Advances in Research on Plant Lectin Receptor Kinases in Abiotic Stress Response: A Postprint

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Abstract

Plants are subjected to various stress factors during growth and development, among which abiotic stress constitutes an extremely important category. Receptor-like kinases (RLKs) are a class of proteins ubiquitously present in plants that can rapidly and effectively respond to stress factors, ultimately triggering a series of biological effects. Lectin receptor-like kinases (LecRLKs) represent a subfamily of RLKs possessing three structural domains: an extracellular lectin domain, a transmembrane domain, and an intracellular kinase domain. Based on the distinct extracellular lectin domains, they can be classified into three types: L-, G-, and C-type. In recent years, substantial research has demonstrated that plant lectin receptor-like kinases play crucial roles in abiotic stress responses. LecRLKs recognize abiotic stress-related signaling molecules, activate downstream signaling pathways such as the MAPK pathway, ROS pathway, and calcium signaling pathway, and regulate gene expression and protein translation to enhance plant stress tolerance. This review summarizes the structural characteristics and classification of plant lectin receptor-like kinases, systematically reviews the functions and mechanisms of LecRLKs in response to abiotic stresses including salt stress, low temperature stress, drought stress, mechanical damage, and phytohormones, and also provides perspectives on future research directions for LecRLKs. This article not only serves as a reference for in-depth understanding of the functions of plant lectin receptor-like kinases in abiotic stress responses, but also provides a theoretical foundation for utilizing LecRLKs in crop stress resistance breeding improvement.

Full Text

Preamble

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Title: Research Advances on Plant Lectin Receptor-Like Kinases in Abiotic Stress Response

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Abstract: Plants are exposed to various stress factors during their growth and development, among which abiotic stress represents a critically important category. Receptor-like kinases (RLKs) are a class of proteins widely present in plants that can rapidly and effectively respond to stress factors, ultimately triggering a series of biological effects. Lectin receptor-like kinases (LecRLKs) constitute a subfamily of RLKs characterized by three structural domains: an extracellular lectin domain, a transmembrane domain, and an intracellular kinase domain. Based on differences in their extracellular lectin domains, LecRLKs can be classified into three types: L, G, and C. In recent years, numerous studies have demonstrated that plant lectin receptor-like kinases play vital roles in abiotic stress responses. LecRLKs recognize abiotic stress-related signaling molecules and activate downstream signaling pathways such as the MAPK pathway, ROS pathway, and calcium signaling pathway, thereby regulating gene expression and protein translation to enhance plant stress resistance. This review summarizes the structural characteristics and classification of plant lectin receptor-like kinases and systematically reviews the functions and mechanisms of LecRLKs in response to various abiotic stresses including salt stress, low temperature stress, drought stress, mechanical damage, and plant hormones. Future research directions for LecRLKs are also discussed. This review not only provides a reference for in-depth understanding of the functions of plant lectin receptor-like kinases in abiotic stress responses but also offers a theoretical basis for utilizing LecRLKs in crop stress resistance breeding.

Keywords: plants, receptor-like kinase, lectin receptor-like kinase, abiotic stress, signal response, mechanism of action

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Plants in nature are subjected to various environmental stresses, and to cope with these diverse biotic and abiotic challenges, they have evolved numerous effective mechanisms during evolution to defend against external environmental pressures. These mechanisms help plants avoid damage from stress while improving their quality and yield. Among plant abiotic stress responses, a class of important proteins—lectin receptor-like kinases (LecRLKs)—plays a key role. LecRLKs are a subfamily of receptor-like kinases (RLKs) that are widely present in plants and have been reported to participate in biotic/abiotic stress responses and plant developmental regulation (Wang et al., 2020). Previous studies have reported that LecRLKs can perceive and transduce various signaling molecules in the environment to participate in abiotic stress responses, including salt stress, low temperature stress, drought stress, mechanical damage, and plant hormones (Vaid et al., 2012; Wang et al., 2020). For example, the lectin receptor-like kinase gene PbLRK138 is involved in plant salt tolerance (Ma et al., 2018), while the LecRK-IX.2 gene participates in plant hormone signaling responses (Luo et al., 2017). Thus, LecRLK-mediated abiotic stress responses are extremely important for maintaining normal plant growth and development.

In recent years, with continuous in-depth research, numerous lectin receptor-like kinases involved in plant abiotic stress responses have been reported, but no comprehensive review has systematically categorized and summarized these studies to date. This article briefly outlines the structural characteristics and classification of plant lectin receptor-like kinases, systematically reviews the signal transduction and regulatory mechanisms by which LecRLKs participate in various abiotic stress responses, and also discusses future research directions.

1. Structural Characteristics and Classification of Lectin Receptor-Like Kinases

Lectin receptor-like kinases are primarily composed of an extracellular lectin domain, a transmembrane domain, and an intracellular kinase domain. The lectin domain has the function of specifically binding carbohydrate molecules, and due to its variability in recognizing different signaling molecules, LecRLKs are divided into three types: L, G, and C (Vaid et al., 2012; Wang et al., 2020). Among these, L-type and G-type exist only in plants, while C-type is mainly found in mammals (Vaid et al., 2013; Wang et al., 2020). L-type LecRLKs contain legume-like extracellular lectin domains, are widely present in leguminous plants, and can recognize extracellular signals to trigger a series of signal responses within plants (Vaid et al., 2012, 2013). G-type LecRLKs belong to the SRK (S-locus receptor kinase) family, participate in flower development, and are associated with self-incompatibility (SI) (Wang et al., 2020). G-type LecRLKs were previously called B-type LecRLKs, and their lectin domains include 12 β-barrel structures with potential affinity for α-D-mannose, although their intrinsic functional mechanisms remain unclear (Vaid et al., 2013). C-type LecRLKs are a class of lectin receptor protein kinases widely present in mammals that can recognize self and non-self and function in a Ca2+-dependent manner (Wang et al., 2020). Few C-type LecRLKs have been discovered in plants; currently, only one such LecRLK has been found in rice (*Oryza sativa*), *Arabidopsis thaliana*, poplar (*Populus* L.), and eucalyptus (*Eucalyptus robusta*), and their specific functions are not yet understood (Bouwmeester & Govers, 2009; Vaid et al., 2012; Peng et al., 2022).

The transmembrane region of LecRLKs consists of 18-25 amino acids, most of which are non-polar, and the sequence shows poor conservation (Morillo & Tax, 2006). The Pi-d2 protein belongs to G-type LecRLKs, and a change in a single amino acid in its transmembrane domain causes loss of protein function, indicating that the transmembrane domain is crucial for maintaining LecRLK function (Chen et al., 2006). Studies have found that the transmembrane domain not only participates in signal transduction and plasma membrane localization but also has ligand recognition functions (Bi et al., 2016; Hohmann et al., 2017).

The kinase domain generally consists of 250-300 amino acids and shows higher conservation compared to the lectin domain. It contains phosphorylation sites on its domain and is primarily involved in external signal transduction (Vaid et al., 2012). Enzyme kinetic studies have found that certain divalent metal cations can promote autophosphorylation and kinase activity of the kinase domain, with Mn2+ and Mg2+ showing better promotion effects than Ca2+ and Zn2+ (Nishiguchi et al., 2002; He et al., 2004).

2.1 Involvement in Salt Stress Response

Among abiotic stresses, high salinity conditions are detrimental to plant growth and development and represent a major cause of crop yield reduction, causing significant economic losses annually. Plants adapt to saline environments through their own genetic regulation under high salt conditions. Studies have shown that various types of lectin receptor-like kinases in *Arabidopsis*, soybean (*Glycine soja*), rice, and pea (*Pisum sativum*) are involved in salt stress responses. Table 1 lists the lectin receptor-like kinase genes involved in salt stress responses.

LecRK-I.3 is an L-type lectin receptor-like kinase gene in *Arabidopsis*. Studies have found that the *Arabidopsis LecRK-I.3* gene is induced by salt stress. Overexpression of the salt-induced ethylene receptor gene *NTHK1* from tobacco in *Arabidopsis* reduces ethylene sensitivity (Zhang et al., 2001; Xie et al., 2002). Deng et al. (2009) confirmed that the *Arabidopsis LecRK-V.2* gene is primarily expressed during seed germination and ceases expression after germination, participating in salt stress responses during early seed development. More importantly, *LecRK-V.2* was verified to function as a positive regulator of ABA responses during seed germination; consequently, functional deficiency mutants of *LecRK-V.2* effectively reduce *Arabidopsis* sensitivity to ABA and salt during early growth and development. The transcription of the L-type lectin receptor-like kinase gene *LecRK-IV.3* in *Arabidopsis* is dually regulated by salt and ABA, playing a positive regulatory role under high salt conditions while negatively regulating ABA responses during seed germination (Xin et al., 2009). Overexpression of *LecRK-IV.3* under high salt environments enhances plant tolerance to salt stress, thereby increasing seed germination rates and green leaf retention

(Huang et al., 2013). Li (2019) found that the *LecRKIII.2* gene enables *Arabidopsis* seedlings to exhibit higher tolerance to salt stress during germination.

GsSRK is a G-type lectin receptor-like kinase gene in soybean that is induced by multiple factors including salt stress, drought stress, and ABA, and regulates plant tolerance to salt and drought stress through an ABA-independent response pathway. Sun et al. (2013) found that overexpression of this gene improves plant salt tolerance, manifested by increased chlorophyll content, reduced ion leakage, enhanced plant height growth, and increased fruit production at the mature stage. Overexpression of *GsSRK* in *Arabidopsis* not only positively regulates plant tolerance to salt stress but also improves yield under saline conditions (Sun et al., 2013). Studies have found that in alfalfa (*Medicago sativa*), overexpression of either the full-length soybean *GsSRK* (*GsSRK-f*) or a truncated version lacking the G-type lectin domain (*GsSRK-t*) can enhance plant salt tolerance, with transgenic lines overexpressing *GsSRK-t* showing better growth performance than those overexpressing *GsSRK-f* (Sun et al., 2018). Zhang et al. (2022) identified *GmLecRLK* as a soybean salt stress-related gene through transcriptional studies; it is primarily expressed in roots and participates in regulating soybean salt tolerance. *GmLecRLK* overexpressing transgenic soybean exhibits tolerance to salt stress and enhanced ability to scavenge reactive oxygen species (ROS) (Zhang et al., 2022). Although these results demonstrate that *GmLecRLK* can improve soybean salt tolerance, its actual regulatory mechanism remains unclear.

The pea L-type *PsLecRLK* gene primarily accumulates in roots and shoots, with its expression significantly upregulated under salt stress conditions. Joshi et al. (2010) found that *PsLecRLK* expression also increases under low temperature and drought stress, but the magnitude of increase is greatest under salt stress. Overexpression of *PsLecRLK* in tobacco reduces ion imbalance and osmotic pressure in transgenic plants, thereby conferring salt tolerance. Vaid et al. (2015) found that plants overexpressing *PsLecRLK* exhibit higher germination rates and green leaf retention under salt stress, prevent ROS accumulation and membrane damage in root tissues, and effectively reduce the Na+/K+ ratio, thereby enhancing plant salt tolerance.

Li et al. (2014) demonstrated that the rice L-type lectin receptor-like kinase *SIT1* is rapidly activated under salt conditions and subsequently phosphorylates downstream effectors MPK3 and MPK6. *SIT1* negatively regulates rice salt tolerance; consequently, as *SIT1* kinase expression increases, plant survival rates decrease. In *Arabidopsis*, the *SIT1* protein kinase increases ROS accumulation under salt stress, thereby inhibiting plant growth and reducing survival under saline conditions (Li et al., 2014). Ma et al. (2018) found that six *LecRLKs* (four L-type and two G-type) in Callery pear (*Pyrus calleryana*) are significantly expressed under salt stress conditions, suggesting they may play a role in regulating abiotic stress. Overexpression of the Callery pear L-type lectin receptor-like kinase gene *PbLEK138* in tobacco causes cell death, thereby improving plant salt tolerance (Ma et al., 2018). Chinese dwarf cherry (*Cerasus* *humilis*) has strong salt tolerance, and eight *ChLecRLK* genes (five G-type, two L-type, and one C-type) have been found to be significantly upregulated under severe salt stress, while five *ChLecRLK* genes (four G-type and one L-type) are significantly expressed under mild salt stress, indicating their active participation in salt stress responses (Han et al., 2021). Peanut (*Arachis hypogaea*) is one of China's major oil crops. Through homologous cloning, an L-type lectin receptor-like kinase gene *AhLecRK9* can be obtained from cultivated peanut. Studies have found that overexpression of peanut L-type lectin receptor-like kinase *AhLecRLK9* in *Arabidopsis* results in plants showing increased sensitivity to salt stress (Huang, 2022).

2.2 Involvement in Low Temperature Stress Response

Like other environmental stresses, low temperature is a key limiting factor for plant growth, largely influenced by geographical location. Low temperature can reduce crop yields, cause poor growth and development, and even hinder reproductive development. Plant cells have evolved complex intracellular signaling networks that can directly or indirectly enhance cold tolerance when encountering cold signals. Table 2 lists the lectin receptor-like kinase genes involved in low temperature stress responses.

The *Arabidopsis* L-type lectin receptor-like kinase *LecRK-V.6* is strongly suppressed when exposed to low temperature (Bouwmeester & Govers, 2009). Lu et al. (2016) found that although *Arabidopsis LecRK-S.7* is not highly expressed at various plant stages, its promoter region contains low temperature stress response elements, indicating that the *LecRK-S.7* gene may be involved in low temperature stress responses. Li (2019) found through low temperature stress treatment of *Arabidopsis* seedlings that the expression level of the *LecRKIII.2* gene first increased and then decreased, suggesting that *LecRKIII.2* may participate in cold stress responses.

Pea *PsLecRLK* expression increases under low temperature conditions, but the magnitude of increase is smaller compared to salt stress (Joshi et al., 2010). After low temperature treatment of rice seedlings at the three-leaf stage, expression of the L-type lectin receptor-like kinase gene *OsLecRK1* is suppressed (Cui, 2012). Liu et al. (2017) identified an L-type lectin receptor-like kinase gene *PnLecRLK1* from an Antarctic moss (*Pohlia nutans*). Studies found that when the *PnLecRLK1* gene is overexpressed in *Arabidopsis* transgenic plants, the plants exhibit enhanced tolerance to low temperature stress (Liu et al., 2017).

2.3 Involvement in Drought Stress Response

As shown in Table 3 , lectin receptor-like kinases have been reported to participate in plant drought stress responses. Chinese dwarf cherry is an important soil and water conservation fruit tree widely planted in northern China with strong drought and salt tolerance (Han et al., 2021). Han et al. (2021) studied Chinese dwarf cherry and found that its *LecRLKs* are not only involved in salt stress responses but are also crucial in responding to drought stress. Research on nine candidate *ChLecRLK* genes selected from 170 *LecRLK* family genes (five G-type *ChLecRLKs*: *ChLecRLK-G22*, *ChLecRLK-G36*, *ChLecRLK-G68*, *ChLecRLK-G82*, and *ChLecRLK-G107*; three L-type *ChLecRLKs*: *ChLecRLK-L17*, *ChLecRLK-L32*, and *ChLecRLK-L42*; and two C-type *ChLecRLKs*: *ChLecRLK-C01* and *ChLecRLK-C02*) showed that these nine genes actively participate in drought stress responses. Under severe drought stress, the expression of eight genes was significantly increased in leaves; under mild drought, the expression of *ChLecRLK-G36*, *ChLecRLK-G68*, and *ChLecRLK-L32* decreased in leaves (Han et al., 2021).

Studies have found that drought stress can induce expression of the soybean *GsSRK* gene, and that *GsSRK* regulates plant drought tolerance through a process independent of the ABA signaling pathway (Ge et al., 2010; Sun et al., 2013). In cucumber, multiple lectin receptor-like kinase genes have been reported to potentially participate in drought stress responses (Haider et al., 2021). Huang (2022) transformed the L-type lectin receptor-like kinase gene *AhLecRK9* obtained from peanut into *Arabidopsis* plants to generate transgenic overexpression (OE) lines. The study found that drought stress inhibited the growth of OE plant shoots, while the underground parts showed relatively elongated growth compared to wild type, indicating that overexpression of *AhLecRK9* enhances drought tolerance in *Arabidopsis*.

2.4 Involvement in Mechanical Damage Response

When plants suffer mechanical damage, it triggers a series of related reactions including membrane depolarization, activation of calcium channels, and plant hormone regulation. LecRLKs play important regulatory roles in mechanical damage stress responses by sensing mechanical damage suffered by plants to participate in abiotic stress responses. Table 4 lists the lectin receptor-like kinase genes involved in mechanical damage stress responses.

LecRK-V.5 is an L-type lectin receptor-like kinase gene in *Arabidopsis* and a member of a multigene family consisting of 45 members (Hervé et al., 1996; Barre et al., 2002; Bouwmeester & Govers, 2009). Hervé et al. (1996) first discovered that *LecRK-V.5* participates in the physiological functions of oligosaccharide and plant hormone signal transduction. Subsequent studies found that the *LecRK-V.5* gene also plays important roles in plant biotic or abiotic stress responses (such as salt stress, low temperature stress, drought, mechanical damage) and plant growth and development processes. Riou et al. (2002) studied the fusion expression of the *LecRK-V.5* gene promoter with the GUS gene and found that the induction of *LecRK-V.5* gene expression after mechanical damage stress is mainly associated with local responses. Mechanical damage typically triggers a series of local responses including cell division induction around the damaged area for tissue repair and healing. From damaged *Arabidopsis* plant tissues, it was found that *LecRK-V.5* gene expression is locally activated and significantly increased after injury (Riou et al., 2002). Studies have found that after *Arabidopsis* is damaged, pectin in the cell wall releases oligogalacturonic acid that induces expression of damage stress response genes through a non-jasmonic acid (JA) pathway, suggesting that such molecules may participate in early damage signal transduction (Benhamou et al., 1990; Riou et al., 2002).

The *Arabidopsis* L-type lectin receptor-like kinase P2K1 has been reported to participate in plant wound responses. P2K1 is the first extracellular ATP (eATP) receptor identified in plants, and through protein sequence alignment, P2K1 protein was found to be LecRK-1.9 (L-type lectin receptor kinase I.9), which is highly expressed under normal conditions (Choi et al., 2014). When plants suffer certain damage, cell rupture releases ATP, and this extracellular ATP can act as a signaling molecule participating in organism growth, development, and stress responses (Tanaka et al., 2014). With the discovery of P2K1 receptor recognition of ATP as a DAMP signal in damage responses, most ATP-responsive genes have also been proven to participate in damage responses (Tanaka et al., 2014). Tanaka et al. (2014) further found that *P2K1* gene mutants show the same response effects to ATP changes and damage, and that overexpression of *P2K1* enhances responses to ATP and damage. This indicates that P2K1 participates in plant damage stress responses, functioning similarly to ATP as a DAMP signal molecule.

In contrast to *LecRK-V.5* in *Arabidopsis*, the *PnLPK* gene in black poplar (*Populus nigra*) shows increased expression when young leaves suffer mechanical damage stress (Nishiguchi et al., 2002). Jasmonic acid (JA) is an important component mediating mechanical damage-induced gene expression (Peña-Cortés et al., 1995). However, Nishiguchi et al. (2002) found that when poplar young leaves suffer mechanical damage, the regulation of *PnLPK* gene expression may be independent of JA- and SA-mediated signal transduction pathways.

In tobacco (*Nicotiana benthamiana*), LecRK1 also participates in mechanical damage stress responses. In mechanically damaged tobacco leaves, the mRNA abundance of the *LecRK1* gene increases (Gilardoni et al., 2011). The L-type lectin receptor-like kinase gene *OsLecRK1* in rice is induced and upregulated after mechanical damage stress (Cui, 2012). Additionally, the pea L-type lectin receptor-like kinase *PsLecRLK* gene has also been reported to participate in mechanical damage responses (Vaid et al., 2015). In pepper (*Capsicum annuum*), *CaLecRK-S.5* has broad-spectrum resistance and plays an important role not only in plant disease resistance but also in mechanical damage stress responses (Woo et al., 2016). Studies have found that damage stress can induce expression of the *CaLecRK-S.5* gene. *CaLecRK-S.5* is a pepper L-type lectin receptor-like kinase gene that cannot induce mitogen-activated protein kinase (MAPK) cascade reactions, ROS bursts, or other response symptoms without external stimulation (Woo et al., 2016, 2020). Woo et al. (2016) studied *CaLecRK-S.5* gene silencing and overexpression and found that in *CaLecRK-S.5* silenced plants, the expression of genes related to damage stress responses decreases; while in *CaLecRK-S.5* overexpressing plants, damage stress can induce stronger MAPK cascade reactions and ROS bursts. This study demonstrates that the pepper

CaLecRK-S.5 gene can respond to damage stress.

2.5 Lectin Receptor-Like Kinases Participate in Plant Hormone Signal Responses

Plant hormones have important physiological functions in regulating plant growth and development. The regulation of plant hormones requires the participation of membrane proteins, and numerous research results indicate that lectin receptor-like kinases (LecRLKs) are involved in plant hormone signal responses.

2.5.1 LecRLKs Participate in Abscisic Acid (ABA) Signal Responses

As shown in Table 5 , lectin receptor-like kinases have been reported to participate in ABA signal responses. According to Xin et al. (2009), multiple LecRLKs in *Arabidopsis* have been confirmed to be transcriptionally regulated by ABA (Xin et al., 2009; Bouwmeester & Govers, 2009). Studies have found that among *Arabidopsis* L-type lectin receptor-like kinases, there is a subfamily called LecRKsA4 comprising four members: *LecRKA4.1*, *LecRKA4.2*, *LecRKA4.3*, and *LecRKA4.4*, which negatively regulate ABA stress during seed germination, thereby inhibiting seed germination (Xin et al., 2009). Xin et al. (2009) further studied *LecRKA4.1* mutants and found that T-DNA knockout mutants of *LecRKA4.1* show a weakly enhanced response to ABA stress in the inhibitory effect on seed germination. Subsequent studies on functional loss mutants of *LecRKA4.2*, *LecRKA4.3*, and *LecRKA4.4* also revealed the same weakly enhanced response. Based on expression studies and transcriptional network regulation analysis of LecRKsA4 genes, *LecRKA4.1* and *LecRKA4.2* were confirmed to participate in regulating the expression of some ABA-responsive genes. Based on the hypothesis that negative regulation of ABA stress responses during seed germination by members of this family has redundant functions, Xin et al. (2009) found that when double or triple mutations of LecRKsA4 member genes occur, the inhibitory effect of ABA on seed germination is more severe. Zhang et al. (2019) found that *LecRKA4.4* also participates in regulating ABA-mediated stomatal opening and closing processes.

Arabidopsis LecRK-V.2 also participates in ABA stress responses during seed germination. Studies have found that *LecRK-V.2* is positively regulated by ABA during seed germination. Unlike the mutant lines of the LecRKsA4 family, functional loss mutants of *LecRK-V.2* can slightly reduce the inhibitory effect of ABA on seed germination (Deng et al., 2009). When the *LecRK-V.5* gene is overexpressed, it can regulate stomatal opening and closing by inhibiting ABA stress responses (Desclos-Theveniau et al., 2012). The pea L-type lectin receptor-like kinase *PsLecRLK* gene also participates in ABA signal responses. After pea is treated with ABA, the *PsLecRLK* gene produces a strong response in the later stage (Vaid et al., 2015). Liu et al. (2017) overexpressed the L-type lectin receptor-like kinase gene *PnLecRLK1* from Antarctic moss in *Arabidopsis* and found that it could increase *Arabidopsis* sensitivity to ABA during seed germination. Additionally, in *PnLecRLK1* overexpressing *Arabidopsis* transgenic plants, the abundance of ABA-responsive gene transcripts significantly increased.

2.5.2 LecRLKs Participate in Salicylic Acid (SA) Signal Responses

As shown in Table 6 , lectin receptor-like kinases have been reported to participate in SA signal responses. Studies have found that the L-type lectin receptor-like kinase *LecRK-IX.2* gene in *Arabidopsis* participates in plant hormone SA signal responses. *LecRK-IX.2* can induce calcium-dependent protein kinase (CPKs) phosphorylation and activate RBohD, thereby causing ROS bursts and enhancing ROS-triggered SA biosynthesis (Luo et al., 2017). *LecRK-IX.2*-mediated cell death requires SA accumulation, and when *LecRK-IX.2* overexpression causes SA elevation, it can lead to cell death. Additionally, *LecRK-IX.2* mutants also participate in responding to flg22-induced *Arabidopsis* SA signal transduction pathways. Studies have shown that functional SA signaling participates in stomatal closure during stomatal immunity (Melotto et al., 2006). Yekondi et al. (2018) suggested that *Arabidopsis LecRK-V.2* and *LecRK-VII.1* may play partial roles in SA-mediated stomatal closure.

In tobacco, LecRK1 inhibits SA accumulation during herbivory. Virus-mediated gene silencing and inverted repeat RNA interference can reduce *LecRK1* expression levels to obtain ir-*LecRK1* plants. Studies have found that in ir-*LecRK1* plants, SA accumulation increases two-fold (Gilardoni et al., 2011).

2.5.3 LecRLKs Participate in Jasmonic Acid (JA) Signal Responses

As shown in Table 7 , lectin receptor-like kinases have been reported to participate in JA signal responses. In *Arabidopsis*, Balagué et al. (2017) found that the L-type lectin receptor-like kinase *LecRK-I.9* participates in JA signal responses. JA can induce *LecRK-I.9* expression, while overexpression of *LecRK-I.9* can change the expression levels of its JA signal response-related transcription factors (TFs). Additionally, overexpression of *LecRK-I.9* also affects the expression of genes involved in JA synthesis and related genes in this signaling pathway. Studies have found that *LecRK-I.9* participates in responding to JA hormone signals and can negatively regulate the MYC branch of the signaling pathway (Balagué et al., 2017). Ethylene (ET) and JA jointly regulate *LecRK-I.9* expression, while SA does not participate in this process (Gimenez-Ibanez & Solano, 2013). Balagué et al. (2017) proposed a regulatory model for *LecRK-I.9* response to JA signal pathways, where *LecRK-I.9* has a positive regulatory effect on JA-mediated defense genes and a negative regulatory effect on JA-mediated damage genes.

Yekondi et al. (2018) found that the L-type lectin receptor-like kinases *LecRK-V.2* and *LecRK-VII.1* participate in stomatal immunity processes and JA-induced stomatal closure processes. When *LecRK-V.2* and *LecRK-VII.1* genes are overexpressed, plants show higher sensitivity to MeJA-mediated stomatal closure processes. *LecRK-V.2* and *LecRK-VII.1* participate in activating MeJA-induced Ca2+ permeable cation channels in guard cells, leading to stomatal closure (Yekondi et al., 2018). Therefore, the *LecRK-V.2* and *LecRK-VII.1* genes may have important functions in the signal cascade process of flg22 perception and MeJA accumulation, thereby causing ROS bursts. Thus, functional *LecRK-V.2* and *LecRK-VII.1* are important components of MeJA-mediated stomatal closure.

Gilardoni et al. (2011) confirmed that LecRK1 participates in insect-mediated suppression of JA-induced defenses in tobacco. Studies have found that in plants with insufficient JA synthesis or low sensitivity to JA, jasmonates can inhibit the expression of *LecRK1* gene mRNA (Gilardoni et al., 2011).

2.5.4 LecRLKs Participate in Ethylene (ET) Signal Responses

As shown in Table 8 , lectin receptor-like kinases have been reported to participate in ET signal responses. Early studies found that ethylene (ET) mediates plant stress responses by regulating ROS production (Mergemann & Sauter, 2000). He et al. (2004) found that the *Arabidopsis* L-type lectin receptor-like kinase *LecRK-I.3* gene is induced by salt stress under the regulation of the ET signaling pathway and ethylene receptor proteins. *NTHK1* is an ethylene receptor gene induced by salt stress discovered in tobacco (Zhang et al., 2001). Studies have shown that in *Arabidopsis* transformed with the *NTHK1* gene, *LecRK-I.3* gene expression is suppressed or delayed (He et al., 2004). In the ethylene overexpression mutant *eto1-1*, *LecRK-I.3* gene shows constitutive expression induced by ethylene (He et al., 2004). In the ethylene-insensitive mutant *ein2-1*, the expression level of *LecRK-I.3* induced by salt is basically the same as in wild type, indicating that *LecRK-I.3* induction by salt stress does not depend on the core component EIN2 of the ethylene signaling pathway (Alonso et al., 1999).

Studies have found that the rice L-type lectin receptor-like kinase *SIT1* positively regulates ET production and mediates salt-induced ethylene signal transduction (Li et al., 2014). In *Arabidopsis*, *SIT1* promotes reactive oxygen species (ROS) accumulation through MPK3/6 and ethylene signal-dependent pathways, thereby inhibiting plant growth and even causing death. Li et al. (2014) confirmed the existence of a *SIT1-MPK3/6* cascade in rice that mediates salt sensitivity by regulating ROS and ethylene homeostasis and signal transduction.

PsLecRLK is a pea L-type lectin receptor-like kinase. When *PsLecRLK* is overexpressed in tobacco plants, ethylene-responsive genes are upregulated (Vaid et al., 2015).

Future Perspectives

Abiotic stresses (salt damage, temperature stress, drought, mechanical damage, and hormone stress) are key factors limiting the yield of most crops and are also major environmental threats to food security. Although many lectin receptor-like kinases have been reported to participate in plant abiotic stress responses, involving multiple signaling molecules and pathways, their underlying mechanisms remain to be further explored.

First, the mechanisms by which LecRLKs recognize ligands and transduce signals in abiotic stress are not well understood. It is known that lectin receptor-like kinases recognize self and non-self signaling molecules and participate in plant biotic/abiotic stress responses through signal transduction. For example, *PnLPK* can participate in mechanical damage responses through non-JA- and SA-mediated signal transduction channels (Nishiguchi et al., 2002). However, systematic studies are lacking on how LecRLKs transmit signals to downstream molecules through their intracellular kinase domains, how they regulate stress responses, how they interact with other signaling pathways, and how they regulate gene expression and protein translation. It is known that lectin receptor-like kinases have kinase domains, and phosphorylation functions are extremely important in signal activation and transduction, but whether phosphorylation functions participate in regulating plant abiotic stress responses has rarely been reported. In-depth research on the kinase activity and phosphorylation functions of lectin receptor-like kinases will further expand research ideas on the involvement of this class of kinases in abiotic stress responses.

Second, the functional diversity and redundancy of LecRLKs have not been deeply exploited. Studies have found that LecRLKs can play different roles under different abiotic stresses, and even have different effects under the same abiotic stress. For example, under low temperature stress, the expression of the *OsLecRK1* gene in rice seedlings is suppressed; while under mechanical damage stress, the expression of the *OsLecRK1* gene is induced and upregulated. This indicates that the same LecRLKs have functional diversity, which may be related to their structural domains, subcellular localization, tissue-specific expression, and other factors. At the same time, functional redundancy or synergistic responses may exist among LecRLKs, leading to inconspicuous or inconsistent results from single gene knockout or overexpression. Therefore, in-depth and systematic functional analysis and research from genetics and molecular biology perspectives are needed. Additionally, current functional studies of lectin receptor-like kinases have mostly focused on single individual kinases, while whether different lectin receptor-like kinases interact with each other and whether they coordinately participate in abiotic stress responses are poorly understood. Investigating the mutual regulatory relationships among lectin receptor-like kinases and elucidating their mechanisms of participation in abiotic stress responses are also worthwhile future research directions.

The application of LecRLKs in crop stress resistance breeding has not yet been popularized. Studies have shown that changing LecRLK expression levels or activity through transgenic or gene editing technologies can improve crop resistance to abiotic stress. For example, overexpression of the *LecRK-IV.3* gene in *Arabidopsis* can enhance plant tolerance to salt stress (Huang et al., 2013).

These studies provide useful references for utilizing LecRLKs in crop stress resistance breeding. However, due to the functional diversity and redundancy of LecRLKs, as well as the limitations of transgenic or gene editing technologies, there have been no successful cases of applying LecRLKs in crop stress resistance breeding to date. Therefore, further screening and identification of LecRLKs with important functions and application potential, as well as the development of more efficient, safer, and more reliable gene manipulation technologies, are key to achieving widespread application of LecRLKs in crop stress resistance breeding. At the same time, deeply understanding the relationship between plant development and stress responses, elucidating the molecular regulatory mechanisms involved, and finding the balance between development and stress resistance are particularly important for crop stress resistance breeding.

Further identification and in-depth research on LecRLKs will help screen out LecRLK candidate genes that meet human needs, thereby engineering crops with greater stress tolerance and resistance. Additionally, improving plant stress resistance can reduce environmental pressure caused by water and fertilizer consumption from low-tolerance crops to a certain extent, which is crucial for sustainable agricultural production and environmental development.

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