

## Plant Lectin Receptor like Kinase Gene Family: Structure and Classification, Signaling Transduction, Physiological Function

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### Abstract

Plant lectin receptor like kinases (LecRLKs) are intron-less *LecRLKs* genes coding transmembrane proteins with amino-terminal extracellular lectin domains, hydrophobic transmembrane domains and carboxyl-terminal intracellular Ser/Thr kinase domains. Up to now, 32 G-type, 42 L-type and 1 C-type LecRLKs from *Arabidopsis* and 72 L-type, 100 G-type and 1 C-type LecRLKs from rice were identified on the basis of extracellular lectin and intracellular kinase domains. Several phylogenetic trees were constructed from the different LecRLKs domain sequences. In plants, although LecRLKs possess conserved sequences, their physiological roles vary to an extent. LecRLKs play crucial roles ranging from plant growth and development to biotic and abiotic stress responses. In this paper, we mainly introduce structure and classification, signal transduction and physiological functions of LecRLKs protein family. This review will lay an overall foundation for further physiological function research of plant LecRLK gene family members.

**KEYWORDS:** Lectin receptor-like kinases; biotic and abiotic; stress response; signal transduction

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### 1. Introduction

Plants are continuously challenged with a wide range of biotic and abiotic stimuli during development (Genre *et al.*, 2009). Perception and transduction of these signals are largely mediated by cell-surface receptors which play fundamental roles in the regulation of cell function in many tissues, but little is known about how they are able to sense and realize signal transduction. Some receptors act as protein kinases which play important roles in plant development and response to various unfavorable environmental conditions (Dombrowski *et al.*, 2012; Jain *et al.*, 2012; Wang *et al.*, 2012). In recent years, the researches on RLK are becoming a focus. The maize CRINKLY4 (*cr4*), a receptor-like kinase, is required to maintain the interlocking of the palea and lemma, and fertility in rice, by promoting epidermal cell differentiation (Pu *et al.*, 2012). Receptor-like kinase present new approaches in tackling drought stress (Marshall *et al.*, 2012). To date, several different types of cell-surface receptors such as receptor-like kinases (RLKs) with perceiving diverse signals and stimuli, have been well studied. Plant receptor-like kinases (RLKs) represents one of the largest gene families and nearly contains at least 610 members, which represent about 2.5% of protein coding genes identified in *Arabidopsis*

(Shiu and Bleecker, 2001, 2003). RLKs are associated with various biological processes such as plant growth and development, disease resistance and stress response which include CLV1 receptor in meristem signaling (Clark, 2001), SRK receptor in signaling from pollen to stigma occurring in self-incompatible *Brassica* species (Andrew *et al.*, 2000) and Xa21 in plant resistance (Ronald, 1998).

Another group of RLKs, functioning as signal sensors, are the lectin receptor like kinases (LecRLKs). Plant LecRLKs are transmembrane proteins with amino-terminal extracellular lectin domains, hydrophobic transmembrane domains and carboxyl-terminal intracellular Ser/Thr kinase domains. Characterization of extracellular lectins is known to bind carbohydrates (Hervé *et al.*, 1999; Swarup *et al.*, 1996) and confers multiple functions. Up to now, there were 32 G-type, 42 L-type and 1 C-type LecRLKs from *Arabidopsis* and 72 L-type, 100 G-type and 1 C-type LecRLKs to be identified from rice on the basis of their annotation and presence of lectin as well as kinase domains (Vaid *et al.*, 2012). However, the exact roles of G and C type were unclear, and meanwhile no evidences showed that function have been elucidated. Three dimension structure and carbohydrate-protein binding specificity of L-type LecRLKs, extracellular domains are similar to soluble legume lectins which are ubiquitous in leguminous seeds, have been elucidated (Bouwmeester and Govers, 2009). In addition, it also showed that the sugar-binding residues of LecRLKs were poorly conserved on the basis of functional conformation. Therefore, it was unlikely that these receptors bind monosaccharide molecules (Andre' *et al.*, 2005; Barre *et al.*, 2002).

It is well established that plant LecRLKs are involved in recognition to extracellular ligands mainly through extracellular lectin domains. They are associated with upstream and downstream components in the signaling events, and then convert external signals to internal signals by means of signal cascade amplification reaction. Unlike animal tyrosine phosphorylation, it was demonstrated that plant LecRLKs phosphorylation amino acid residue site occurred in Ser/Thr (He *et al.*, 2004).

Plant LecRLKs play key roles not only in plant growth and development but also in the adaptative response to various extracellular stimuli such as disease resistance and stress response. The structure and classification, signaling transduction and stress resistance about LecRLKs will be introduced in this paper. Furthermore, we will also introduce great application value of plant LecRLKs members in the aspect of increasing agricultural industry by improving some resistance genes expression which are beneficial to crop growth and yield.

## 2. Structure and Classification of LecRLKs

### 2.1 The structure of LecRLKs

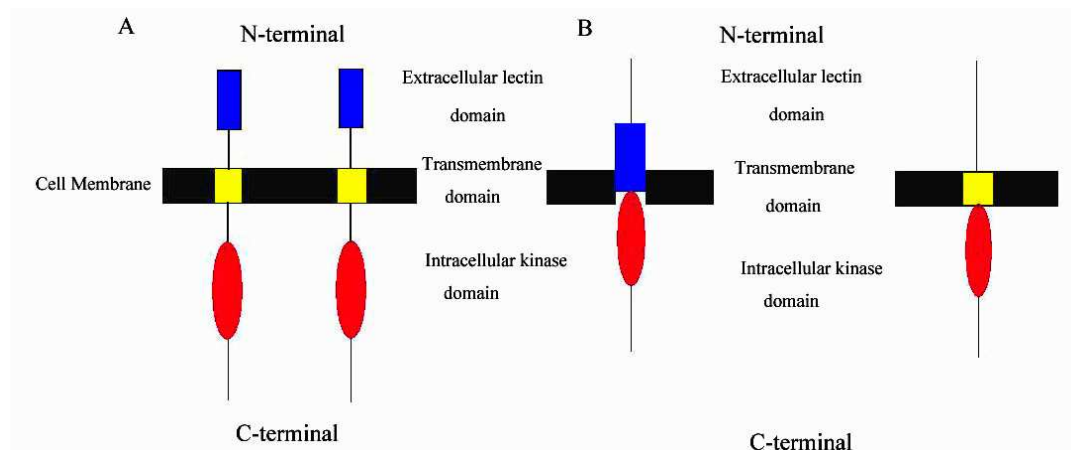
In higher plants, LecRLKs are a class of proteins, which include an extracellular lectin domain, a transmembrane domain, and an intracellular Ser/Thr kinase domain (Fig.1A). In recent years, some researchers have detailed introductions about the three structure domains of LecRLKs (Barre *et al.*, 2002). Protein structural analysis showed that extracellular domains consisted of some  $\beta$  sheet strands and  $\alpha$  helices, and meanwhile formed localized loops which were responsible for dimerization (Rini, 1995). Sequence analysis and molecule modeling of plant LecRLKs showed their differences reflected in extracellular lectin domains. The amino acid sequence comparison of the lectin domains showed a percentage of similarity close to 32% for all the aligned

sequences, therefore, the amino acid residues forming the hydrophobic cavity of the legume lectin monomer were extremely conserved in LecRLKs family. It was such a cavity capable of binding extracellular signal molecules such as carbohydrate to play a crucial role in transmitting these external signals, and meanwhile it was so far demonstrated that LecRLKs could bind oligosaccharides as ligands not monosaccharides because of possessing a highly conserved hydrophobic cavity in their extracellular lectin domains (Barre *et al.*, 2002).

Intracellular C-terminal catalytic region was composed of the upstream kinase domain that was essential to LecRLKs function, poor conservative juxtamembrane domain and downstream C-terminal domain. C-terminal domains were considered to interact with downstream proteins in signal transduction to finish signal transmission (Schlessinger, 2000; Hubbard and Till, 2000). More Ser/Thr than Tyr distributes in C-terminal, and meanwhile related studies demonstrated that the phosphorylated amino acid residues site in Ser/Thr. A decade ago, a striking observation was found that truncating the entire kinase domain would cause functional loss of CLV1 (Clark *et al.*, 1997; Trotochaud *et al.*, 1999). Therefore, the importance of C-terminal kinase domain is self-evident.

Transmembrane region was just like a joint between extracellular lectin domain and intracellular kinase domain, so it played a very important role in constructing an intact LecRLKs structure. It consisted of three coterminous parts including external juxtamembrane region located in the downstream of lectin-like domain, the hydrophobic membrane-spanning helix, and the juxtamembrane region located in the cytoplasm just upstream the catalytic kinase domain. Downstream and upstream regions were poorly conserved to cause diversity. Almost all the LecRLKs family members had a conserved region about five amino acids residues acting as a "stop-transfer" signal which determined signal to transfer or stop in membrane-spanning helix. Consequently, such a transmembrane region was supposed to directly or indirectly play a substantial role in determining signal transmission to continue or terminate.

However, not all the LecRLKs have a normally intact LecRLKs structure, and the previous studies showed that AT4g28350 and AT3g46760 proteins were in absence of transmembrane domain and lectin domain, respectively (Krogh *et al.*, 2001)(Fig.1B).



**Fig.1** Basic structure of the lectin receptor-like kinases. LecRLKs constitute of extracellular lectin domain, transmembrane domain and intracellular kinase domain.

However, based on structure characteristics LecRLKs can be divided into complete and incomplete normal structure. A. A normally complete LecRLKs structure. B. Two LecRLKs coded by *At4g28350* and *AT3g46760* with missing part of the structure domain.

## 2.2 The classification of LecRLKs

In plants, with the further exploration of RLKs, more and more members were identified and classified into LecRLKs subfamily (Hervé *et al.*, 1999; Swarup *et al.*, 1996). The differences among LecRLKs members were mainly reflected in extracellular lectin domains. Based on extracellular sequence homology comparison analysis, phylogenetic trees were constructed (Vaid *et al.*, 2012; Bouwmeester and Govers, 2009). The construction of the phylogenetic trees of *Arabidopsis LecRLKs* members laid a solid foundation for us to study *LecRLKs* homologous genes functional similarity.

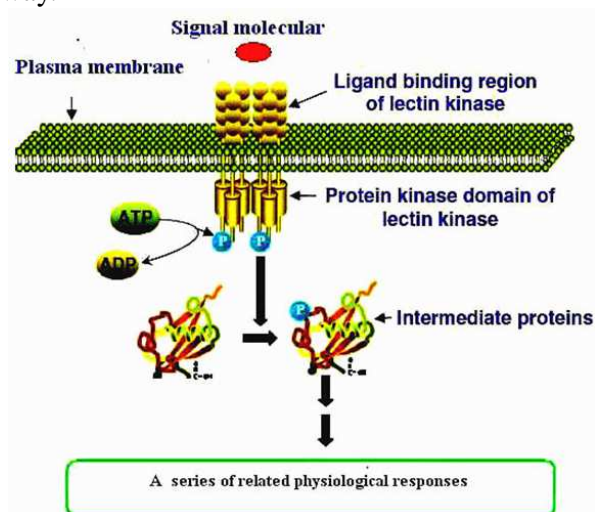
Based on the specific extracellular lectin domains, LecRLKs could be well distinguished. Current researches show that LecRLKs in *Arabidopsis thaliana* were divided into three types: G, C and L. G, C and L represented GNA-related, calcium-dependent and legume-like LecRLKs, respectively. It showed they had different functions (Andre´ *et al.*, 2005; Naithani *et al.*, 2007; Cambi *et al.*, 2005). There were 32 G-type, 42 L-type and 1 C-type LecRLKs from *Arabidopsis* and 72 L-type, 100 G-type and 1 C-type LecRLKs to be identified from rice on the basis of their annotation and presence of lectin as well as kinase domains. C-type was scarce and had only one member. The precise roles of G and C type were unclear, and no evidences showed that their functions in ligand binding were elucidated. L-type were widespread in legume plants and were currently studied extensively among them (Shiu and Bleecker, 2003; Clark, 2001; Vaid *et al.*, 2012). However, besides the studies of LecRLKs in *Arabidopsis thaliana*, some LecRLKs of other plants were also being studied, such as NbLRK1 in tobacco (Kanzaki *et al.*, 2008), CaMBL1 in pepper (De Hoff *et al.*, 2009), rice blast resistance *pid-2* (Chen *et al.*, 2004, 2006) and PsLecRLKs in legume (Joshi *et al.*, 2009).

## 3. LecRLKs Signaling Transduction

### 3.1 Introduction of LecRLKs signaling transduction

The growth and development of organisms have to be regulated by a steady stream of endogenous and exogenous signals. The first step of the signals reach the cell membrane, and then they are recognised and transmitted by membrane receptor. RLKs, a kind of cell membrane protein receptors, act as external signal receiver. For example, CLV1 received a signal that regulates cell proliferation in the meristematic regions (Williams *et al.*, 1997), and meanwhile CLV1 ligand was found (Trotochaud *et al.*, 2000). In recent years, it showed that some LecRLKs combined with some other pathways such as ethylene and ABA signaling pathways to jointly regulate plant growth (He *et al.*, 2004; Desclos-Theveniau *et al.*, 2012). Although previous studies identified some LecRLKs family members with a combination of genetic and biochemical approaches, the exact roles in signal transduction are not sure. LecRLKs signaling network are still fragmented even if an increasing number of LecRLKs have been identified. LecRLKs, acting as a network junction in transduction processes, associates with the upstream and downstream components to constitute a signaling network.

Generally speaking, LecRLKs convert information from extracellular to intracellular to regulate plant growth. The device of signal transmission constitutes of upstream ligand, intermediate receptor and downstream component (Fig.2). The LecRLKs acting as receptor is well-known, however, related evidences of upstream and downstream component and how LecRLKs to interact with them are still deficient. Therefore, it is of great significance to know the target proteins interacting with LecRLKs for mapping a complete signal pathway.



**Fig.2** The picture shows a preliminary overview of signal event transduced by LecRLKs. When extracellular signal molecules bind extracellular lectin domain, it would make dimerization, and then intracellular kinase domain is phosphorylated. Similar to other membrane protein kinases, progressively phosphorylating downstream components would pass on along the signal pathway. Finally, related physiological reactions will respond to the external stimulus signal (Shiu and Bleecker, 2003).

### 3.2 Signal transduction controlled by LecRLKs phosphorylation and dephosphorylation

Extracellular signals are firstly recognised by receptors on membrane and then these signals get to downstream through enzymatic cascade reaction. It is such a process that progressively enlarges the weak input signal into a strong output signal, which results in a variety of physiological responses. A decade ago, signal transduction of some receptor kinases in plants were clearly investigated (Torii, 2000) and the ways of action generally including the phosphorylation and dephosphorylation were well-known.

When external ligands bind to extracellular lectin domains, it will result in LecRLKs dimerization, and subsequently a series of enzyme cascade reactions are activated to amplify signals. Finally, related physiological reactions will appear. When LecRLKs dimerization happened, phosphorylation was an important mechanism in the regulation of the kinase activity to transmit these messages (Karin and Hunter, 1995), which had been found to modulate protein-protein interactions in some receptor-like kinases (Williams *et al.*, 1997; Stone *et al.*, 1994). Depending on the phosphorylation sites, we all knew that phosphorylation sites could be located in Ser/Thr and Tyr. In higher plants, LecRLKs phosphorylation site was confirmed to occur in Ser/Thr not in Tyr (Shiu and Bleecker, 2001; Hardie, 1999; Sopory and Munshi, 1998). Related experiments confirmed that PnLPK phosphorylation site in Ser/Thr residues not in Tyr residue. The C-terminal

catalytic domain of PnLPK showed significantly higher autophosphorylation activity than the full-length PnLPK protein when incubated in the presence of  $Mn^{2+}$ . The phosphorylation activity of PnLPK was also detected using  $\beta$ -casein as substrate, and then phosphoamino acid analysis indicated that PnLPK was a Ser/Thr kinase (Nishiguchi *et al.*, 2002). In *Arabidopsis*, the AtLecRK2 phosphorylation site was also in Ser/Thr. The phosphorylated AtLecRK2 kinase domain was hydrolyzed with HCl, then subjected to two-dimensional thin-layer electrophoresis and autoradiographed, and ultimately the autoradiograph revealed that the phosphorylated amino acids were Ser/Thr (He *et al.*, 2004). These LecRLKs autophosphorylation could not be in absence of the metal ion activation. PnLPK was activated in the assistance of  $Mn^{2+}$  (Nishiguchi *et al.*, 2002). NgRLK1 was autophosphorylated with higher activity in the presence of  $Mn^{2+}$  than  $Mg^{2+}$  (Kim *et al.*, 2010).

#### 4. Physiological Function of LecRLKs

In the previous study, lectins were reported to have the important roles in plant defense (Chrispeels and Raikhel, 1991). Lectins were demonstrated as recognition molecules in organisms (Sharon and Lis, 1998). The interacting partners and coexpression data of the *LecRLKs* genes revealed the importance of gene family in physiology and stress related responses (Vaid *et al.*, 2012). Recent research showed that lectin-mediated resistance impaired plant virus infection at the cellular level (Yamaji *et al.*, 2012). Meanwhile, there were some evidences showing that LecRLKs could impair virus invasion. In addition, LecRLKs were also involved in some other physiological processes. So far, functions of plant LecRLKs can be divided into three broad categories including resistance response, regulation of plant development and phytohormone regulation.

##### 4.1 Resistance response

Plants inevitably suffer the impact of a variety of abiotic stresses and biotic stresses such as salt, drought, cold, wounding and pathogen invasion. Plants have established multilayered defense mechanisms to gain stress resistance (Chisholm *et al.*, 2006). Members of protein kinases played a central role and signaling pathway was studied in plant-microbe interaction (Antolín-Llovera *et al.*, 2012). When pathogens attacked plants, PRR recognizing pathogen induces PAMP to prevent infection, and then triggered effector immunity which induced a hypersensitive response (HR) with localized cell death and defense genes expression that suppressed the growth and spread of pathogens postentry (Chisholm *et al.*, 2006; Jones and Dangl, 2006; Eitas and Dangl, 2010). Continuum in plant cell wall (CW) and cell membrane (CM) played a key role in defense function, and was also regulated by regulatory proteins which interacted with special pathogen surface protein (IPI-O) to initiate defense (West *et al.*, 1998; Mellersh and Heath, 2001).

LecRK79, LecRK1.9 and At5g60300 in *Arabidopsis thaliana* were demonstrated to act as continuum to defend pathogens (Bouwmeester and Govers, 2009; Bouwmeester *et al.*, 2011; Gouget *et al.*, 2006). NbLRK1 in tobacco LecRLKs combining with INF1 protein in phytophthora induced HR reaction to protect plant from infecting. However, HR was retarded in mutant (Kanzaki *et al.*, 2008). CaMBL1 in pepper played a key role in regulating cell death and defense responses after plants encountering pathogens

(Hwang, 2011). Pid(t)-2 in rice LecRLKs played an important role in preventing rice blast when *Magnaporthe grisea* infected rice (Chen *et al.*, 2004, 2006) Some plants prevented pathogen invasion through opening and closing of stomata. For example, related experiment showed that LecRK-V.5 negatively regulated stomata opening and such a regulation only appeared in early days. It was found that ROS accumulated in *lecrk-v.5* mutant, high concentration of ROS triggered stoma closure (Desclos-Theveniau *et al.*, 2012; Nicaise *et al.*, 2009). The ABA was also observed to participate in regulating stoma size (Klüsener *et al.*, 2002). Therefore, there was a possibility that LecRLKs controlled stoma size mainly by regulating ABA. Deletion of *LecRK-I.8* gene was identified to show a much reduced induction of PR-1 in response to *Pieris brassicae* eggs to impair PAMP-triggered immunity (Gouhier-Darimont *et al.*, 2013).

Salt stress has become a major threat to plant growth and crop productivity. It virtually affected many aspects of plant basic life such as water loss which results in plant death (Zhu, 2002). Many changes appearing under these stresses have been documented (Zhu, 2001). Some of them are capable of directly or indirectly causing fast plant death or dying gradually. To address this problem, it is of great significance to find related genes increasing resistance to salt stress. After years of research, the good news were that related genes have been found to associate with resistance to salt stress. People have found several LecRLKs were involved in salt stress signaling pathway. *PsLecRLK* in legume was a salt-induced gene and its expression levels elevated when exposed to high salt, and then transferring *PsLecRLK* gene to bacteria, finally culturing in NaCl medium. Results showed that significant enhance in salt-tolerant capabilities. In summary, *PsLecRLK* gene was a resistance gene and induced by salt stress (Joshi *et al.*, 2009). There was a research showing that *AtLecRLK2* had a functional similarity with *PsLecRLK*, and meanwhile *AtLecRLK2* was also negatively regulated by ethylene (He *et al.*, 2004). When plants suffer wounding, we know that systemin, a polypeptide signal for plant defense genes, is involved in the local and systemic activation of defense responses against wounding (Bergey *et al.*, 1999; Ryan and Pearce, 1998). Overexpression of *GsSRK* in *Arabidopsis* promoted seed germination, as well as primary root and rosette leaf growth during the early stages of salt stress, and meanwhile it was also showed that expression levels of *GsSRK* were largely induced by ABA and drought stresses (Sun *et al.*, 2012). However, we could also find some RLKs are involved in repairing wounding. For example, *Nt-Sd-RLK* took effect during wounding (Sanabria *et al.*, 2012). Wound-induced *rgs-CaM* gets ready for counterresponse to an early stage of viral infection (Tadamura *et al.*, 2012). *PnLPK* was determined to be a member of the LecRLKs. Wounding of the young leaves would increase the amount of *PnLPK* mRNA (Nishiguchi *et al.*, 2002).

#### 4.2 Regulation of plant growth and development

During plant growth and development, organisms start the endogenous genes expression by the perception and transduction of exogenous signals. Meanwhile, the expressions of endogenous genes determine the plant growth condition. In some cases, the deletion of related genes will result in severe defection in phenotype and physiological conditions. The transmission of these signals were mostly in the aid of transmembrane receptor protein kinases such as *CLAVATA* controlling the number of SAM, *HAESA* controlling floral organ shedding and *ERECTA* regulating cell

proliferation and organ growth (Jinn *et al.*, 2000; Canales *et al.*, 2002; Torii *et al.*, 1996). The rice wall-associated receptor-like kinase gene OsDEES1 played a role in female gametophyte development (Wang *et al.*, 2012). Some LecRLKs can also be found to play a key role in regulating these processes of growth and development. *At3g53810* coding SGC LecRLK is essential for normal pollen development. *At3g53810* deletion mutants will result in pollen abortion with appearing pollen grain deformity, contraction, sticking together and mature pollen grains smaller than wild-type plants (Wan *et al.*, 2008). Along with aging processes, *LecRK-a1* gene expression level could be found to show the gradual increase. When using oligomeric galactan glucuronide treatment or suffering wounding, *LecRKA-1* gene expression level was significantly elevated (Riou *et al.*, 2002). The extracellular lectin structure of LecRLKs determined that some LecRLKs were involved in the legume-rhizobia symbiosis (Herve' *et al.* 1996; Hirsch, 1999). Research of symbiotic nitrogen fixation signaling pathway about legume model plant *Medicago truncatula* showed 4 MtLecRLKs proteins (MtLecRK1;1,MtLecRK7;1,MtLecRK7;2,MtLecRK7;3) were involved in this plant signal event (Navarro-gochicoa *et al.*, 2003).

#### 4.3 Phytohormone regulation

Plants struggled to adapt to their surroundings during their lifetime (Zhang *et al.*, 2011), and then they were regulated by a series of phytohormones to jointly control plant growth and development. Importance of phytohormones regulating plant establishment was self-explanatory, and meanwhile more and more evidences were proposed to support this viewpoint. For example, the phytohormones participated in an  $s6$  kinase signal transduction pathway in *Arabidopsis* (Turck *et al.*, 2004).

The message transmission of phytohormones was partly regulated by transmembrane protein kinases. A plasma membrane receptor kinase, GHR1, mediates abscisic acid- and hydrogen peroxide-regulated stomatal movement in *Arabidopsis* (Hua *et al.*, 2012). STUNTED (STU), a receptor-like cytoplasmic kinase (RLCK) VI family gene, mediated control of cell proliferation by GA in *Arabidopsis* (Lee *et al.*, 2012). Our studies demonstrated that LecRK-b2 (encoded by *At1g70130*) was involved in ABA signaling pathway and positively regulated ABA. It also had an important regulatory role in the processes of salt and osmotic stress. Dual-luciferase transient expression assay confirmed that the transcription factor ABSCISIC ACID INSENSITIVE3 (ABI3) could activate the luciferase under driving of *LecRK-b2* promoter. *LecRK-b2* transcription expression level was found to be down-regulated in *abi3* during seed germination. Furthermore, *LecRK-b2* loss-of-function mutation reduced the salt and osmotic sensitivity during early development stage of *Arabidopsis* (Deng *et al.*, 2009). On the contrary, A4 subfamily including *At5g01540* (*LecRK4.1*), *At5g01550* (*LecRK4.2*), and *At5g01560* (*LecRK4.3*) had a negative regulation of ABA sensitivity. *lecrk4.1-1* mutant enhanced ABA sensitivity. The double interference mutant *lecrk4.1;LecRK4.2* (RNAi) plants showed the increased sensitivity to the ABA (Xin *et al.*, 2009).

Apart from the above physiological roles, the part of plant proteins with legume lectin domains were involved in anti-tumor effect. ConA with the induction of apoptosis was regulated by mitochondria (Lei and Chang, 2006,2009). PHA-E (hemagglutinin) with legume lectin domain had anti-leukemia function (Xia and Ng, 2006). Purple bean lectins achieved the boycott to liver cancer HepG2 cells through the formation of



apoptotic bodies proliferation, and GNA-lectins were also associated with the anti-cancer effect (Liu *et al.*, 2009; Peng *et al.*, 2009). Therefore, plant proteins with lectin domain may be substantial antineoplastic (Fu *et al.*, 2011; Liu *et al.*, 2010).

## 5. Concluding Remarks

In contrast to animals, plants can not move when encountering outside stimulus all their life, therefore, plants need more anti-stress capabilities to make them to adapt to environmental fluctuations. Perception and transduction of these extracellular signals are mediated by functional continuum between the plant cell wall (CW) and the plasma membrane (PM), functioning as cell wall integrity sensors (Bouwmeester and Govers, 2009; Humphrey *et al.*, 2007). LecRLKs function as sensors to convert external information to the cytoplasm (Ringli, 2010). LecRLKs with extracellular lectin domain is distinguished from other transmembrane proteins. Up to now, there were 32 G-type, 42 L-type and 1 C-type LecRLKs from *Arabidopsis* and 72 L-type, 100 G-type and 1 C-type LecRLKs to be identified from rice on the basis of their annotation and presence of lectin as well as kinase domains. It is exciting that we have a preliminary understanding of their basic characteristics such as structure, classification, and function. Meanwhile, it is well established that LecRLKs work in signaling transduction mainly through phosphorylation and dephosphorylation to transmit these external signals. However, the LecRLKs downstream components and the natural ligands are not clear, so the related signaling pathways should be improved in the further studies. The good news is that, in recent years, several upstream or downstream interacting components in the signal pathways have been well studied (Shiu and Bleeker, 2001). To deeply study the mechanism of action in a variety of signal transduction pathways is beneficial to a better understanding of signal molecular events. Once these signaling pathways have been extensively studied and the related functional genes are found, subsequently it is possible to map a network model of the plant cell signal transduction pathways. Completion of drawing signal spectrum will be of great significance to improve crop plants to be in accordance with plant breeding by regulating the gene expression of the signaling network.

More and more studies showed that RLK members were involved in tissue or organ architecture and agronomic traits. A MAPK cascade downstream of ERECTA regulated *Arabidopsis* inflorescence architecture by promoting localized cell proliferation (Meng *et al.*, 2012). Expression of truncated ERECTA protein from *Arabidopsis thaliana* would modify tomato growth (Villagarcia *et al.*, 2012). We all know currently that the most meaningful studies of LecRLKs are to bring resistance genes among them to agricultural production to increase yield. With the deterioration of the ecological environment and ecological crisis, economically important plants are suffering from abiotic and biotic stress factors. Salt stress and pathogen invasion, ultimately increasing risk of low production or crop failure, are always the main threats to crop economy. Therefore, it is an urgent need to find some stress resistance genes. Studies showed that some *LecRLKs* genes had stress resistance, and so we can make full use of modern genetic engineering techniques to make crop plants obtain resistance. Such a breakthrough will increase crop yield, and then relieve population pressure.

In this article, we have introduced LecRLKs from structure, classification, signaling transduction and related physiological function including resistance response, regulating plant growth and phytohormone regulation, and the most important is that the application

prospect of improving practical production and possible drug development. Taken together, this article will provide a reference to the further research for physiological and biochemical functions and applications of LecRLKs in plants.

### Acknowledgements

This research was supported by grants from the National Natural Science Foundation of China (31071076; 30871325; 30600368), the Program for New Century Excellent Talents in University (NCET-10-0363 to X. Guo), the Excellent Youth Foundation of Hunan Province (11JJ1005), the Project Sponsored by the Scientific Research Foundation for the Returned Overseas Chinese Scholars, the State Education Ministry ([2011]1139 to X. Guo), and the SIT Project of Hunan University, 2011, 2012 and 2013.

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