Cai *et al. Phytopathology Research (2024) 6:58*
https://doi.org/10.1186/s42483-024-00279-0

Phytopathology Research

REVIEW **Open Access**

Receptor-like proteins: decision-makers of plant immunity

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Abstract

Receptor-like proteins (RLPs) are crucial pattern-recognition receptors on the surface of plant cells, which are involved in almost all processes of the plant life cycle. Recently, the evolution of high-throughput sequencing technology has strengthened the appraisal and identification of increasing numbers of RLPs and has primarily improved our understanding of the roles of RLPs in various biological processes. Here, we review the classification and evolutionary characteristics of RLPs and their regulatory roles in pattern-triggered immunity (PTI) and effector-triggered immunity (ETI). In particular, we summarize the ligands recognized by RLPs, their co-receptors, and downstream signalling cascades mediated by RLPs. To summarize, this review offers beneficial guidance for researchers in at-a-glance comprehension of the function of RLPs. It also puts forward the prospect of mining broad-spectrum candidate genes in light of the research on the disease resistance mechanism of RLPs and current challenges in disease resistance breeding.

Keywords Receptor-like proteins, Pattern recognition receptors, PAMP-triggered immunity, Effectors, Effector-triggered immunity

Background

To accomplish the lengthy life cycle, plants cannot locomote and thus must take out survival strategies to overcome environmental stress conditions and attacks of pathogenic microbes. During the plant-pathogen coevolution, plants have formed an efficient innate immune system to detect the signals from potentially harmful microorganisms and initiate rapid defence responses. Plant innate immunity is a two-layer immune system composed of pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) (Jones and Dangl 2006; Dodds and Rathjen 2010). PTI, characterized as horizontal or basal resistance, is initiated by plasma membrane-localized pattern-recognition receptors (PPRs) upon perception of pathogen-associated molecular patterns (PAMPs) (Macho and Zipfel 2014). Most identified PRRs are members of receptor-like kinases (RLKs) and receptor-like proteins (RLPs) (Gu et al. 2017). ETI is defined as vertical resistance and is primarily initiated by intracellular or transmembrane immune receptors by recognizing either effector structures or effector-mediated manipulations of host targets (Cui et al. 2014).

As one class of essential membrane-localized proteins, RLPs are widely distributed in the genomes of all tested Angiosperms and have emerged as a significant class of signalling proteins (Jamieson et al. 2018). From 50 to nearly 500 RLPs have been determined in each plant via genome-wide identification (Fritz-Laylin et al. 2005; Kang and Yeom 2018; Restrepo-Montoya et al. 2020; Yang et al. 2021; Álvarez-López et al. 2022; Kang et al. 2022; Yu et al. 2023). To date, the increased investigations revealed the versatile functions of RLPs in PTI and ETI (Wang et al. 2008, 2018; Larkan et al. 2015; Saur et al. 2016; Wu et al. 2016; Catanzariti et al. 2017; Yang et al. 2017, 2023; Yin et al. 2021; Fan et al. 2022). Compared to RLKs, RLPs maintain a prolonged immune response, indicating their crucial and specific

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functions upon stress (Wan et al. 2019). Here, we outline the research progress of RLPs on plant immunity and discuss potential orientations for resistance breeding in the future.

Domain structure of RLPs

RLPs possess one or more extracellular ligand-binding domains (ED) similar to RLKs but lack a C-terminal cytoplasmic kinase domain (KD) (Fritz-Laylin et al. 2005; Fig. 1). Most RLPs contain an N-terminal signal peptide, a single transmembrane region (TM) and a short cytoplasmic tail (Jamieson et al. 2018). However, a few proteins containing a glycosylphosphatidylinositol (GPI) anchor instead of TM are also regarded as RLPs (Broner et al. 2002). In rice, GPI-anchor modification causes the failure localization of chitin receptor OsCEBiP on the plasma membrane, indicating that GPI anchoring is integral to

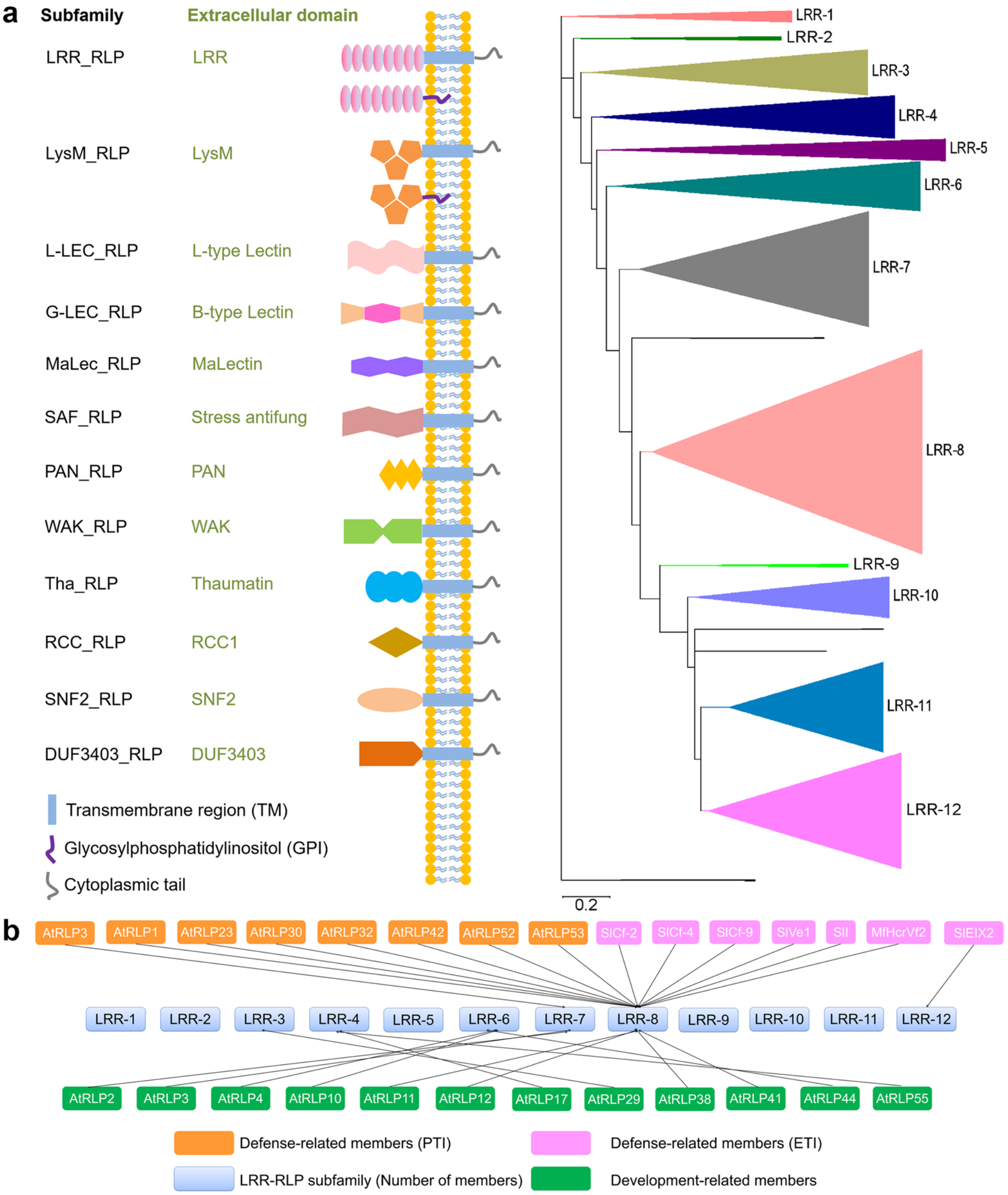

Fig. 1 Evolution and functional diversification of RLPs. **a** The main structure and classification of RLPs. LRR, Leucine-rich repeat; LysM, Lysin motif; L-type lectin, Legume lectin; B-type Lectin, Bulb-type lectin; Stress-Antifung, Formerly known as DUF26 (Domain of Unknown Function); PAN, Plasminogenlapple/nematode protein domain; WAK, Wall associated kinase; RCC1, Regulator of Chromosome Condensation 1; SNF2, sucrose nonfermenting 2; DUF3403, Domain of Unknown Function. **b** Clustering of the development and defence-related RLP members in each RLP subfamily

its localization (Gong et al. 2016). Various EDs, such as leucine-rich repeat (LRR), lectin or lectin-like, galectin-like, stress-Antifung, RCC1, and thaumatin domains, etc., have been found distributed on the N terminal of the RLPs and responsible for the extracellular signalling perception (Jamieson et al. 2018; Yu et al. 2023).

Plant-derived extracellular leucine-rich repeats (LRRs) contain 22–23 amino acids and form a LxxLxxLxLxxNxLSGxIPxxLGx consensus (Hohmann et al. 2017). RLPs containing LRRs, known as LRR-RLPs, most commonly exist in plants. There are at least 57 and 90 members in the model plant *Arabidopsis thaliana* and *Oryza sativa*, respectively, and more members in most woody plants (Fritz-Laylin et al. 2005; Yu et al. 2023). Arabidopsis LRR-RLPs typically have 16–28 LRR repeats (Belkhadir et al. 2014). LRRs recognize various ligands, including sterols, lipids, sugars, peptides, lipopeptides, and nucleic acids (Jamieson et al. 2018). However, for some LRR-RLPs in plants and oomycete pathogens, only a part of LRRs are the recognizer for plant-microbe interaction (Catanzariti et al. 2017; Pei et al. 2023). Therefore, besides identifying critical LRR-RLPs regulating plant resistance, additional experiments are needed to determine the crucial LRR domains of LRR-RLPs on immunity regulation.

Lectin or lectin-like domains, typically including legume-like (L-type) lectins, G-type lectins, calcium-dependent (C-type) lectins, and the lectin-like Lysin-motifs (LysM), frequently exist in plant RLK superfamily, and some are also discovered from RLPs (Vaid et al. 2013; Naithani et al. 2021). Among the tested 17 plant species belonging to Angiosperm, the number of L-type and G-type lectin RLP family members varies from 1 to 8 and 0 to 4, respectively; in contrast, LysM RLPs show a conserved range from 3 to 5 members, whereas few C-lectin RLPs are found (Yu et al. 2023). The ligands of LysM-RLPs, such as CEBiP, are well characterized as chitin or oligosaccharides peptidoglycan (PGN) (Willmann et al. 2011; Liu et al. 2012a; Shinya et al. 2012; Gong et al. 2016). Additionally, the extracellular L-type lectin domain of LecRK-I.9 or P2K2 and LecRK-I.8 directly binds to extracellular ATP and NAD$^+$, respectively, and thus is determined as the potential receptors for these compounds (Choi et al. 2014; Wang et al. 2017; Pham et al. 2020). An RLK member LORE, which contains a G-type lectin domain, was confirmed to recognize bacterial 3-hydroxy fatty acids (3-OH-FAs) (Ranf et al. 2015; Kutschera et al. 2019; Schellenberger et al. 2021). However, whether the L-type and G-type lectin domains of RLPs can also recognize and bind to these compounds is unclear.

Many other domains, such as malectin, stress-Antifung, thaumatin, PAN, RCC1, and GUB_WAK_bind, have also been identified from plant RLPs. Malectin, stress-Antifung, and EGF domains were widely detected from RLPs of Angiosperms, but other domains were only found from RLPs in some dicots (Yu et al. 2023). The malectin domain of several RLKs is well clarified, which binds to multiple cysteine-rich peptides named Rapid Alkalinization Factors (RALFs) (Ge et al. 2017; Franck et al. 2018; Gonneau et al. 2018). For RLKs containing GUB_WAK_bind domains, AtWAK1 is demonstrated as a receptor of oligogalacturonides (OGs), whereas AtWAK2 can bind to the de-esterified charged galacturonic acid backbone common in pectin (Kohorn et al. 2009; Brutus et al. 2010). Besides, both TaCRK3 and its stress-Antifung domain, also named DUF26, obviously inhibit the growth of *Rhizoctonia cerealis* and contribute to the resistance of wheat. However, the ligands of this domain are not yet determined (Guo et al. 2021). Interestingly, a recent study identified RALR, the first LRR-RLP protein receptor in Poplar, that recognizes antimicrobial peptides (AMPs) (Lintz et al. 2023).

In summary, our understanding of the functions of the RLP domains is largely limited, although their structures are already well characterized. Besides several EDs, such as LysM, the functional analyses of the domains mentioned above mainly focus on RLKs; however, it is unclear whether these domains possess similar functions in RLKs. Structural prediction via tools such as AlphaFold and DeepMSA2/DMFold (Jumper et al. 2021; Zheng et al. 2024) and further functional investigation may shed light in the future.

Expansion and duplication events

The scientific classification of RLPs is the basis for subsequent exploration of family expansion and gene duplication events. RLPs were preliminarily classified into different subfamilies based on the types of EDs (Restrepo-Montoya et al. 2020; Silva et al. 2022). Reliable further classification is needed considering the large size of LRR-RLP family members. A phylogenetic tree of Arabidopsis LRR-RLPs was constructed based on the sequence of the C3-F region (Fritz-Laylin et al. 2005). Recently, we classified almost all of the LRR-RLPs predicted from 19 plant species into 12 subfamilies based on a phylogenetic tree constructed using whole amino acid sequences (Yu et al. 2023; Fig. 1). However, it is still not known if the RLP members in the same phylogenetic group share similar functions.

The high dynamics of the genome evolution have been observed in angiosperms compared to other land plants. Several subfamilies of RLKs or subgroups of LRR-RLKs, such as WAKs and LRR-XI, are rapidly expanded during their evolution, which is mainly driven by frequently occurring gene duplication events and usually results in diversified functions (Innan and Kondrashov 2010). The expansion of several defence-related gene groups is primarily caused by tandem duplication (Melissa et al. 2009; Mao et al. 2021). Among 24 RLP subfamilies from 19 plant species, RLPs display both species- and subfamily-specific expansion (Yu et al. 2023). In Arabidopsis, RLP subfamily LRR.8_RLP exhibits a high expansion rate resulting from whole-genome duplication (WGD) and tandem duplication (TD).

Interestingly, for the 27 functionally investigated RLPs in Arabidopsis, 13 out of 15 functionally determined RLPs associated with disease resistance belong to LRR.8_RLP subfamily, whereas 11 members are related to cell growth and development distributed in five subfamilies (Fig. 1). Moreover, several subfamilies, such as LRR.7_RLP, LRR.11_RLP, LRR.12_RLP, and Tha_RLP, are rapidly expanded in Rosaceae and several members were determined as critical genes regulating *Valsa canker* resistance (Yu et al. 2023). These observations indicate that many species- and subfamily-specific expansion events occurred during the evolution of RLPs, which is vital for land plants adapting to complex and changeable environments. In the near future, extensive practices are needed to elucidate the exact relationship between gene expansion events and corresponding functions. In addition, functional investigation on the receptor-like cytoplasmic kinase VII members based on mutant construction suggests that tandem duplicated members in each clade display functional redundancy (Rao et al. 2018). It is still being explored whether functional redundancy also widely exists in the RLP superfamily.

RLPs recognize appropriate ligands to activate PTI

PRRs are membrane-localized receptors that recognize PAMPs as highly conserved molecules secreted by microbes for their fitness or survival (Boller and Felix 2009). Numerous PAMPs have been well characterized, including bacterial flagellin, elongation factor Tu, lipopolysaccharides, peptidoglycan, and fungal chitin, and these PAMPs are not related to the pathogen virulence (Thomma et al. 2011). To prevent pathogen invasion, PRRs could recognize PAMP molecules or PAMPs and activate PTI (Table 1) (Schwessinger and Ronald 2012; van den Burgh and Joosten 2019; Defalco and Zipfel 2021). So far, PRRs include two types of cell surface proteins: receptor-like kinases (RLKs) and receptor-like proteins (RLPs). We focus on summarizing the role of RLPs in stimulating plant immunity.

RLPs recognize multiple PAMPs

An increasing number of RLPs belong to LRR-RLPs, and LysM-RLPs are determined as typical PRRs that mediate plant resistance to infection by a wide range of pathogens (Fig. 2). Several members were confirmed as receptors for multiple PAMPs and mediate broad-spectrum disease resistance.

LRR-RLP members could recognize various PAMPs from pathogenic bacteria and fungi. *AtRLP1/ReMAX* of Arabidopsis precisely functions as a PRR and sensing eMax signal derived from *Xanthomonas* (Jehle et al. 2013). In *Nicotiana benthamiana*, *NbRE02* (*NbCSPR*) underlies age-dependent immune responses directly associating with and responding to bacterial cold shock protein CSP22 (Saur et al. 2016; Wang et al. 2016). AtRLP32 recognizes the structural fold of proteobacteria's translation-initiation factor (If-1) and confers resistance against *Pseudomonas syringae* infection (Fan et al. 2022). Aside from bacterial PAMPs, several fungal and oomycete PAMPs could also be perceived by LRR-RLP members. *N. benthamiana* RXEG1 has been demonstrated to sense the glycoside hydrolase XEG1 secreted from oomycete *Phytophthora sojae* (Wang et al. 2018). TaRLP1.1 is required to fully resist the biotrophic fungus *Puccinia striiformis* f. sp. *tritici* (*Pst*) (Jiang et al. 2013). In wild potato (*Solanum microdontum*), the LRR-RLP ELICITIN RESPONSE (SmELR) discerns elicitin INF1 and positively regulates potato resistance to *Phytophthora infestans* (Du et al. 2015). Further research indicates that Responsive to ELicitins (REL) also recognizes elicitins in *N. benthamiana* and mediates *Phytophthora* resistance, but REL and ELICITIN RESPONSE (ELR) differ in how they bind and recognize elicitins (Chen et al. 2023).

Moreover, NbEIX2, AtRLP30, and AtRLP42/RBPG1 recognize necrotrophic fungi-produced PAMPs ethylene-inducible xylanase (EIX), sclerotinia culture filtrate elicitor1 (SCFE1), and endopolygalacturonases (PGs), respectively (Ron and Avni 2004; Zhang et al. 2013, 2014; Yin et al. 2021). AtRLP23 perceives a conserved 20-amino-acid fragment present in most necrosis and ethylene-inducing peptide (Nep1)-like proteins, thereby mediating immune activation (Albert et al. 2015). It is interesting that an LRR-RLP NbRE02 is able to recognize multiple PAMPs and trigger resistant reactions against both bacteria and fungi. As a sensor for bacterial csp22, NbRE02 also perceives small cysteine-rich protein VmE02 from apple canker pathogen *Valsa mali* and contributes to the resistance of *N. benthamiana* against multiple filamentous phytopathogens (Saur et al. 2016; Nie et al. 2021). Another novel cell surface receptor, NbREli, senses and directly binds to *Pythium periplasm* elicitin PpEli2, and confers broad-spectrum disease resistance (Yang et al. 2023).

Table 1 Summary of the identified RLP resistance genes

Gene	Ligands	Gene synonyms	Subgroup	Species	Type	Associated receptor	Function	Reference(s)
AtRLP1/ReMAX	eMax	AT1G07390	*LRR-8*	*Arabidopsis*	LRR	SOBIR1	Pattern-triggered immunity	(Jehle et al. 2013)
AtRLP30	Sclerotinia culture filtrate elicitor1 (SCFE1)	AT3G05360	*LRR-8*	*Arabidopsis*	LRR	SOBIR1, BAK1	Pattern-triggered immunity, influences non-host resistance towards *Pseudomonas syringae* pv. *phaseolicola* (*Psp*)	(Ellendorff et al. 2008; Wang et al. 2008; Zhang et al. 2013)
AtRLP32	Proteobacterial translation initiation factor IF1	AT3G05650	*LRR-8*	*Arabidopsis*	LRR	SOBIR1	Pattern-triggered immunity	(Fan et al. 2021)
AtRLP3	/	AT1G17250	*LRR-7*	*Arabidopsis*	LRR		Resistance to the vascular wilt fungus *Fusarium oxysporum*	(Shen et al. 2013)
AtRLP23	nlp20	AT2G32680	*LRR-8*	*Arabidopsis*	LRR	SOBIR1, SERK3/BAK1	Pattern-triggered immunity	(Liebrand et al. 2013)
AtRLP42/RBPG1	Endopolygalacturonases (PGs)	AT3G25020		*Arabidopsis*	LRR	SOBIR1, SERK	Pattern-triggered immunity	(Zhang et al. 2014)
AtLYM2	Chitin	AT2G17120	*LysM-RLP*	*Arabidopsis*	LysM		Pattern-triggered immunity	(Petutschnig et al. 2010; Shinya et al. 2012)
AtLYM1	Oligosaccharides peptidoglycan (PGN)	AT1G21880	*LysM-RLP*	*Arabidopsis*	LysM	CERK1	Pattern-triggered immunity	(Willmann et al. 2011; Shinya et al. 2012)
AtLYM3	Oligosaccharides peptidoglycan (PGN)	AT1G77630	*LysM-RLP*	*Arabidopsis*	LysM	CERK1	Pattern-triggered immunity	
OsLYP4	Oligosaccharides peptidoglycan (PGN)	LOC_Os09g27890		Rice	LysM	CERK1	Pattern-triggered immunity	(Liu et al. 2012)
OsLYP6	Oligosaccharides peptidoglycan (PGN)	LOC_Os06g10660		Rice	LysM	CERK1	Pattern-triggered immunity	
OsCEBiP	Chitin	LOC_Os03g04110		Rice	LysM	OsCERK1	Pattern-triggered immunity	(Shimizu et al. 2010)
HvCEBiP	Putative chitin receptor gene	KAE8808384.1		Barley	LysM		Defence against fungal pathogens	(Tanaka et al. 2010)
SlCf-2	Avr2	U42444	*LRR-8*	Tomato	LRR	SOBIR1, BAK1	Effector-triggered immunity	(Jones et al. 1994)
SlCf-4	Avr4	AJ002235	LRR-8	Tomato	LRR	SOBIR1, BAK1	Effector-triggered immunity	
SlCf-9	Avr9	Solyc12g008380.1	*LRR-8*	Tomato	LRR	SOBIR1, BAK1	Effector-triggered immunity	
SlVe1	Ave1	AY262016	*LRR-8*	*Solanum lycopersicoides*	LRR	SOBIR1, BAK1	Effector-triggered immunity	(Kawchuk et al. 2001)
SlI	Avr1	Solyc11g011180.1	*LRR-8*	Tomato	LRR	SOBIR1, SERK3/BAK1	Effector-triggered immunity	(Catanzariti et al. 2017)

Table 1 (continued)

Gene	Ligands	Gene synonyms	Subgroup	Species	Type	Associated receptor	Function	Reference(s)
SlEIX2	Ethylene-inducible xylanase (EIX)-like protein	Solyc07g008630.1	*LRR-12*	Tomato	LRR		Pattern-triggered immunity	(Ron and Avni 2004)
NbEIX2	Ethylene-inducible xylanase (EIX)-like protein	Niben-101Scf00975_98677–103,769	*LRR-12*	*Nicotiana benthamiana*	LRR		Pattern-triggered immunity	(Yin et al. 2021)
NbRXEG1	The glycoside hydrolase XEG1 from *Phytophthora sojae*	Niben-101Scf03925_116219–121,385		*Nicotiana benthamiana*	LRR	SOBIR1, BAK1	Pattern-triggered immunity	(Wang et al. 2018)
NbRE02	Small cysteine-rich protein VmE02 from *Valsa mali* bacterial cold-shock protein (csp22)	Niben101Scf03240g00007.1		*Nicotiana benthamiana*	LRR	SOBIR1, BAK1	Pattern-triggered immunity	(Saur et al. 2016; Nie et al. 2021)
GrLyp1	Chitin	Gorai.002G205600.1		Cotton	LysM		Recognize chitin signals	(Xu et al. 2017)
MtLYM2	Chitin-related molecules	Medtr3g097500.1		*Medicago truncatula*	LysM			(Fliegmann et al. 2011)
MfHcrVf2	/	AJ297740		Apple	LRR		Resistance to the apple scab fungus *Venturia inaequalis*	(Belfanti et al. 2004)
MmLYP1	Chitin	MG182078		*Morus multicaulis*	LysM	MmLYK2	Pattern-triggered immunity	(Lv et al. 2018)
BnLepR3	AvrLm1	JX880110		*Brassica napus*	LRR	SOBIR1	Effector-triggered immunity	(Larkan et al. 2013)
BnRlm2	AvrLm2	KM097068		*Brassica napus*	LRR	SOBIR1	Effector-triggered immunity	(Larkan et al. 2015)
SmELR	Elicitin INF1	MK388409.1		potato	LRR	SOBIR1, BAK1	To confer enhanced resistance to late blight	(Du et al. 2015)
REL	Elicitins	Niben101Scf02826g01005.1		*Nicotiana benthamiana*	LRR	SOBIR1, BAK1	Required for ELI-triggered immune responses	(Chen et al. 2023)
NbREli	PpEli2	Niben101Scf02826g01005.1		*Nicotiana benthamiana*	LRR	SOBIR1, BAK1		(Yang et al. 2023)
AtRLP53	/	AT5G27060	*LRR-8*	*Arabidopsis*	LRR	SOBIR1, BAK1	Pattern-triggered immunity	(Chen et al. 2022)
AtRLP52	/	AT5G25910	*LRR-8*	*Arabidopsis*	LRR		Resistance against the powdery mildew pathogen	(Ramonell et al. 2005)

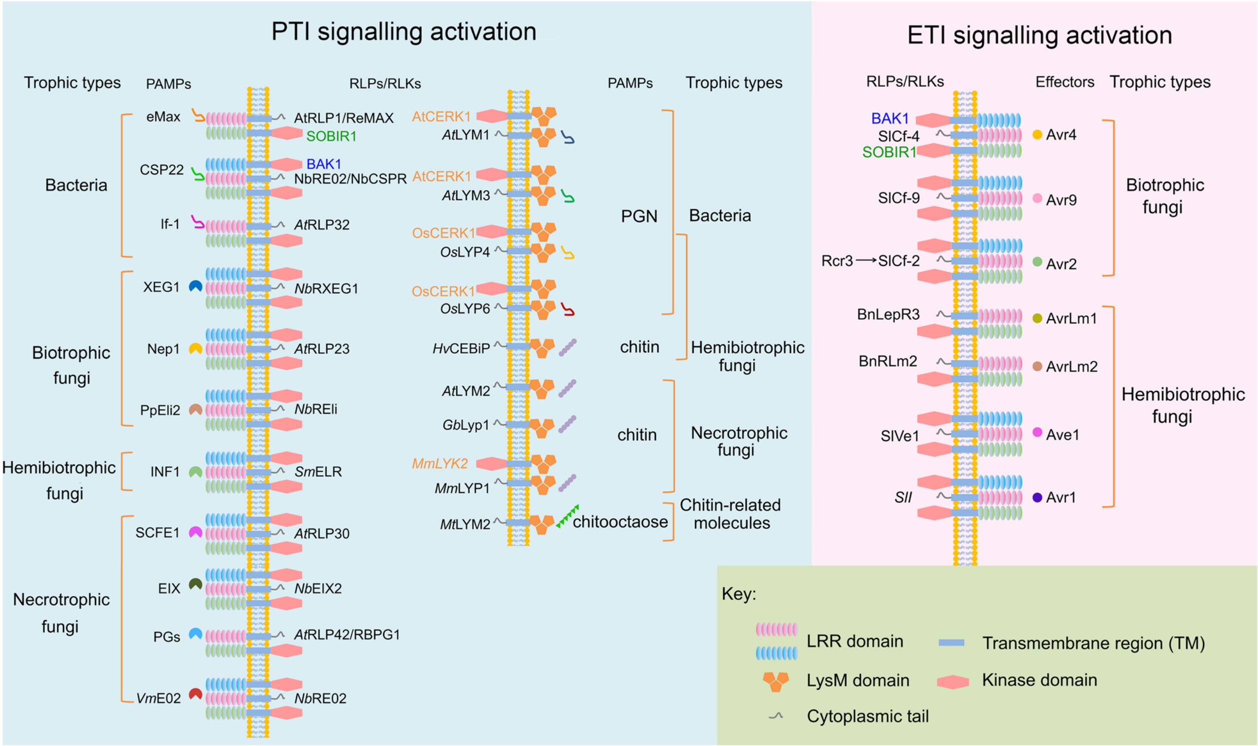

Fig. 2 Molecular models for the RLP recognition of different pathogen-related molecular patterns (PAMPs) and different effectors activating PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI), respectively. With regards to LRR-RLPs, upon perception of PAMPs, the RLP-type PRRs form a complex with BAK1 (BRI1-ASSOCIATED KINASE-1) and SOBIR1 (SUPPRESSOR OF BIR1-1) probably through BAK1/SOBIR1 interaction with the PRR-bound ligand, whereas CERK1 and LYK2 act as a core partner of part LysM-RLPs in plants and activate downstream signal pathways. Moreover, several pathogen-derived effectors, e.g. Avr4, Avr9, AvrLm1, AvrLm2, Avr2, Ave1, and Avr1, are also recognized by LRR RLPs SlCf-4, SlCf-9, BnLepR3, BnRLm2, SlCf-2, SlVe1, and SlI. In addition, Cf-2-mediated resistance upon Avr2 perception requires the extracellular tomato cysteine protease Rcr3. LRR-RLPs constitutively interact with SOBIR1. BAK1 is also required for some LRR-RLPs' function

All the systemically studied LysM-RLPs can specifically bind to chitin or oligosaccharides peptidoglycan (PGN) and contribute to host resistance against a broad range of pathogenic microbes. AtLYM2 has been determined as a PRR that recognizes chitin signals and mediates resistance to necrotrophic fungi *Botrytis cinerea* and *Alternaria brassicicola* (Petutschnig et al. 2010; Shinya et al. 2012; Faulkner et al. 2013; Narusaka et al. 2013). In contrast, AtLYM1, AtLYM3, OsLYP4, and OsLYP6 specifically bind PGN to trigger resistance to bacterial pathogens (Willmann et al. 2011; Liu et al. 2012a; Shinya et al. 2012). Conservatively, the homologs of chitin receptor CEBiP in barley (HvCEBiP) and cotton (GbLyp1) also act as important chitin sensors and induce defence responses against hemibiotrophic fungi *Magnaporthe oryzae* and necrotrophic fungus *Verticillium dahliae*, respectively (Tanaka et al. 2010; Xu et al. 2017). MtLYM2 is a homolog of CEBiP in *Medicago truncatula* and acts as a specific binding protein like CEBiP (Fliegmann et al. 2011). The above findings indicate that the recognition by most LysM-RLPs in plants depends on binding to chitin or PGNs. On the contrary, two LysM-RLP members in rice, OsLYP4 and OsLYP6, function as dual receptors for PGNs and chitin in rice, mediating bacterial and fungal resistance (Liu et al. 2012a).

Signalling partners of RLPs in PTI

Owing to RLPs' lack of typical cytoplasmic signalling domains, receptor/co-receptor complex formation is instrumental for LRR-RLP-mediated signal transduction (Gust and Felix 2014). At present, the interaction relationships between RLPs and LRR-RLK members SOBIR1 and BAK1 and LysM-RLK members CERK1 and LYK2 are confirmed. These interacting protein pairs synergistically regulate downstream signal cascades (Burgh et al. 2019).

Plant receptor-like protein kinase BAK1 acts as a co-receptor and forms receptor complexes with multiple RLKs to regulate diverse cellular signalling (Li et al. 2010). SOBIR1 is a suppressor of the LRR-RLK BIR1 (BAK1-interacting RLK-1), and functions as a positive defence regulator (Liebrand et al. 2014). These receptors are also confirmed as co-receptors of a variety of LRR-RLP members and collaboratively mediate immune activity against multiple microbes. In *N. benthamiana*, the association of a complex with BAK1 and SOBIR1 is indispensable for the recognition of the glycoside hydrolase 12 protein XEG1 by RXEG1 and the induction of downstream signal cascades (Wang et al. 2018). These two receptors are also associated with RE02 and regulate immune responses induced by VmE02, a PAMP from the phytopathogenic fungus *Valsa mali* (Nie et al. 2021). Upon ligand binding, AtRLP23 forms a constitutive, ligand-independent complex with the SOBIR1 and recruits BAK1 into a tripartite complex to mediate NLPs (Necrosis and ethylene-inducing peptide 1-like proteins)-triggered immunity (Albert et al. 2015). In line with this, the complex of SOBIR1 and ELR recruits BAK1/SERK3 to recognize elicitin proteins from *Phytophthora* species and activates basal resistance of wild potato *S. microdontum* (Du et al. 2015; Domazakis et al. 2018). Other LRR-RLPs, such as REli and NbCSPR in *N. benthamiana* and RLP30 and RLP53 in *A. thaliana*, are also constitutively associated with SOBIR1 and BAK1 in a pathogen-induced manner (Saur et al. 2016; Zhang et al. 2021; Chen et al. 2022; Yang et al. 2023). The above discoveries suggest that the complex of SOBIR1 and BAK1 is indispensable for subsequent signal transduction of a large number of LRR-RLPs during PAMP perception. However, NbSOBIR1 and its close homolog are not essential for the function of NbCSPR, although NbBAK1 can form a constitutive complex with both NbSOBIR1 and NbCSPR (Saur et al. 2016), indicating that csp22-triggered immune signalling is probably regulated by an unknown functional redundant protein(s).

Chitin Elicitor Receptor Kinase1 (CERK1) was characterized as a critical component for chitin signalling in plants and mediates plant immunity against both bacterial and fungal pathogens (Shimizu et al. 2010; Willmann et al. 2011). Typically, OsCERK1, a well-investigated LysM-RLK in rice, is required for OsCEBiP to transduce chitin signalling cascades. Upon perception of chitin, homodimerization of the OsCEBiP was induced, which recruits OsCERK1 to form an immune complex and further causes the homodimerization and phosphorylation of OsCERK1 and subsequent activation of immune response (Shimizu et al. 2010; Hayafune et al. 2014; Liu et al. 2016) (Fig. 3). The OsCEBiP paralogs, OsLYP4 or OsLYP6, have also been shown to bind to OsCERK1 and form receptor complexes to perceive PGN and chitin-derived signals (Liu et al. 2012a; Nasir et al. 2017). In Arabidopsis, CERK1 does not directly bind PGNs but is required for the activation of defenses and immunity to bacterial infection via binding with LysM domain proteins AtLYM1 and AtLYM3 (Willmann et al. 2011; Liu et al. 2012b). In addition, MmLYP1, a chitin-binding protein, physically interacts with the homolog of OsCERK1, MmLYK2 (Lv et al. 2018). These findings suggest that CERK1 conservatively acts as a core partner of many LysM-RLPs in plants and activates downstream signal pathways.

In summary, numerous LRR-RLPs and LysM-RLPs are crucial to plant PTI response via binding with specific PAMPs. SOBIR1/BAK1 and CERK1 emerged as crucial connectors to link the perception of LRR-RLPs and LysM-RLPs, respectively, and initiate subsequent immune responses. Nevertheless, whether other RLKs act as co-receptors remains to be explored. Besides, discovering the key resistance regulators in other RLP subfamilies is vital for our systemic understanding of RLPs on plant PTI.

RLPs can also be activated by avirulence proteins

Intracellular nucleotide-binding leucine-rich repeat (NLR) receptors detect effector proteins (virulence factors secreted into the host cell cytoplasm by pathogenic microbes) to induce effector-triggered immunity (ETI). NLRs are the largest group of resistance (R) proteins that detect specific effector proteins secreted by pathogens for their colonization and result in ETI (Cui et al. 2014; Peng et al. 2015). Typically, ETI displays a race-specific defence network and remarkable programmed cell death at the site of infection, termed a hypersensitive response (HR) (Coll et al. 2011). Compared to PTI, ETI activates robust and prolonged responses and appears more directly associated with transcriptional regulation of defence gene expression due to its localization (Peng et al. 2015). Besides the NLR superfamily, some LRR-RLP subfamily members are also characterized as R proteins and can activate typical ETI (Jamieson et al. 2018) (Fig. 2).

LRR-RLP members Cf-2, Cf-4, Cf-5, and Cf-9 confer plant race-specific resistance via binding to effector Avr2, Avr4, Avr5, and Avr9, respectively (Jones et al. 1994; Dixon et al. 1996, 1998; Thomas et al. 1997; Rooney et al. 2005; Huang et al. 2024). Ve1 and I in tomato and LepR3 and RLM2 in *Brassica napus* could also recognize specific effectors and mediate race-specific defence responses (de Jonge et al. 2012; Larkan et al. 2013; Larkan et al. 2015; Catanzariti et al. 2017). In addition, HcrVf2, a homolog of *Cladosporium fulvum* resistance genes, which appeared to be the functional gene for resistance against *Venturia inaequalis* avirulent isolates but not for virulent isolates, was considered as an R gene (Belfanti et al. 2004; Joshi et al. 2011; Table 1). Therefore, a large number of LRR-RLPs act as R genes to recognize specific effectors, activate ETI, and contribute to plant race or isolate specific resistance. The discovery of R genes is mainly focused on model plants such as Arabidopsis and tomato; identification of other R genes in LRR-RLPs, even other RLP

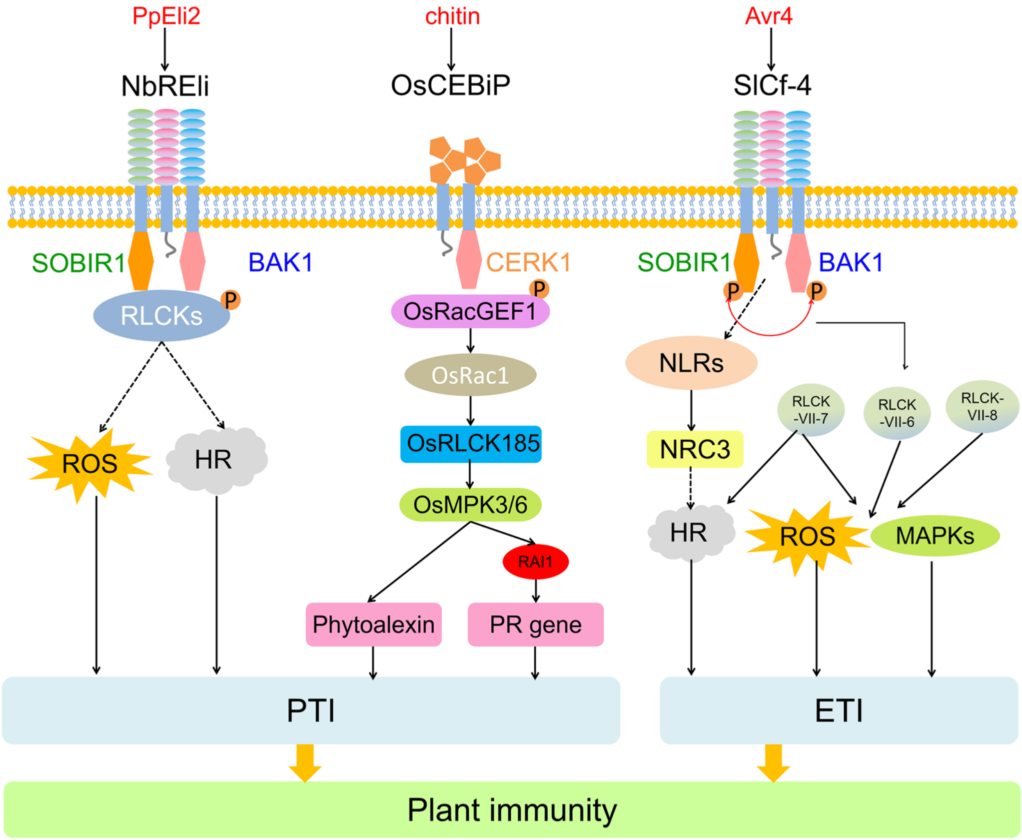

Fig. 3 Diagram of pattern-triggered immunity (PTI) signalling in response to PAMPs and effector-triggered immunity (ETI) signalling in response to plant effectors. During various pathogen infections, many PAMPs/DAMPs are recognized by plasma membrane-localized RLP complexes. The LRR-RLPs NbREli and LysM-RLPs OsCEBiP recognize PpEli2 and chitin, respectively. REli recognizes PpEli2 and forms a complex with two co-receptors, BAK1 and SOBIR1, to trigger the downstream immune responses, including HR cell death and ROS burst. Chitin is sensed by OsCEBiP. Activated OsCEBiP binds to the co-receptor OsCERK1 to form the OsCEBiP-OsCERK1 complex that initiates OsRacGEF1-dependent chitin signalling pathways. The OsCEBiP-OsCERK1 complex mediates the phosphorylation of OsRacGEF1 (a guanine nucleotide exchange factor for OsRac1), activating the small GTPase OsRac1. Subsequently, the OsRAI1 transcription factor is activated, further upregulating the expression of defense-related genes, leading to disease resistance. OsRLCK185 is essential for chitin-triggered immune responses. In *N. benthamiana*, Cf-4 requires the intracellular nucleotide-binding domain leucine-rich repeat-containing receptor (NLR) NRC3 to trigger a confluent cell death response upon detecting the fungal effector Avr4. Following the perception of Avr4 by Cf-4, the kinase domains of SOBIR1 and BAK1 directly phosphorylate each other. Avr4/Cf-4 can trigger ROS accumulation and MAPK activation in RLCK-VII-6, -7, and – 8-dependent manner, whereas members of RLCK-VII-7 are also required for the Avr4/Cf-4-induced HR

subfamilies that contribute to plant resistance, is essential for resistance breeding in the future.

RLPs modulate downstream immune outputs in PTI and ETI

Both PTI and ETI initiate a complex downstream signal cascade. Typically, PTI activates a series of cellular responses, such as activation of receptor-like cytoplasmic kinases (RLCKs), phosphorylation of substrate protein, rapid Ca^{2+} influx, reactive oxygen species (ROS) burst, initiation of MAPK cascades, callose deposition, alteration of hormonal networks, and activation of defence gene expression (Schwessinger and Ronald 2012; van den Burgh and Joosten 2019; Defalco and Zipfel 2021). By contrast, ETI is characterized by a robust and prolonged defence and is often accompanied by local programmed cell death (PCD) related to hypersensitive response (HR), which may further cause systemic acquired resistance (SAR) to restrict subsequent infection of the pathogen (Saijo and Loo 2020). Recent investigations show that ETI and PTI can involve similar defence responses, including massive ROS production, activation of kinases, and induction defence genes (Yuan et al. 2021). Indeed, SlNRC4a, a member of the NRC family, associates with LeEIX2 and positively regulates LeEIX2/EIX-mediated downstream immune signalling outputs (Leibman-Markus et al. 2018). Besides, ADR1s are required for RLP23-nlp20-induced transcriptional defences, which include a prominent ethylene response (Pruitt et al. 2020). Moreover, the cell surface receptor-like protein Cf-4 requires the intracellular NLR protein NRC3 to trigger a confluent cell death response upon detection of the fungal effector Avr4 in the leaves of *N. benthamiana.* Traditionally, the signalling pathways of cell surface receptor-mediated immunity and intracellular NLR-mediated immunity are believed to be different in nature, but this finding links the NLR resistosome model to cell surface PRR-induced hypersensitive cell death. However, further experiments are required to elucidate when this NRC helper NLR family member has evolved to connect with the pattern recognition receptor-triggered signalling pathway (Mesarich et al. 2016; Kourelis et al. 2022) (Fig. 3). This indicates that plant immunity activated by some PRRs can be classified as PTI, while others can be classified as ETI. Therefore, multiple studies have introduced other terms to classify immune responses (van der Burgh and Joosten 2019; Ding et al. 2020; Lacaze and Joly 2020). Nevertheless, each term has advantages and disadvantages and should be used cautiously. For example, the classification of the acronyms PTI and ETI is beneficial in avoiding confusion between autoimmunity and pathogen-induced immunity (Ngou et al. 2022).

As essential signalling molecules, ROS was characterized as a key regulator for plant development and stress responses. A series PRRs belonging to LRR-RLPs, such as NbCSPR, RXEG1, NbEIX2, REli, RBPG1, and RE02, are required for PAMPs activated ROS production (Zhang et al. 2013; Saur et al. 2016; Wang et al. 2018; Nie et al. 2020; Yin et al. 2021; Yang et al. 2023). ROS burst could also be conferred by R protein Cf-2 and Cf-9 and further involved in immunity triggered intracellularly (Dixon et al. 1996; van der Burgh and Joosten 2019). For the LysM-RLP subfamily, only some members are involved in ROS regulation. The levels of ROS triggered by the purified PGN declined by about 40% in RNAi lines of either LYP4 or LYP6 compared to the wild type but recovered in overexpression lines (Liu et al. 2012a). By contrast, ROS generation induced by chitin oligosaccharide GN8 was not impaired in the *AtCEBiP*-knockout (KO) mutant (Shinya et al. 2023). Nevertheless, little attention is paid to the detailed relationships between RLPs and critical proteins that affect ROS production. The PM-localized NADPH oxidase RBOH family members in plants function in apoplastic ROS production (Suzuki et al. 2011). As an additive player in defenses associated with BAK1, SOBIR1, and FLS2, receptor-like cytoplasmic kinase BIK1 controls ROS signalling via phosphorylation of RbohD (Kadota et al. 2014). These discoveries indicated that co-receptors of LRR-RLPs take vital roles in eliciting ROS signalling.

MAPK is a crucial signalling function downstream of PRRs and R proteins and is considered an essential component in plant immunity (Zhang and Zhang 2022). For LRR-RLPs, MAPKs induced by PAMPs are significantly impaired by silencing of NbCSPR (Saur et al. 2016) but were improved by overexpression of PpEli2 (Yang et al. 2023). SCFE1-containing fraction is specifically sensed by RLP30, and SCFE1-triggered MAPK activation requires BAK1 (Zhang et al. 2013). Furthermore, nlp20-inducible MAPK activation in wild-type plants was abolished in RLP23 mutants *rlp23*-1 and *rlp23*-2 (Albert et al. 2015). Aside from LRR-RLPs, the activation of MKK4 and MPK3/6 was also detected from LysM-RLP member OsCEBiP, OsLYP4, and OsLYP6 (Akamatsu et al. 2013) (Fig. 3). These investigations suggest that activation of MAPKs is a common signalling event downstream of most RLPs.

Phytohormones have pivotal roles in regulating immune responses with a complex network for rapidly adapting to an abiotic environment (Pieterse et al. 2012). Among these, ethylene and jasmonic acid (JA) are crucial for plant resistance against necrotrophs, whereas salicylic acid (SA) prevents biotroph attacks. Besides, auxin, abscisic acid (ABA), and other hormones are also involved in plant immunity. A large number of AtRLP genes were differentially expressed upon exposure to different hormones (Wu et al. 2016). Indeed, PAMPs, such as the 22-kD fungal protein EIX and eMAX, could induce ethylene biosynthesis, but the induction was substantially abolished by silencing of target receptors in host cells (Ron and Avni 2004; Jehle et al. 2013).

Functional investigation demonstrates that the mutation of either RLP23, the receptor of nlp20, or the co-receptor BAK1 and SOBIR1 results in significantly weakened ethylene generation, indicating that the signalling activation is mainly dependent on the receptor and co-receptors (Albert et al. 2015). Receptor-like protein ELT1 promotes brassinosteroid signalling via associating with and suppressing the endocytosis-mediated degradation of receptor BRI1 (Yang et al. 2017). SA signalling is involved in the ETI activated by Cf-2 and Cf-9, two typical R proteins in the LRR-RLP subfamily (Dixon et al. 1996). These findings suggest that various LRR-RLPs specifically mediate plant hormonal signalling during the immune response. Apart from LRR-RLPs, few reports mentioned that the hormone signal associated with LysM-RLPs and other RLP subfamily members initiated an immune response.

Cell death mechanisms are integral to plant defence against widely varied pathogenic microbes (Zebell and Dong 2015). The HR-related cell death adjacent to the infection site limited the spread of biotrophic pathogens, whereas it is favourable for further infection of necrotrophic microbes (Mengiste 2012). Cell death is involved in both PTI and ETI initiated by LRR-RLPs (Dixon et al. 1996; Suzuki et al. 2011; Domazkis et al. 2018; Chen et al. 2022). The REli or its co-receptors BAK1 and SOBIR1 are indispensable for perceiving elicitin PpEli2 and induction of HR-like cell death (Yang et al. 2023). Similarly, the Avr4-triggered HR was also obviously compromised when SOBIR1 was silenced (Liebrand et al. 2013). This suggests that co-receptors modulate the shared signalling hubs of cell death in both PTI and ETI regulated by LRR-RLPs. In addition, the cell death activated by various LRR-RLPs was precisely simultaneous with the accumulation of ROS, a well-characterized key regulator for cell death (Nie et al. 2021; Yang et al. 2023). However, it is unclear if ROS accumulation is a potential positive feedback to promote cell death.

Various other limmune responses initiated by RLPs cause the enhancement of host resistance. LRR-RLP member RLP23 and LysM-RLP member LYM2 are required for callose deposition activated by specific PAMPs (Faulkner et al. 2013; Albert et al. 2015), but the influence of RLP-induced ETI on callose deposition has rarely been documented. As an essential entrance of pathogen infection, stomata influence plant resistance via its movement (Melotto et al. 2006). Arabidopsis LRR-RLP member *TOOMANY MOUTHS* (*TMM*; *AtRLP17*) is expressed in proliferative postprotodermal cells and regulates stomatal distribution by controlling meristem formation as well as initiation of stomatal precursor cells (Nadeau et al. 2002). Besides, the LysM-RLP member LYM2 senses the chitin signal to modulate the molecular flux between cells, while LYP4 and LYP6 recognize bacterial PGN and fungal chitin to mediate alkalinization response (Liu et al. 2012a; Faulkner et al. 2013). Moreover, RLPs trigger immune responses along with up-regulation of a large number of defense-related genes. OsRLP1 associates with OsSOBIR1 to mediate rice resistance against rice black-streaked dwarf virus and results in differential expression of more than 800 genes, involving multiple defense-related GO terms such as jasmonic acid, oxidation-reduction responses, peroxidase activity, chitin-binding, and systemic acquired resistance (Zhang et al. 2021). Numerous PTI-related genes could be induced by various LRR-RLPs and LysM-RLPs. These include pathogenesis-related (*PR*) genes (*PR1*, *PR2*, *PR4*, and *PR5*), cytochrome P450 (*CYP71A13* and *CYP71D20*), WRKY transcription factor (*WRKY7* and *WRKY22*), and other PTI marker genes (*Acre31*, *PTI5*, and *FRK1*) (Willmann et al. 2011; Saur et al. 2016; Nie et al. 2021; Yin et al. 2021; Chen et al. 2022; Yang et al. 2023). Nevertheless, our understanding of the exact gene expression networks regulated by RLPs is limited.

To sum up, RLPs could initiate a series of signal networks, and some signals, such as ROS burst and up-regulation of defence gene expression, shared the signal hubs of both PTI and ETI. The development of modern omic analytic technology, such as single-cell sequencing, spatial transcriptomics, and 4D-proteomics, provides new opportunities for a comprehensive exploration of the downstream signal networks regulated by RLPs.

The balance of plant immunity and growth regulated by RLPs

In most cases, improving disease resistance comes with a noticeable reduction in growth and yield. Various hormones, such as brassinosteroids (BR), ABA, SA, JA, and ethylene (ET), have emerged as crucial regulators of the growth-immunity trade-off, and some of these are also regulated by RLPs, although the detailed molecular mechanisms underlying this role are not well clarified (Lozano-Durán and Zipfel 2015; Ning et al. 2017). Some members of MYB, WRKY, NAC, bZIP, MADS, and bHLH transcription factors have been confirmed to be involved in this trade-off. Nevertheless, several essential genes have been recently identified that positively regulate plant disease resistance but not at the cost of yield reduction (Wang et al. 2022, 2023).

BR and ABA signalling mediate either growth or defence responses by activating distinct downstream signal pathways. BRs promote the kinase activity of its receptor BRASSINOSTEROID INSENSITIVE 1 (BRI1), induce changes in gene expression, and control seed germination, etiolation, vegetative growth, stomata development, flowering, and fertility (Lozano-Durán and Zipfel 2015). In normal growth conditions, BR signals promote the expression of BRASSINAZOLE BRASSINAZOLE RESISTANT 1 (BZR1) and bHLH HOMOLOG OF BR ENHANCED EXPRESSION2 INTERACTING WITH INCREASED LEAF INCLINATION1 BINDING bHLH1 (HBI1), two positive regulators of BR-regulated growth and negative regulators of immunity. On the contrary, PAMP treatment activates immune responses and suppresses growth by inhibiting the expression of HBI1 and transcription factors WRKY11, WRKY15, and WRKY18 (Lozano-Durán and Zipfel 2015). In Arabidopsis, RLP44 acts as a critical modifier of BR signalling via association with the BR receptor complex and inhibition of pectin de-methylesterification in the cell wall. RLP44 is required for normal growth and stress responses (Wolf et al. 2014). Apart from BRs, ABA can be considered as an isoprenoid compound that regulates developmental processes, which also plays both positive and negative roles in plant immunity depending on the type of pathogens (Denancé et al. 2013). Indeed, mutation of RLP17 resulted in stomatal clustering across the leaf epidermis and decreasing sensitivity to ABA, suggesting that it plays a role in ABA-induced alternation of chlorosis and growth (Wang et al. 2008). The above investigations indicate that some RLPs mediating BRs and ABA signals are involved in balancing plant growth and development.

Mutation of the *CLAVATA2* (*CLV2*) and its homologous genes results in the enlarging of shoot and flower meristems, as well as alterations in the development of the gynoecia, flower pedicels, and stamens (Guo et al. 2010; Hanemian et al. 2016). The carpel number phenotype of the *clv2* mutant could be largely rescued by *AtRLP2* and *AtRLP12* when expressed under the control of the *CLV2* promoter (Wang et al. 2010). *AtRLP3* and *AtRLP11* display similar functions to their duplicated genes *AtRLP2* and *AtRLP12*, respectively (Wu et al. 2016). However, mutations in the *CLAVATA1* (*CLV1*) and *CLAVATA2* (*CLV2*) genes also confer enhanced resistance of Arabidopsis against bacterial wilt disease caused by *Ralstonia solanacearum* via a miR169-dependent pathway (Hanemian et al. 2016). In addition, many RLPs could affect tissue growth and development. *AtRLP4*/*AtPDO2*, predicted as a putative developmental ortholog, is ubiquitously and highly expressed across almost all the developmental stages and organs, confirming a potential basic function in plant development (Wang et al. 2008). Evidence of mutations of other RLPs suggests that *AtRLP20*, *AtRLP24*, *AtRLP27*, *AtRLP28*, and *AtRLP35* may participate in the development of lateral roots and pollen of plants (Wang et al. 2008). Among these, RLP20 was confirmed to be responsive to the infection of *P. syringae* (Macho and Zipfel 2014). Whether these RLPs balance the growth and immunity in plants is largely unknown.

Collectively, several RLPs emerged to balance plant growth and immunity by regulating the BRs and ABA signalling pathways. Otherwise, many RLPs modulate plant immunity via induction of the signals that regulate cell growth and defense. Furthermore, recent investigations reveal that several vital genes positively regulate plant disease resistance but do not reduce the production (Wang et al. 2022, 2023). Therefore, a far-sighted and significant step is to discover critical RLPs contributing to plant immunity but not affecting agronomic traits of crop plants.

Conclusion and prospects

The relationships between evolutionary characteristics and the function of RLPs

For the RLK superfamily, the relationships between evolutionary characteristics and functions have been preliminarily established by analysing gene expansion and duplication events (Melissa et al. 2009). The RLPs were divided into Putative Developmental Orthologs (PDOs) and Validated Defence RLPs (VDRs) based on multi-omics analysis and incomplete experimental validation (Steidele and Stam 2020). Our recent investigation classified the RLPs based on expansion ratio, expression pattern, and co-expression module, some of which could well distinguish the RLPs involved in growth or stress responses, indicating the potential correlation between the evolutional characteristics and the functions (Yu et al. 2023). The complete phylogenetic trees for each of the LRR-RLK subclades were inferred, and the deepest nodes of the whole gene family were reconstructed via an improved method based on iterative hidden Markov model searching and phylogenetic inference (Man et al. 2020). For practical purposes, the improved methods for evolutional characteristics and additional functional validation could enhance our understanding of this puzzle.

Screening of key RLPs for disease-resistance breeding

Numerous RLPs involved in both PTI and ETI regulation were determined using large-scale screening and functional investigations. However, almost all identified genes are in the LRR-RLP and LysM-RLP subfamily. In fact, for EDs of some RLK subfamilies, such as L-Lectin and stress-Antifung domains, the functions of plant defense, even antifungal activity, were continually uncovered (Choi et al. 2014; Pham et al. 2020; Guo et al. 2021), suggesting the existence of other RLP subfamily members on resistance regulation. Therefore, it is meaningful to take some practice in screening for the essential genes mediating disease resistance from other RLP subfamilies, which can further be used to improve crop yield and quality.

Many resistance genes are associated with balancing plant growth and defence responses. Several hormone signals, such as BR and ABA, are involved in this balance but were modulated by RLPs. Mutation of numerous defence-related RLPs displays no differences in growth characteristics compared to the wild type plants. Few investigations have been focused on whether the RLPs-regulated defence responses have to cope with the costs of growth reduction. In addition, plant NLR autoactivation usually results in defence but disappears when integrated domains are modified (Bentham et al. 2023). Therefore, deep investigations on the function of specific domains or amino acid residues might eliminate the trade-off between growth and defence conferred by resistance regulators.

Elaboration of the signal networks downstream RLPs

The detailed molecular networks are still largely elusive, although continuous investigations have confirmed the vital roles of RLPs on plant immunity acting as PRRs or R genes. BAK1/SOBIR1 and CERK1 have been well characterized as core partners for disease-resistance-related LRR-RLPs and LysM-RLPs, respectively. It is inconclusive that other PRRs may act as co-receptors for defense-related RLPs. Besides, several core PRRs emerge as co-receptors for numerous defense-related members of RLKs and RLPs (Jamieson et al. 2018). Nevertheless, the detailed similarities and differences of downstream signal cascades initiated by RLPs and RLKs are still elusive, although the slower but prolonged immune response is regulated by RLPs (Wan et al. 2019).

Moreover, ETI displays race-specific resistance but activates more rapid and robust responses than PTI, but some defence signals could be initiated in both PTI and ETI (Yuan et al. 2021). One of the significant challenges is illustrating how the molecular pathways are regulated by RLPs acting as PRRs or R genes. Gene editing, third-generation sequencing technology, and TurboID-based proximity labeling (Feng et al. 2023) may help elucidate these issues.

Abbreviations

RLPs	Receptor-like proteins
RLKs	Receptor-like kinases
PTI	Pattern-triggered immunity
ETI	Effector-triggered immunity
PPRs	Pattern-recognition receptors
PAMPs	Pathogen-associated molecular patterns
ED	Extracellular ligand-binding domains
KD	Kinase domain
TM	Transmembrane region
GPI	Glycosylphosphatidylinositol
LRR	Leucine-rich repeat
PGN	Peptidoglycan
WGD	Whole-genome duplication
TD	Tandem duplication
CERK1	Chitin Elicitor Receptor Kinase1
NLR	Nucleotide-binding Leucine-rich Repeat
HR	Hypersensitive
RLCKs	Receptor-like cytoplasmic kinases
ROS	Reactive oxygen species
PCD	Programmed cell death
SAR	Systemic acquired resistance
SA	Salicylic acid
JA	Jasmonic acid
ABA	Abscisic acid
BR	Brassinosteroids
ET	Brassinosteroids

Acknowledgements

The authors would like to thank China National Knowledge Infrastructure (CNKI) for providing access to e-resources.

Author contributions

MC and CZ outlined the manuscript. MC wrote the manuscript and made the figures. MC, CZ, HY, and ES revised the manuscript. All authors read and approved the final manuscript.

Funding

This research was funded by the Science and Technology Major Project of Gansu Province (22ZD6NA045) and by the National Natural Science Foundation of China (32260741).

Data availability

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 3 June 2024 Accepted: 22 August 2024

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