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Plant plasma membrane-resident receptors: Surveillance for infections and coordination for growth and development[FA]

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ABSTRACT

As sessile organisms, plants are exposed to pathogen invasions and environmental fluctuations. To overcome the challenges of their surroundings, plants acquire the potential to sense endogenous and exogenous cues, resulting in their adaptability. Hence, plants have evolved a large collection of plasma membrane-resident receptors, including RECEPTOR-LIKE KINASEs (RLKs) and RECEPTOR-LIKE PROTEINs (RLPs) to perceive those signals and regulate plant growth, development, and immunity. The ability of RLKs and RLPs to recognize distinct ligands relies on diverse categories of extracellular domains evolved. Co-regulatory receptors are often required to associate with RLKs and RLPs to facilitate cellular signal transduction. RECEPTOR-LIKE CYTOPLASMIC KINASEs (RLCKs) also associate with the complex, bifurcating the signal to key signaling hubs, such as MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) cascades, to regulate diverse biological processes. Here, we discuss recent knowledge advances in understanding the roles of RLKs and RLPs in plant growth, development, and immunity, and their connection with co-regulatory receptors, leading to activation of diverse intracellular signaling pathways.

Keywords: co-regulatory receptors, plant growth and development, plant immunity, RECEPTOR-LIKE KINASE (RLK), RECEPTOR-LIKE PROTEIN (RLP), signal transduction

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INTRODUCTION

Plants are regularly exposed to microbial pathogen invasions and variable environmental conditions that need to be continuously monitored. Thus, plants rely on plasma membrane-localized receptors that recognize exogenous and endogenous signals and trigger proper responses to ensure a balanced modulation of growth, development, immunity, and stress adaptation (De Smet et al., 2009; Couto and Zipfel, 2016; Tang et al., 2017).

These receptors mainly consist of RECEPTOR-LIKE KINASEs (RLKs) and RECEPTOR-LIKE PROTEINs (RLPs), which have been expanded across the plant kingdom. As evidence of their biological relevance, the *Arabidopsis thaliana* genome is predicted to encode more than 600 RLKs and 57 RLPs, and the rice (*Oryza sativa*) genome encodes more than 1 000 RLKs and 90 RLPs (Shiu and Bleecker, 2003; Shiu et al., 2004; Fritz-Laylin et al., 2005).

Recent studies have shown that various receptors perceive specific ligands; however, the perception could lead to converged signaling pathways that will regulate diverse physiological and biological processes (Chen et al., 2019; Zheng et al., 2019). In this review, we discuss the roles of RLKs and RLPs in regulating distinct pathways that control plant immunity, growth, and development. Moreover, we discuss the relationship between the receptors and the co-regulatory receptors that result in the activation of diverse intracellular signaling pathways.

GENERAL FEATURES OF RLKS AND RLPS

The plant's ability to adapt to different environmental conditions has likely resulted in the evolution of a wide variety of RLKs and RLPs that can recognize a broad range of ligands, including peptides, lipids, steroids, proteins, among others. A classical RLK consists of a unique ligand-binding extracellular domain, a single transmembrane domain, and an intracellular kinase domain, while a typical RLP shares a very similar structure with an RLK apart from the intracellular kinase domain (Figure 1) (Shiu and Bleecker, 2001; Wang et al., 2008). An RLP lacks the kinase domain. Instead, it possesses a short cytoplasmic tail (Wang et al., 2008; Jamieson et al., 2018). The perception of a ligand in the apoplast, by an RLK, particularly for the leucine-rich repeat (LRR) RLKs, usually leads to its hetero-dimerization with a co-regulatory RLK that will result in phosphorylation and activation of ligand–receptor complexes (Couto and Zipfel, 2016; Hohmann et al., 2017; Tang et al., 2017). Subsequently, the kinase domains of RLKs transduce the signal through a cascade of phosphorylation events, which ultimately leads to the plant cellular response to the cognate ligands (Couto and Zipfel, 2016; Hohmann et al., 2017; Tang et al., 2017). On the other hand, a similar process occurs for RLPs, but due to lacking the kinase domain, RLPs depend on one or several receptor kinases to activate intracellular signaling (Couto and Zipfel, 2016; Jamieson et al., 2018).

Based on the heterogeneity of their ligand-binding motifs, RLKs and RLPs are classified into 12 subgroups, including LRR, lysin motif (LysM), lectin, wall-associated kinases (WAK), malectin-like, proline-rich, cysteine-rich repeat, and self-incompatibility locus (S-Locus) (Shiu and Bleecker, 2001; Dievart et al., 2020). LRR is the most common motif of the extracellular domain of RLKs and RLPs, comprising more than 200 and 50 members, respectively, in *Arabidopsis* (Shiu and Bleecker, 2001; Wang et al., 2008; Lehti-Shiu et al., 2009). In recent years, several advances have been made in uncovering novel functions of RLKs and RLPs with LysM and lectin extracellular domains. LysM receptors can be classified into two clades, LYKs for LysM-RLKs and LYRs for LysM-RLPs, based on the presence or absence of a functional intracellular kinase domain, and usually bind to polysaccharide ligands or are involved in polysaccharide-mediated signaling. (Limpens et al., 2003; Arrighi et al., 2006; Buendia et al., 2018; Jamieson et al., 2018). In *Arabidopsis*, five LysM RLKs, and three LysM RLPs have been identified (Shinya et al., 2015). Furthermore, lectin domains often perceive ligands

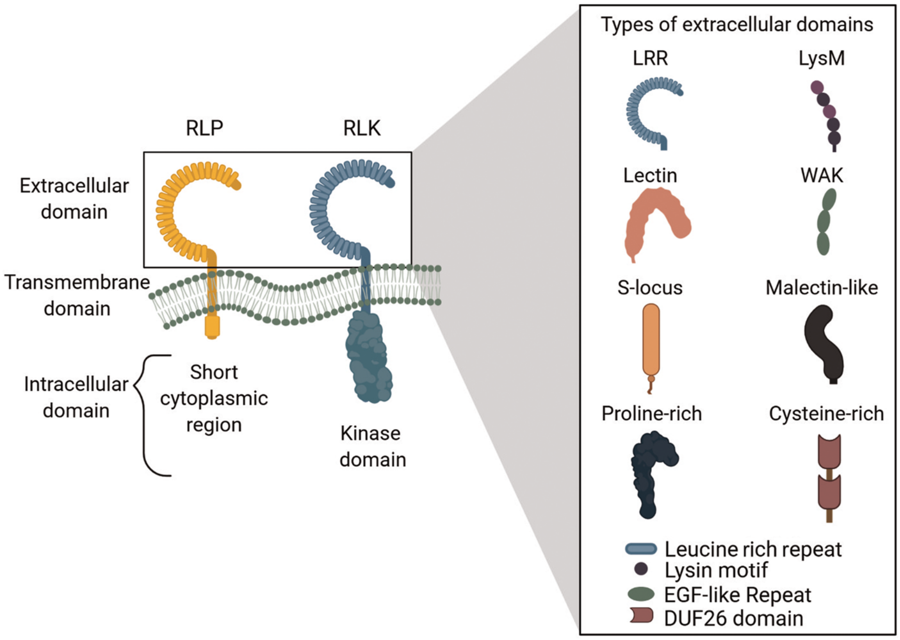

Figure 1. Schematic portrayal of plant cell-surface receptors

Plants have evolved cell surface receptors to recognize self and non-self signals to activate defense response and promote plant growth and development. A classical RECEPTOR-LIKE KINASE (RLK) contains an extracellular domain, transmembrane domain and a kinase domain. Meanwhile, the RECEPTOR-LIKE PROTEIN (RLP) possesses an extracellular domain, transmembrane domain and a short cytoplasmic region, but lacks a cytoplasmic kinase domain. RLKs and RLPs are classified in several subgroups based on the diverse composition of the extracellular domains. These include: leucine-rich repeat (LRR) domain; LysM, constituted by lysin motifs; lectin; wall-associated kinases (WAK), comprised of epidermal growth factor-like repeat; S-locus domain; malectin-like; proline-rich; and cysteine-rich repeat, consisting of DUF26 domain. Created with BioRender.com.

composed of glycans and carbohydrates and can be classified into three subfamilies, including L-type, C-type, and G-type lectin domain (Vaid et al., 2013; Lannoo and Van Damme, 2014; Jamieson et al., 2018). In *Arabidopsis*, the L-type lectin comprises of 45 RLKs and six RLPs, while the G-type lectin comprises of 39 RLKs and three RLPs, and only one RLK C-type lectin has been predicted (Lannoo and Van Damme, 2014; Bellande et al., 2017; Jamieson et al., 2018). Further, RLKs and RLPs can also be distinguished based on the roles they play in the plant life cycle, forming part of a remarkable surveillance system that modulates plant immune responses, growth, and development (De Smet et al., 2009; Couto and Zipfel, 2016; Tang et al., 2017).

THE ROLES OF RLKS AND RLPS IN PLANT IMMUNITY

Plant immune system

Plants have a robust immune system that is modulated by a two-tiered perception system. The first layer is activated upon recognition of MICROBE/PATHOGEN-ASSOCIATED MOLECULAR PATTERNS (MAMPs/PAMPs) by PATTERN-RECOGNITION RECEPTORS (PRRs), which are plasma membrane-localized RLKs and RLPs (Figure 2A) (Jones and Dangl, 2006; Boller and Felix, 2009). Collectively, this line of immunity is known as PAMP-TRIGGERED IMMUNITY (PTI). MAMPs/PAMPs correspond to essential conserved regions of pathogen or microbial components. Likewise, PTI can also be activated upon the detection of DAMAGE-ASSOCIATED MOLECULAR PATTERNS (DAMPs), which are molecules secreted by the plants as a result of exposure to biotic and abiotic stresses (Figure 2A) (Gust et al., 2017; Tang et al., 2017; Ortiz-Morea and Reyes-Bermudez, 2019). Activation of PTI leads to an increase of intracellular calcium, activation of MITOGEN-ACTIVATED PROTEIN KINASE (MAPK), a burst of reactive oxygen species (ROS), activation of CALCIUM-DEPENDENT PROTEIN KINASEs (CDPKs), massive transcriptional reprogramming, stomata closure, callose deposition, and so forth (Figure 2A) (Wu et al., 2014; Couto and Zipfel, 2016; Yu et al., 2017; Wang et al., 2020a, 2020b, 2020c). Currently, despite the large number of genes predicted to encode RLKs and RLPs, only a small portion have been characterized, and few ligands are identified (Figure 2B; Table 1). Most of the characterized PRRs belong to the LRR subgroup.

PAMP-TRIGGERED IMMUNITY responses contribute to plants effectively fighting off non-adapted microbes and provide restricted protection against host-adapted pathogens (Jones and Dangl, 2006; Boller and Felix, 2009). Nevertheless, most of the host-adapted microbes can overcome the first line of defense by deploying and delivering effectors into the plants that will target specific components of PTI and block its activation or interfere with host physiology and other defense barriers resulting in the EFFECTOR-TRIGGERED SUSCEPTIBILITY (ETS) (Jones and Dangl, 2006). To fend off infections, plants have evolved intracellular NUCLEOTIDE-BINDING LEUCINE-RICH REPEAT PROTEINs (NB-LRRs), also known as resistance proteins (R proteins), which can indirectly or directly recognize effectors and trigger another line of defense called EFFECTOR-TRIGGERED IMMUNITY (ETI) (Jones and Dangl, 2006; Cui et al., 2015). Activation of ETI often induces programmed cell death at the infection sites known as the hypersensitive response (HR) to reduce the pathogen growth (Jones and Dangl, 2006; Cui et al., 2015).

LRR-RLKs as PRRs for the plant immune system

The first and best-characterized immune-related PRR in *Arabidopsis* is the LRR-RLK FLAGELLIN SENSING 2 (FLS2) that perceives the bacterial flagellin and the cognate peptide flg22 (Gómez-Gómez and Boller, 2000). FLS2 orthologs have been found in tomato (*Solanum lycopersicum*), a wild relative of tobacco (*Nicotiana benthamiana*), grapevine (*Vitis vinifera*), and rice (Hann and Rathjen, 2007; Robatzek et al., 2007; Takai et al., 2008; Trdá et al., 2014). The diversification of PRRs results from modifications that have occurred over time following the evolution of the pathogens (Steinbrenner, 2020). Therefore, analogous MAMPs may be recognized by distinct and/or convergent PRRs. For instance, tomato has evolved another LRR-RLK, SlFLS3, that perceives flgII-28, a variation of the flg22 epitope (Hind et al., 2016).

Another well-studied LRR-RLK PRR is ELONGATION FACTOR-TU (EF-Tu) RECEPTOR (EFR) that recognizes the bacterial EF-Tu (elf18), a very abundant and conserved protein in bacteria (Kunze et al., 2004; Zipfel et al., 2006). Similar to what was observed for flagellin, a second EF-Tu epitope (EFa50) was found in rice, suggesting that rice may have evolved PRRs that can recognize bacterial EF-Tu. Even though elf18 is a specific MAMP for Brassicaceae species, rice plants can recognize another region of the EF-Tu epitope (Furukawa et al., 2014).

Several other LRR-RLKs have been identified as PRRs throughout the plant kingdom. For instance, csp22 is a peptide from bacterial COLD-SHOCK PROTEIN (CSP) that is perceived by LRR-RLK CSP RECEPTOR (SlCORE) in tomato (Wang et al., 2016). In addition, the MAMP RaxX from *Xanthomonas oryzae pv. oryzae* (Xoo) was reported as essential for activation of PTI responses mediated by OsXA21, an LRR-RLK from rice (Pruitt et al., 2015). Although remarkable progress has been made in identifying and characterizing new pairs of MAMPs/PRRs, a handful of identified PRRs lack recognition of their cognate ligands. For instance, NEMATODE-INDUCED LRR-RLK 1 (NLR1) is required for nematode-mediated defense response activation in *Arabidopsis*; however, its corresponding ligand is yet to be identified (Mendy et al., 2017).

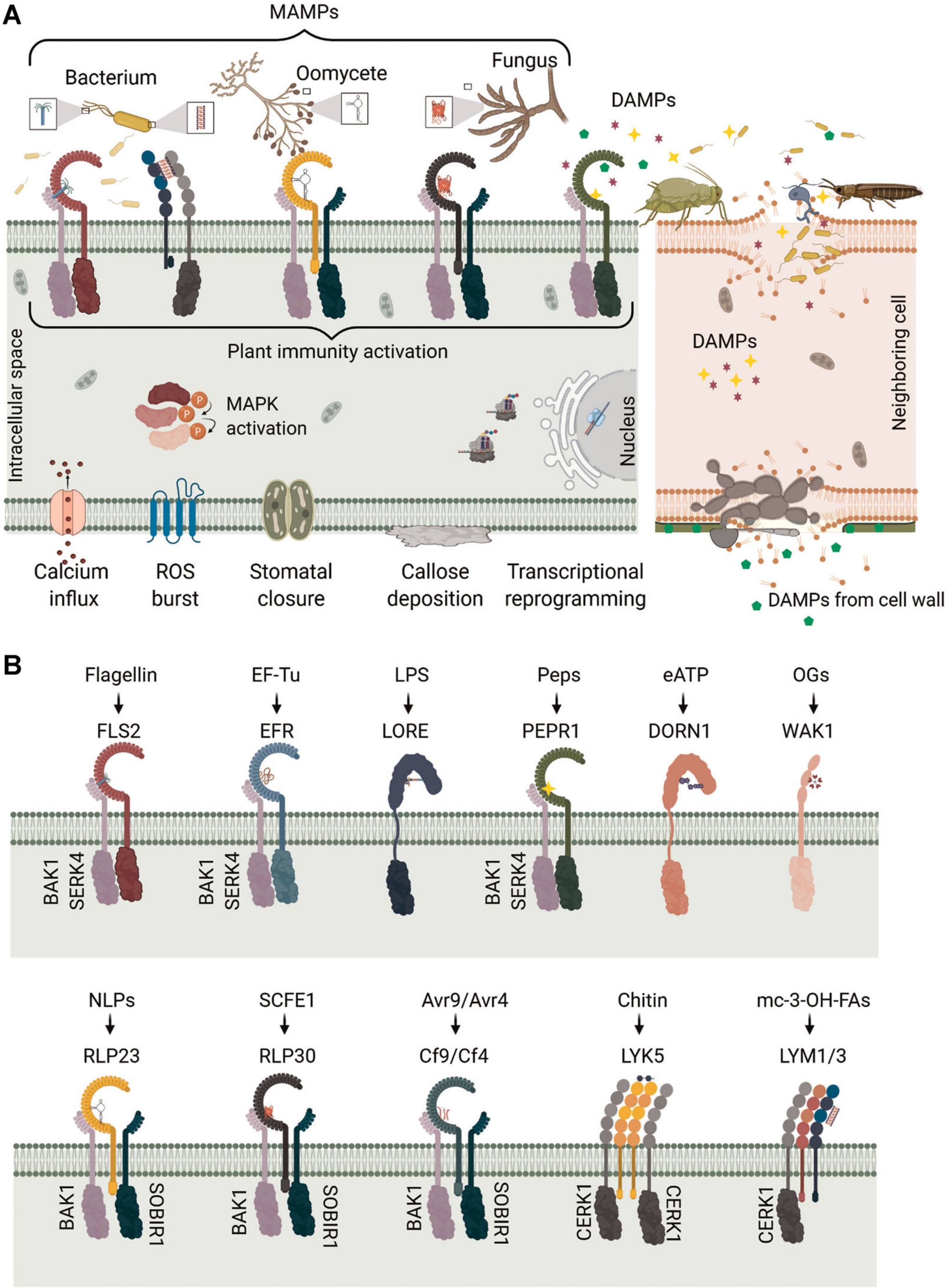

Figure 2. Continued

Besides detecting MAMPs, LRR-RLKs can also perceive DAMPs and activate the immune signaling in response to physical wounding and herbivore attack. The RLK PEP1 RECEPTOR1 (PEPR1) and PEPR2 in *Arabidopsis* recognize the so-called PLANT ELICITOR PEPTIDE (PEP1 through 8) in response to wounding (Krol et al., 2010; Yamaguchi et al., 2006, 2010). Furthermore, PEP1 also acts mutually with another plant peptide family known as PAMP-INDUCED PEPTIDES (PIPs) to magnify the immune response triggered by flagellin (Hou et al., 2014). In *Arabidopsis*, PIP1 is recognized by RECEPTOR-LIKE KINASE 7 (AtRLK7) (Hou et al., 2014).

LRR-RLKs also perceive signals from parasitic plants. For instance, the obligate parasitic plant *Orobanche cumana* can

Table 1. RLKs and RLPs in plant immunity

Receptor name	Extracellular domain	Plant	Ligand	Ligand origin	Co-receptors
RECEPTOR-LIKE KINASE					
FLS2	LRR	*Arabidopsis*	flg22	Bacteria	BAK1, BKK1
FLS3	LRR	Tomato	flgII-28	Bacteria	BAK1
EFR	LRR	*Arabidopsis*	elf18	Bacteria	BAK1, BKK1
CORE	LRR	Tomato	csp22	Bacteria	BAK1
Xa21	LRR	Rice	raxX	Bacteria	SERK2
NLR1	LRR	*Arabidopsis*	?	Nematode	
PEPR1/PEPR2	LRR	*Arabidopsis*	Peps	Plants	BAK1, BKK1
RLK7	LRR	*Arabidopsis*	PIP1	Plants	BAK1, BKK1
DORN1	Lectin	*Arabidopsis*	eATP	Plants	
LYK4/LYK5	LysM	*Arabidopsis*	chitin	Fungi	
CERK1	LysM	*Arabidopsis*	chitin	Fungi	
LORE	LysM	*Arabidopsis*	LPS	Bacteria	
WAK1	WAK	*Arabidopsis*	OGs	Plants	
CERK1	LysM	Rice	chitin	Fungi	
LecRK-VI.2	Lectin	*Arabidopsis*	β-aminobutyric acid	Bacteria	
OsLecRK	Lectin	Rice		Bacteria, fungi, insects	
RECEPTOR-LIKE PROTEIN					
SlCf9	LRR	Tomato	Avr9	Fungus	BAK1, SOBIR1
SlCf2	LRR	Tomato	Avr2	Fungus	BAK1, SOBIR1
SlCf4	LRR	Tomato	Avr4	Fungus	BAK1, SOBIR1
SlCf5	LRR	Tomato	Avr5	Fungus	BAK1, SOBIR1
LeEIX1/LeEIX2	LRR	Tomato	EIX	Fungi	BAK1, SOBIR1
NbCSPR	LRR	Tobacco	csp22	Bacteria	BAK1
RLP23	LRR	*Arabidopsis*	NLPs	Bacteria, fungi, oomycete	BAK1, SOBIR1
RLP30	LRR	*Arabidopsis*	SCFE1	Fungi	BAK1, SOBIR1
RLP42	LRR	*Arabidopsis*	PGs	Fungi	SOBIR1
CuRe1	LRR	Tomato	Cuscuta factor	Parasitic plant	
CEBiP	LysM	Rice	chitin	Fungi	
LYP4/LYP6	LysM	Rice	PGNs/chitin	Bacteria, Fungi	
LYM1/LYM3	LysM	*Arabidopsis*	PGNs	Bacteria	

Notes: Receptor names are included with the extracellular domain composition, organism identified, ligand recognized, origin of the ligand, and known co-regulatory proteins. RLK, RECEPTOR-LIKE KINASE; RLP, RECEPTOR-LIKE PROTEIN.

Figure 2. Receptor complexes in plant immunity

(**A**) Plants perceive external and internal signals to regulate diverse biological processes. Several conserved regions from microbe-associated molecular patterns (MAMPs) are recognized by RECEPTOR-LIKE KINASEs (RLKs) and RECEPTOR-LIKE PROTEINs (RLPs) to activate plant immunity. RLKs and RLPs often recruit co-regulatory receptors to amplify and transduce the signal into downstream mitogen-activated protein kinase (MAPK) cascades which in turn are phosphorylated and transduce the signal into the nucleus, resulting in transcriptional reprogramming. In addition, early and late immune responses are also activated upon MAMP perception, including cytosolic calcium influx, reactive oxygen species (ROS) burst, stomatal closure, and callose deposition. (**B**) Upon perception of a wide variety of MAMPs and DAMAGE-ASSOCIATED MOLECULAR PATTERNs (DAMPs), leucine-rich repeat (LRR)-RLKs and LRR-RLPs associate with co-receptors such as SOMATIC EMBRYOGENESIS RECEPTOR KINASEs (SERKs) to transduce the extracellular signals into the plant cell to activate immunity. The bacterial elicitors flg22 and elf18 are perceived by the LRR-RLKs FLS2 and EFR, respectively, which then, associate with BAK1 and BKK1 to activate PTI. Plant Lec-RLK LORE percieves bacterial LPS. The DAMP Peps are perceived by LRR-RLK PEPR1 and PEPR2 that subsequently associate with BAK1 and BKK1 to amplify plant immune responses. Additionally, the Lec-RLK DORN1 binds to eATP in response to wounding. The WAK-RLK WAK1 recognizes oligogalacturonides (OGs) originating from fungi to activates defense. Further, the immune activation in response to the fungal-derived MAMPs NLP, SCFE1, and Avr9/4 are regulated by LRR-RLPs RLP23, RLP30, and Cf9/4, respectively, which is then associated with LRR-RLK SOBIR and BAK1. The perception of chitin by LysM-RLP LYK5 induces the complex formation with LysM-RLK CERK1. In addition, LysM-RLK CERK1 also associates with LysM-RLPs LYM1 and LYM3 to activate immunity upon perception of bacterial PGN. Created with BioRender.com.

infect the roots of susceptible sunflowers (*Helianthus annuus*), leading to yield losses (Duriez et al., 2019). Resistant varieties of sunflowers possess the LRR-RLK HAOR7 that prevents the parasitic plant from attaching to the roots (Duriez et al., 2019).

LRR-RLPs as PRRs for the plant immune system

In addition to LRR-RLKs, members of LRR-RLPs perceive MAMPs and regulate plant immune activation (Figure 2B and Table 1). Although RLPs lacks the kinase domain to transduce the signal from the plasma membrane, it has been suggested that LRR-RLPs constitutively associate with SUPPRESSOR OF BIR 1-1 (SOBIR1) to form a bimolecular complex with an RLK to initiate the signal transduction (Gust and Felix, 2014).

The first identified LRR-RLP belongs to tomato, SlCF-9, which confers resistance to pathogen *Cladosporium fulvum* (Cf) bearing the avirulence gene Avr9 (Jones et al., 1994). Subsequently, a few other LRR-RLPs were identified as PRRs for resistance genes, such as SlCf-2, SlCf-4, and SlCf-5 (Thomas et al., 1997; Dixon et al., 1996, 1998). Although these LRR-RLPs require binding to ligands to activate PTI, the evidence of direct binding does not occur. Instead, they perceive the inhibitory effect of the avirulence proteins on the specific plant cysteine proteases such as Rcr1, Rcr2, and Rcr3 (Hammond-Kosack et al., 1994; Rooney et al., 2005). In tomato perception of the ETHYLENE-INDUCED XYLANASE (eix) from fungi *Trichoderma* spp. requires the LRR-RLPs LeEIX1 and LeEIX2 (Ron and Avni, 2004; Zipfel, 2008). Although LeEIX1 and LeEIX2 can bind to eix elicitor, only LeEIX2 can transduce the signal to induce plant defense, whereas LeEIX1 acts as a decoy receptor and suppresses the immune response activated by LeEIX2 (Ron and Avni, 2004; Bar et al., 2010). Unlike in tomato, the csp22 perception in tobacco is accomplished by an LRR-RLP called RECEPTOR-LIKE PROTEIN REQUIRED FOR CSP22 RESPONSIVENESS (NbCSPR) (Saur et al., 2016).

In *Arabidopsis*, LRR-RLP RLP23 confers resistance to a widespread microbial elicitor from bacteria, fungi, or oomycetes called NECROSIS- AND ETHYLENE-INDUCING PEPTIDE 1 (NEP1)-LIKE PROTEINs (NLPs) (Böhm et al., 2014; Albert et al., 2015). Meanwhile, LRR-RLP RLP30 triggers PTI in response to the fungal elicitor SCLEROTINIA CULTURE FILTRATE ELICITOR 1 (SCFE1) from *Sclerotinia sclerotiorum* (Zhang et al., 2013). Additionally, the fungal ENDOPOLYGALACTURONASE (PGs) was reported as MAMP perceived by the LRR-RLP RLP42, also known as RESPONSE TO BOTRYTIS POLYGALACTURONASES 1 (RBPG1) (Zhang et al., 2014). Moreover, LRR-RLPs are also able to detect MAMP elicitors from parasitic plants. For instance, the first of its kind is the tomato LRR-RLP CUSCUTA RECEPTOR 1 (SlCuRe1), which can perceive a small peptide factor from the parasitic plant, *Cuscuta reflexa* (Hegenauer et al., 2016).

Recent studies have shown that the conservation of RLKs and RLPs has taken place across land plants. Nevertheless, compared with the widespread preservation of RLKs, RLPs are less conserved but show a degree of conservation within the specific plant genus (Jamieson et al., 2018; Steinbrenner, 2020). As revealed by a recent study, most of the characterized LRR-RLPs from tomato and *Arabidopsis* are classified into different clades with no evident orthology between them (Steinbrenner, 2020). For instance, *Arabidopsis* LRR-RLPs 30, 23, and 42 are grouped within the *Arabidopsis* clade, whereas the tomato LRR-RLPs Cf-4 and Cf-5 are placed in the tomato clade. Albeit the LRR-RLPs LeEIX1, LeEIX2, and CuRe1 are not placed in a clade as specific as the above mentioned LRR-RLPs, they are still classified within particular species groups (Steinbrenner, 2020).

RLKs and RLPs with a distinct extracellular domain as PRRs for the plant immune system

Although LRR comprises the most common extracellular domain of RLKs and RLPs, there are others with peculiar extracellular domains that also play a role in the activation of plant immune responses upon the presence of MAMPs and DAMPs (Figure 2B and Table 1). For instance, chitin, the primary component of the fungal cell wall, is perceived by a complex formed by the LysM-RLKs LYSIN MOTIF RECEPTOR KINASE 5 (LYK5), LYSIN MOTIF RECEPTOR KINASE 4 (LYK4), and CHITIN ELICITOR RECEPTOR 1 (CERK1), also known as LYK1 (Kaku et al., 2006; Miya et al., 2007; Cao et al., 2014; Xue et al., 2019). The receptors in this complex have a differential contribution to recognizing the elicitor and activation of defense response. For instance, LYK5 is the primary receptor of chitin, whereas LYK4 acts as a scaffold protein to increase the immune response (Cao et al., 2014; Xue et al., 2019). Meanwhile, CERK1 binds to LYK5 in a chitin-dependant manner, and the binding is required for CERK1 phosphorylation and transduction of the signal from the membrane to the intracellular space to activate PTI (Cao et al., 2014). Several lectin receptors have been identified and characterized recently. For instance, LECTIN RECEPTOR KINASE-VI.2 (LecRK-VI.2) from *Arabidopsis* is required to activate PTI in response to *Pseudomonas syringae* and *Pectobacterium carotovorum* bacteria (Singh et al., 2012). In rice, LECTIN RECEPTOR-LIKE KINASE (OslecRK) plays a role in rice resistance to pathogens, including bacteria, fungi, and insects (Cheng et al., 2013). Additionally, a lectin S-domain RLK LIPOOLIGOSACCHARIDE-SPECIFIC REDUCED ELICITA TION (LORE) was reported to recognize medium-chain 3-hydroxy fatty acids (mc-3-OH-FAs) from bacterial LPS (Kutschera et al., 2019). Furthermore, a WAK domain RLK, WALL-ASSOCIATED KINASE 1 (WAK1), can recognize the oligogalacturonides (OGs) released during fungal infection (Brutus et al., 2010). This receptor can activate MAMPs and DAMPs in response to both immunity and development. Moreover, it has been shown that the malectin-like domain RLK, FERONIA (FER) that belongs to the *Catharanthus roseus* RLK1-LIKE (CrRLK1L) subfamily, modulates immune signaling by functioning as a scaffold protein that positively regulates the ligand-induced PRR complexes formation (Stegmann et al., 2017). Interestingly, ANXUR1 (ANX1) and ANX2, the closest homolog of FER, function as a molecular link regulating two-tiered plant immunity by association with both PRR and NB-LRR protein complexes (Mang et al., 2017); however, how ANXs differentially modulated plant PTI and ETI is not clear.

Along with the various RLKs with distinct extracellular domains, several RLPs with LysM motifs have been extensively studied. For instance, the rice receptor CHITIN ELICITOR BINDING PROTEIN (OsCEBiP) was reported to play a critical role in the perception and activation of downstream signaling in response to chitin (Shimizu et al., 2010). Later on, similar to *Arabidopsis*, the RLK OsCERK1 was also identified as a crucial component of the chitin-mediated immune signaling in rice (Shimizu et al., 2010). Additional to its function in chitin recognition, OsCERK1, together with LYSM DOMAIN-CONTAINING PROTEIN 4 (LYP4) and LYP6, also play a role in perceiving bacterial peptidoglycan (PGN) (Liu et al., 2012). Similarly, in *Arabidopsis*, CERK1 also associates with two LysM-RLPs called LYSIN-MOTIF 1 (LYM1) and LYM3 to activate PTI in response to bacterial PGN (Willmann et al., 2011).

In addition, RLKs with a distinctive extracellular domain play a role in amplifying the PTI responses and activating plant defense upon DAMP perception. For instance, DOES NOT RESPOND TO NUCLEOTIDES 1 (DORN1) is an RLK with an extracellular lectin domain and binds to the extracellular adenosine triphosphate (eATP) in response to physical wounding (Choi et al., 2014).

THE ROLES OF RLKS AND RLPS IN PLANT DEVELOPMENT

Plasticity of plant growth and development

In contrast with animals, plants have the ability to form and regenerate organs throughout their life cycle and dynamically adjust their body architecture in response to environmental conditions. Therefore, plants rely on pluripotent stem cells that compose the meristems to promote their growth and development. These cells are not specialized, and they continuously divide to generate new cells that subsequently induce the differentiation of all cell types (Heidstra and Sabatini, 2014; Greb and Lohmann, 2016).

The embryonic phase includes the establishment of the shoot apical meristem (SAM), the root apical meristem (RAM), and the first vascular stem cells. Afterward, in the post-embryonic phase, the SAM induces the development of leaves, flower primordia, side branches, and stem tissue (Kitagawa and Jackson, 2019). Meanwhile, the RAM induces the elongation and the formation of primary and lateral roots (Kitagawa and Jackson, 2019). In addition, the vascular tissue of the primary root, hypocotyl, and cotyledons is derived from the first vascular stem cells. In contrast, the vascular tissue of newly formed organs such as leaves, lateral roots, and stem is derived from the apical meristems (Zhu et al., 2020). The vascular tissue allows the plant to grow radially, resulting in the thickening of the stem tissue (Kitagawa and Jackson, 2019).

Moreover, plants also undergo cell elongation, where the plant grows toward a stimulus, such as light, water, physical contact, and gravity. The steady formation of new organs and tissues by meristems demands a robust control of plant growth and development processes regulated by hormones, plant growth regulators (PGR), and signals from other plant cells (Drisch and Stahl, 2015; Galli and Gallavotti, 2016). Several plant hormones function in preserving the meristem activity. For instance, auxin and cytokinin coordinate cell differentiation and division (Pierre-Jerome et al., 2018). Furthermore, ethylene and brassinosteroid (BR) are responsible for regulating senescence and the control of cell elongation and cell division, respectively (Pierre-Jerome et al., 2018).

Interestingly, during the last decades, an increasing number of RLKs and RLPs have been found to play crucial functions in regulating different aspects of plant growth and development, with the LRR-RLKs and LRR-RLPs as the dominant group (Figure 3; Table 2).

LRR-RLKs in plant growth and development

One of the best well-characterized LRR-RLK involved in plant growth and development is BRASSINOSTEROID INSENSITIVE 1 (BRI1) (Li and Chory, 1997). BRI1 is the receptor of brassinosteroids, and it can regulate plant response to light, cell elongation, root growth, stomata development, and stress response (Li and Chory, 1997; Gudesblat et al., 2012; Zhu et al., 2013; Nolan et al., 2020). Another key regulator of plant development is the phytohormone PHYTOSULFOKINE (PSK), which is responsible for cell division and cell expansion and perceived by the LRR-RLK PSK RECEPTOR 1 (PSKR1) (Matsubayashi, 2002; Matsubayashi et al., 2006; Wang et al., 2015). Additionally, the peptide PLANT PEPTIDE CONTAINING SULFATED TYROSINE 1 (PSY1) also regulates the cell division and expansion in *Arabidopsis*, after being distinguished by an LRR-RLK named as PSY1 RECEPTOR (PSY1R) (Amano et al., 2007). Moreover, the LRR-RLKs ERECTA, ERECTA-LIKE 1 (ERL1), and ERL2 play a role in stomatal development, reproductive organ development, and trigger cell differentiation, upon recognition of EPIDERMAL PATTERNING FACTOR 1 (EPF1) and EPF2 (Shpak et al., 2004; Lee et al., 2012; Shpak, 2013). A recent study identified another peptide, CLAVATA3/ESR-RELATED 9/10 (CLE9/10), which also plays a role in stomatal development upon being recognized by HAESA-LIKE 1 (HSL1) (Qian et al., 2018). Furthermore, a peptide called INFLORESCENCE DEFICIENT IN ABSCISSION (IDA), upon perception by HAESA (HAE) and HAESA-LIKE 2 (HSL2) receptors, triggers lateral root emergence and cell abscission of the floral organ after pollination (Cho et al., 2008; Kumpf et al., 2013).

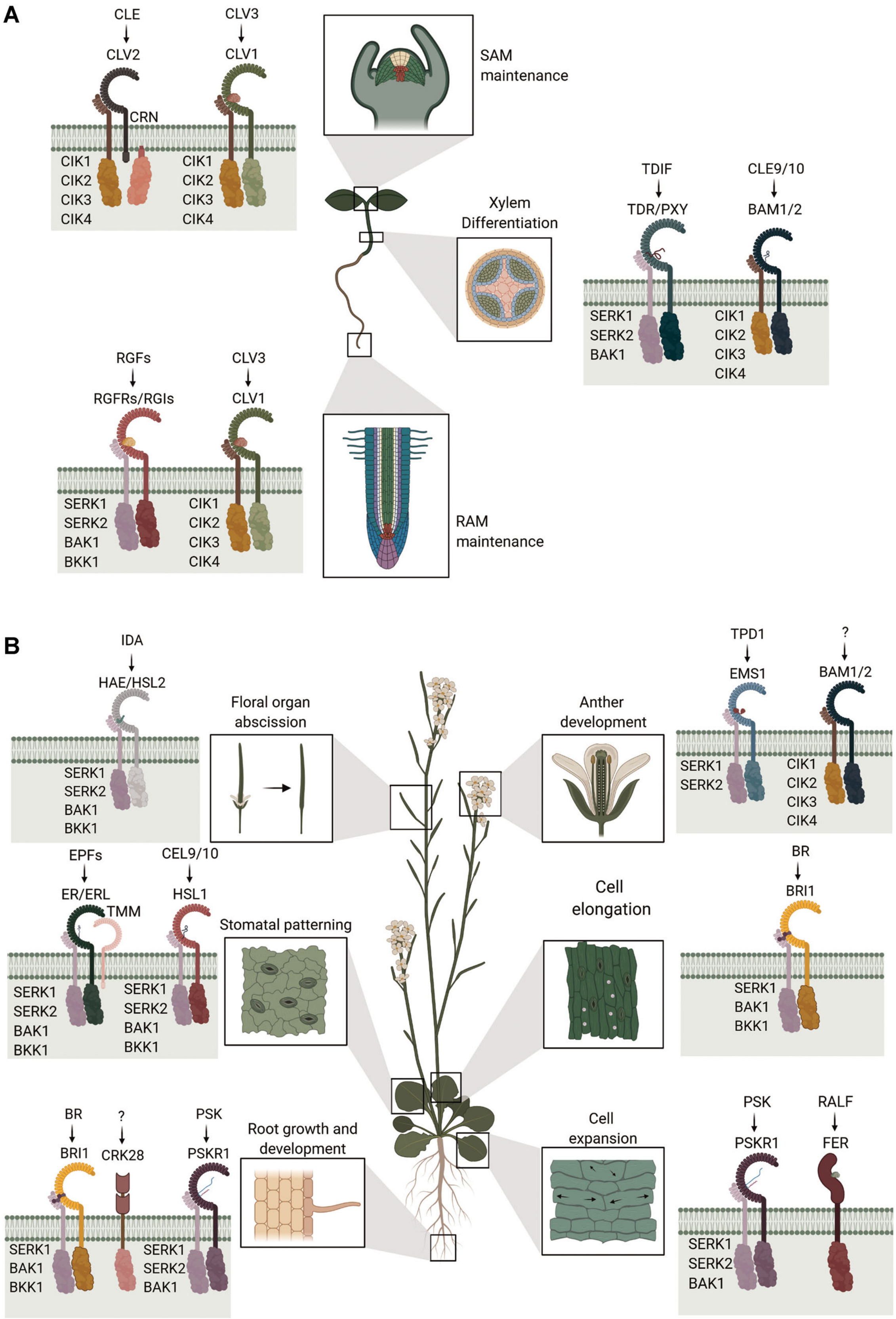

Figure 3. Continued

Table 2. RLKs and RLPs in plant growth and development

Receptor name	Extracellular domain	Ligand	Co-regulatory receptors	Function
RLK				
BRI1	LRR	BR	SERK1, BAK1, BKK1	Cell elongation and plant growth
PSKR1	LRR	PSK	SERK1, SERK2, BAK1	Cell division and cell expansion
PSYR1	LRR	PSY1	SERK1, SERK2, BAK1	Cell division and cell expansion
ERECTA	LRR	EPFs	SERK1, SERK2, BAK1	Stomatal patterning
ERL1/ERL2	LRR	EPFs	SERK1, SERK2, BAK1	Stomatal patterning
HAE/HSL2	LRR	IDA	SERK1, SERK2, BAK1, BKK1	Floral organ abscision
HSL1	LRR	CLE9/10	SERK1, SERK2, BAK1	Stomatal patterning
CLV1	LRR	CLV3	CIK1, CIK2, CIK3, CIK4	SAM and RAM maintenance
RGFR1 to 5	LRR	RGFs	SERK1, SERK2, BAK1, BKK1	RAM maintenance
BAM1/2	LRR		CIK1, CIK2, CIK3, CIK4	Anther development
TDR (PXY)	LRR	TDIF	SERK1, SERK2, BAK1	Xylem differentiation
EMS1 (EXS)	LRR	TPD1	SERK1, SERK2	Male sporogenesis
LePRK1 to 3	LRR			Polen tube growth
SUB	LRR			Tissue morphogenesis
MUS/MUL	LRR			Root development
FERONIA	Malectin-like	RALF		Plant reproduction, root growth and cell expansion
CRK28	Cysteine-rich			Plant growth and root organogenesis
OsESG1	S-domain			Root development
OsSRK1	S-domain			Leaf development
OsLecRK5	Lectin			Gametophyte development
ANX1/2	Malectin-like			Plant reproduction
HERK1/ANJ	Malectin-like			Plant reproduction
BUPS1/2	Malectin-like			Plant reproduction
SGC	Lectin			Pollen development
GhLecRK	Lectin			Fiber development
OsLecRK	Lectin			Seed viability and germination
RLP				
TMM (RLP17)	LRR	EPFs	SERK1, SERK2, BAK1	Stomatal patterning
CLV2	LRR	CLE	CIK1, CIK2, CIK3, CIK4	SAM and RAM maintenance
FEA2	LRR			SAM maintenance
RLP44	LRR			BR regulation and plant growth

Notes: Receptor names are included with their extracellular domain composition, cognate ligands, co-regulatory proteins and functions. BR, brassinosteroid; RAM, root apical meristem; RLK, RECEPTOR-LIKE KINASE; RLP, RECEPTOR-LIKE PROTEIN; SAM, shoot apical meristem.

The plant stem cells' maintenance demands a sensitive regulation of the cell division and differentiation in the meristems. Taking that into consideration, in *Arabidopsis*, a peptide named CLAVATA 3 (CLV3) is perceived by an LRR-RLK known as CLAVATA1 (CLV1), which in turn, regulates transcription factors responsible for the maintenance of SAM (Brand et al., 2000; Ogawa et al., 2008; Pierre-Jerome et al., 2018). The peptide CLE9/10, additional to its

Figure 3. Receptor complexes in plant growth and development
(**A**) Plant stem cells, located at the meristems, are responsible for plant growth during the embryonic and post embryonic phase. To maintain the shoot apical meristem (SAM) and root apical meristem (RAM), leucine-rich repeat-RECEPTOR-LIKE KINASEs (LRR-RLK) CLV1 perceive the peptide CLV3 and subsequently form a complex with the co-regulatory proteins CIKs. Similarly, LRR-RLP (RECEPTOR-LIKE PROTEINs) CLV2 also associates with CIKs and a cytoplasmic RLK CORYNE (CRN) in response to CLV3 and regulate SAM and RAM. LRR-RLKs RGFRs form a complex with SOMATIC EMBRYOGENESIS RECEPTOR KINASEs (SERKs) to control RAM upon perception of ROOT GROWTH FACTORs (RGFs). The xylem differentiation is regulated by LRR-RLK complexes TDR/PXY-SERKs and BAM1/BAM2-CIKs after perception of TDIF and CLE9/10, respectively. (**B**) Plant hormones and other peptides are also perceived by several RLKs and RLPs to regulate development and growth process. The floral organ abscission is regulated by LRR-RLK HAE/HSL2 associated with SERKs upon recognition of INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) peptides. Brassinosteroid (BR) is the hormone perceived by LRR-RLK BRI1 to regulate cell elongation and root growth and development. In addition, the root growth is also regulated by cysteine-rich RLK CRK28 and LRR-RLK PSKR1-SERKs complex upon PHYTOSULFOKINE (PSK) perception. Further, the PSKR1-SERKs complex control cell expansion, which can also be regulated by Malectin-RLK FERONIA (FER) in response to RAPID ALKALINIZATION FACTOR (RALF) peptides. The stomatal patterning and development is controlled, respectively, by the complexes LRR-RLP/RLK TMM-ER/ERL-SERKs in response to EPFs and LRR-RLK HSL1-SERKs in response to CLE9/10. Further, in the anther development, the peptide TPD1 is perceived by the complex LRR-RLK EMS1-SERKs. LRR-RLK BAM1/2 together with CIKs can also regulate anther development. Created with BioRender.com.

function in stomatal patterning, is perceived by the receptors BARELY ANY MERISTEM 1 (BAM1), BAM2, and BAM3 to promote xylem development (Qian et al., 2018). Furthermore, BAM receptors are also involved in anther development and the maintenance of the meristem function (DeYoung et al., 2006; Hord et al., 2006). Another receptor, RECEPTOR-LIKE PROTEIN KINASE 2 (RPK2), was also reported to play a role in meristem maintenance and anther development (Mizuno et al., 2007; Kinoshita et al., 2010). Moreover, the CLE peptide/receptor complex also regulates the differentiation and proliferation of the vascular stem cells. Namely, the CLE peptide TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY (TDIF) is recognized by the TDIF RECEPTOR (TDR), also known as PHLOEM INTERCALATED WITH XYLEM (PXY) (Fisher and Turner, 2007; Hirakawa et al., 2008). Further, the receptors ROOT GROWTH FACTOR (RGF) RECEPTOR 1–5 (RGFR1 to RGFR5) recognize the peptide RGF leading to a fine-tuned control of the root meristem development (Ou et al., 2016; Shinohara et al., 2016).

Several ligand-receptor complexes have also been identified as critical components of plant reproduction. For instance, a small protein called TAPETUM DETERMINANT1 (TPD1) can induce the specialization of anther cells after being perceived by the RLK EXCESS MICROSPOROCYTES1 (EMS1) or EXTRA SPOROGENOUS CELLS (EXS) (Canales et al., 2002; Zhao et al., 2002; Yang et al., 2003; Jia et al., 2008). In tomato, the POLLEN-SPECIFIC RECEPTOR KINASES 1 (LePRK1), LePRK2, and LePRK3 family regulate pollen germination and pollen tube growth (Tang et al., 2002, 2004; Huang et al., 2014). Further, recent studies revealed new receptors as a critical component in regulating plant growth and development processes. For instance, the *Arabidopsis* STRUBBELIG (SUB) receptor is involved in tissue morphogenesis and controls the composition of the plant cell wall (Chaudhary et al., 2020). Meanwhile, the kinase-inactive RLKs MUSTACHES (MUS) and MUSTACHES-LIKE (MUL) can control lateral root development (Xun et al., 2020). Although MUS and MUL are *in vitro* kinase-inactive RLKs, they are phosphorylated by an unidentified kinase in planta (Xun et al., 2020).

LRR-RLPs in plant growth and development

Along with LRR-RLKs, several LRR-RLPs have also been reported to function as crucial components of the plant growth and development system (Figure 3). However, they often require another RLK to transduce the signal. For instance, the receptor TOO MANY MOUTHS (TMM) or RLP17 regulates the stomatal patterning through complex formation with ERECTA and ERL1 upon the perception of EPF1 and EPF2 in *Arabidopsis* (Lin et al., 2017). Similarly, CLAVATA 2 (CLV2) interacts with CLV1 in response to CLV3, which leads to the regulation and maintenance of SAM, RAM, and organ development (Kayes and Clark, 1998; Jeong et al., 1999). Besides this pathway, CLV2 also interacts with the RECEPTOR-LIKE CYTOPLASMIC KINASE (RLCK) CORYNE (CRN) to form a complex and independently perceive CLV3 to regulate the meristems (Müller et al., 2008; Bleckmann et al., 2010; Guo et al., 2010; Somssich et al., 2016). Meanwhile, FASCIATED EAR 2 (FEA2), a CLV2 homolog in maize, was identified to function in the shoot meristem proliferation and positively affect floral meristem (Taguchi-Shiobara et al., 2001). Furthermore, RECEPTOR-LIKE PROTEIN (RLP44) mediates brassinosteroid activation to regulate plant growth and cell wall integrity upon pectin modification (Wolf et al., 2014).

RLKs and RLPs with distinct extracellular domains in plant growth and development

Apart from the LRR extracellular domain, several RLKs and RLPs with distinct extracellular domains also contribute to plant growth and development. The malectin domain RLK FER takes part in the hormone signaling and female fertility in *Arabidopsis* (Li et al., 2016). Further, FER also perceives the peptide RAPID ALKALINIZATION FACTOR (RALF) in order to regulate the primary root growth and plant cell expansion (Haruta et al., 2014). Other malectin-like RLKs involved in plant reproduction are HERCULES RECEPTOR KINASE 1 (HERK1) and ANJEA (ANJ). During fertilization, HERK1 and ANJ interact with FER to regulate pollen tube reception (Galindo-Trigo et al., 2020). Additionally, malectin-like RLKs BUDDHA'S PAPER SEAL 1/2 (BUPS1/2) and ANX1/2 were reported to play a role in plant reproduction by controlling the pollen tube's cell wall integrity during fertilization (Boisson-Dernier et al., 2009; Miyazaki et al., 2009; Ge et al., 2017). The BUPS-ANX receptor complex recognizes RALF4 and RALF19 peptides (Ge et al., 2017).

CYSTEINE-RICH RECEPTOR-LIKE KINASE 28 (CRK28) was shown to regulates the growth and development of the root and shoot system, and to fine-tune abscisic acid signaling in germination and early root growth (Pelagio-Flores et al., 2020). In rice, several RLKs with distinct extracellular domains have been reported recently. For instance, an S-domain receptor-like kinase OsESG1 plays a role in early crown root development through auxin regulation (Pan et al., 2020). Meanwhile, the S-RECEPTOR-LIKE KINASE 1 (OsSRK1) contributes to the salt tolerance response in rice and regulates the leaf width (Jinjun et al., 2020). Another rice RLK identified is the LECTIN RECEPTOR KINASE 5 (OsLecRK5) which controls the callose deposition, which is crucial for male gametophyte development (Wang et al., 2020a). The male sterility in *Arabidopsis* is also controlled by a lectin RLK named SMALL GLUED-TOGETHER (SGC) Lectin RLK, which plays a crucial role in pollen development (Wan et al., 2008). In cotton, the RLK GhlecRK regulates fiber development (Zuo et al., 2004). Additional to its role in immunity, the rice OslecRK can also regulate seed viability and germination (Cheng et al., 2013).

REGULATION OF RLKS AND RLPS

Upon recognizing a ligand, RLKs and RLPs often rely on co-regulatory receptors to transfer the signal from the apoplast to the cell interior. The plant response to a ligand depends on the differential phosphorylation in the kinase domains of the complexes formed at the plasma membrane (Figure 4) (Perraki et al., 2018; Burgh and Joosten, 2019).

Co-regulatory RLKs

Currently, it is known that the co-regulatory RLKs can interact constitutively or in a ligand-dependent manner with a ligand-perceiving receptor (Liebrand et al., 2014). They function as co-receptors and play a role in amplifying the ligand-receptor complex signals transmitted to the downstream cascade by transphosphorylation (Liebrand et al., 2014).

SOMATIC EMBRYOGENESIS RECEPTOR KINASES as positive regulators in plant immunity and plant growth and development

SOMATIC EMBRYOGENESIS RECEPTOR KINASES (SERKs) are a subgroup of LRR-RLK that operate as co-receptors for several RLKs that regulate immunity, growth, and development (Figures 2B, 3A, B) (Ma et al., 2016). SERK was first identified in carrot, *Daucus carota* SERK (DcSERK), where it functions as a marker of embryogenesis (Schmidt et al., 1997). After that, SERK homologs were identified in other species such as *Arabidopsis thaliana*, rice, cotton, tomato, among others (Ito et al., 2005; Mantelin et al., 2011; Sakamoto et al., 2012; Gao et al., 2013; Shi et al., 2014; Aan den Toorn et al., 2015).

In *Arabidopsis*, SERK3/BRI1-ASSOCIATED KINASE 1 (BAK1) and its closest homolog SERK4/BAK1-LIKE1 (BKK1), hereafter BAK1 and BKK1 respectively, play a positive role in

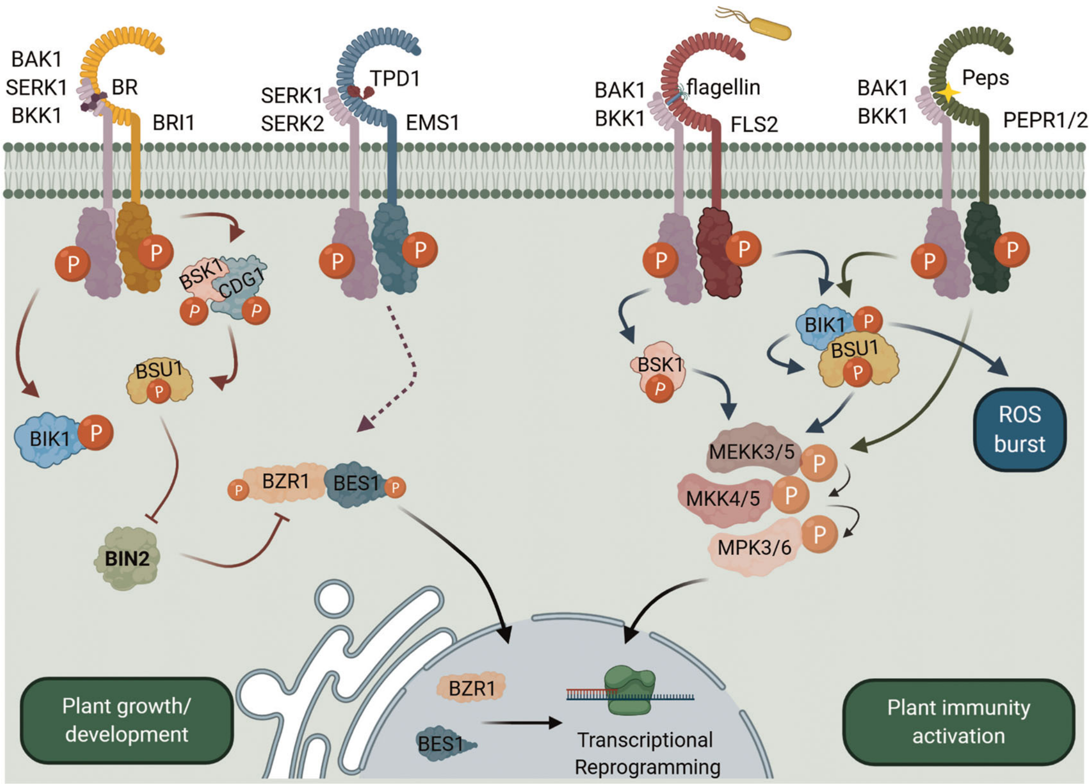

Figure 4. Shared signaling regulating plant growth, development, and immunity
Upon perception of the ligands, several RECEPTOR-LIKE KINASEs (RLKs) and RECEPTOR-LIKE PROTEINs (RLPs) transduce the signal into the plant cell employing shared key components. For instance, upon brassinosteroid (BR) perception, BRI1 associates with BAK1, which phosphorylate BSK1 and CDG1 and release BIK1 from BRI1. Subsequently, BSK1 and CDG1 phosphorylate BSU1 which in turn deactivate BIN2 allowing the dephosphorylated BZR1 and BES1 to enter the nucleus and induce the activation of BR-related genes. EXCESS MICROSPOROCYTES1 (EMS1) form a complex with SERK1/2 in response to TPD1 regulating anther development. Recent studies have shown that upon EMS1-SERKs (SOMATIC EMBRYOGENESIS RECEPTOR KINASEs) complex formation, BZR1 and BES1 activate anther development genes. In the presence of bacterial infections, FLS2 binds to BAK1/BKK1 and subsequently phosphorylate BIK1 resulting in reactive oxygen species (ROS) burst. BSK1 and BIK1-dependent BSU1 phosphorylation also occur leading to mitogen-activated protein kinase (MAPK) activation. Further, PEPR1 and PEPR2 also associate with BAK1 and BKK1 in response to Peps and subsequently phosphorylate BIK1. Later, the MAPK cascade is activated in response to both flg22 and Peps perception and results in transcriptional reprogramming to activate immunity. Maroon arrows indicate the pathway activated by BRI1; meanwhile the purple arrows represent the pathway activated by EMS1. The blue arrows indicate the pathway activated by FLS2, while the green arrows represent the pathway activated by PEPR1/2. Black arrows indicate converged pathways. Circled P represents phosphorylation events. Created with BioRender.com.

MAMP-triggered immunity by complexing with PRRs (Figure 2B) (Roux et al., 2011). For instance, the PRRs FLS2 and EFR, in response to bacterial MAMPs flg22 and elf18, respectively, require BAK1 and BKK1 to form a complex and subsequently activate defense response (Chinchilla et al., 2007; Roux et al., 2011). Similarly, the tomato receptors SlFLS3 and SlCORE, the tobacco NbCSPR, and the rice receptor OsXa21 also recruit SERKs to positively regulate plant response to bacterial effectors (Chen et al., 2014; Hind et al., 2016; Saur et al., 2016; Wang et al., 2016). On the other hand, ANX1 and ANX2 negatively regulate plant immune response by associating BAK1 and FLS2 and disrupting the complex formation (Mang et al., 2017). In addition to activating response to bacterial infections, SERKs are also involved in defense response to oomycetes and fungi. For instance, the activation of PTI by tomato receptors SlCf9 and SlCf4, in response to fungal elicitors, is dependent on SERKs (Liebrand et al., 2013; Postma et al., 2016). Likewise, RLP23 relies on BAK1 to activate defense response to fungi and oomycetes in *Arabidopsis* (Albert et al., 2015). The PTI activation by DAMPs also depends on SERKs. For example, PEPR1 and PEPR2 bind in a ligand-dependent manner with BAK1 and BKK1 to form a heterodimer complex and activate intracellular signaling (Postel et al., 2010; Roux et al., 2011).

On the other hand, SERKs also play a pivotal role in plant growth and development (Figure 3). Upon BR perception, BRI1 recruits BAK1 to form a complex and regulate plant response to light, root growth, cell elongation, and stress response (Li and Chory, 1997; Li et al., 2002; Nam and Li, 2002; Zhu et al., 2013). Later, it was reported that SERK1 and BKK1 act redundantly with BAK1 to regulate the BR-mediated signaling (Gou et al., 2012). Another example is the PSKR1 receptor that mobilizes SERK1, SERK2, and BAK1 to form a stable complex and regulate root growth and cell expansion in response to PSK (Wang et al., 2015). Furthermore, the PSY1R receptor is also able to interact with SERKs to mediate PSY1 signal transduction after phosphorylation, and subsequently regulate cell expansion and cell division (Oehlenschlæger et al., 2017). In *Arabidopsis*, SERK1 and SERK2 are also known to play a role in embryogenesis (Albrecht et al., 2005). They associate with EMS1/EXS to regulate male-gametophyte development. SERKs also carry out additional functions in growth and development. For instance, the stomatal opening and closure are vital for efficient gas and water exchange with the environment (Nadeau and Sack, 2002). The stomatal cell patterning is regulated by EPFs that are recognized by the receptors ER and ERL1. The distribution patterns in *serks* quadruple mutants are similar to *er/erl1* mutants, indicating that SERKs play a redundant role in regulating stomatal patterning (Meng et al., 2015). SERKs complex with ER and ERL1 upon EPF peptide perception. Moreover, SERKs were also reported to control floral organ abscission redundantly. In this process, the plant peptide IDA is recognized by the receptors HAE and HSL2 that recruit SERKs to activate downstream signaling and promote the detachment of floral organs (Meng et al., 2016). Further, SERKs are also involved in the development of root meristem and xylem differentiation, acting as co-receptors of RGFR 1–5 and TDR, respectively (Song et al., 2016; Zhang et al., 2016).

Altogether, the co-regulatory SERKs are versatile and capable of regulating distinct signaling pathways to maintain the plant balance between immunity and growth and development.

Negative regulators of plant immunity, growth, and development

Although the SERK family positively regulates plant immunity and plant growth development, negative regulators are critical for maintaining the plant homeostasis by simultaneously attenuating the responses activated by SERKs. For instance, the LRR-RLK BAK1-INTERACTING RECEPTOR-LIKE KINASE 2 (BIR2) constitutively interacts with BAK1 to avoid binding FLS2 before flg22 exposure (Halter et al., 2014; Kumar and Van Staden, 2019). Meanwhile, another RLK from the BIR family, BIR3, negatively regulates BR signaling by constitutively binding with BAK1 and BRI1, thus preventing the complex formation until the ligand perception (Imkampe et al., 2017). Furthermore, the MEMBRANE STEROID-BINDING PROTEIN 1 (MSBP1) interacts with the extracellular domain of BAK1, which rapidly induces its endocytosis, resulting in a negative impact in BR signaling (Song et al., 2009). Additionally, PROTEIN PHOSPHATASE 2A (PP2A), a serine/threonine protein, negatively regulates plant immunity by controlling the kinase activity of BAK1 (Segonzac et al., 2014). Another example of negative regulation is the ubiquitination of FLS2 by the E3-ubiquitin ligases PLANT U-BOX 12 (PUB12) and PUB13 that culminate in the FLS2 degradation and attenuation of PTI (Lu et al., 2011).

The role of SUPPRESSOR OF BIR1-1 (SOBIR1) in plant immunity, growth, and development

An additional co-regulatory LRR-RLK, SUPPRESSOR OF BIR1-1 (SOBIR1), was initially described as a positive regulator of the cell death pathway (Gao et al., 2009). Apart from this, SOBIR1 also constitutively interacts with other LRR-RLPs leading to the formation of functional signaling receptor complexes (Figure 2b) (Gao et al., 2009; Leslie et al., 2010; Gust and Felix, 2014; Liebrand et al., 2013, 2014). RLP23 requires SOBIR1 to form a complex together with BAK1 to activate immune responses to NLP peptides (Albert et al., 2015). Further, tomato receptors SlCf9, SlCf4, LeEIX1, and LeEIX2 also interact with SOBIR1 homolog in tomato in response to fungus (Liebrand et al., 2013). Moreover, the tomato receptor SlCuRe constitutively associates with tomato SOBIR1 to activate defense against the parasitic plant *Cuscuta reflexa*. (Hegenauer et al., 2016). A recent study also described a new role of SOBIR1 in plant growth and development. Alongside ERECTA, SOBIR1 regulates secondary xylem formation (Milhinhos et al., 2019).

The role of CLV3-INSENSITIVE RECEPTOR KINASEs in plant growth and development

Recently, a new class of co-receptors was described as regulators of stem cell homeostasis. Like the SERK family, the CLV3-INSENSITIVE RECEPTOR KINASE 1 (CIK1) to CIK4 are also members of the subclass LRR II of the RLK family. CIKs were reported to play a role as co-receptors of CLV1 and RPK2 in response to the CLV3 peptides to regulate meristem maintenance (Figure 3A) (Hu et al., 2018; Xu and Jackson, 2018). Subsequently, a new study reported that CIKs also bind to RPK2 and BAM1/2 receptors to regulate the differentiation of anther cells (Figure 3B) (Cui et al., 2018).

RECEPTOR-LIKE CYTOPLASMIC KINASEs relaying the signaling

RECEPTOR-LIKE CYTOPLASMIC KINASEs bear a kinase domain similar to RLKs. However, they lack the extracellular domain and the transmembrane domain (Lin et al., 2013b; Liebrand et al., 2014). RECEPTOR-LIKE CYTOPLASMIC KINASEs associate with the RLK complexes at the plasma membrane to transmit the intracellular signal via transphosphorylation. They play critical roles in plant immunity, growth, and development (Lin et al., 2013b).

The role of RLCKs in plant immunity

A well-known RCLK in plant immunity is BOTRYTIS-INDUCED KINASE 1 (BIK1) (Veronese et al., 2006; Lu et al., 2010; Laluk et al., 2011). BIK1 associates with FLS2 and BAK1 complex. Upon flg22 perception, BIK1 is phosphorylated by FLS2 and BAK1. Subsequently, BIK1 is released from the complex to transduce the signal, leading to ROS bursts (Figure 4) (Lu et al., 2010; Zhang et al., 2010). Further, recent studies have shown that the release of BIK1 from the PRR complex and its activation is dependent on ubiquitination by E3 ubiquitin ligases RHA3A and RHA3B (Ma et al., 2020). BIK1 can also directly interact with several other PRR complexes, including EFR, PEPR1, PEPR2, and CERK1 (Zhang et al., 2010; Liu et al., 2013). In addition, upon flg22 perception, BIK1 can phosphorylate the phosphatase BRI1-SUPPRESSOR1 (BSU1), which in turn triggers MAPK activation (Park et al., 2019). Similar to BIK1, avrPphB SENSITIVE 1 (PBS1), PBS1-LIKE 1 (PBL1), and PBL2 belong to subfamily VII of the RLCKs and interact with the previously mentioned PRRs to initiate PTI responses (Zhang et al., 2010; Laluk et al., 2011). Recently, RLCK VII members were reported to act downstream of PRRs, activating MAPK cascades by direct phosphorylation (Bi et al., 2018; Rao et al., 2018).

In tomato, PTO-INTERACTIN 1 (PTI1) was reported to be a positive regulator of PTI activation in response to FLS2 and FLS3 activation upon bacterial MAMPs (Schwizer et al., 2017). Further, CERK1 also interacts with PBS1-LIKE 27 (PBL27) to regulate PTI activation induced by chitin (Shinya et al., 2014; Yamada et al., 2016). In rice, OsCERK1 phosphorylate and associate with the RLCK OsRLCK185 in response to chitin leading to activation of MAPK and calcium channels (Yamaguchi et al., 2013; Wang et al., 2019). Interestingly, some RLCKs can be targeted by pathogens in order to overcome plant immunity activation. For instance, the bacteria *Xanthomonas campestris* pv *campestris* enhances virulence and inhibits plant immunity by targeting the RLCKs, BIK1 and RPM1-INDUCED PROTEIN KINASE (RIPK) (Feng et al., 2012). RIPK positively regulates the ETI response activation through phosphorylation of RPM1-INTERACTING PROTEIN 4 (RIN4) induced by the *Pseudomonas syringae* effectors AvrRpm1 and AvrB (Kim et al., 2005; Chung et al., 2011; Liu et al., 2011). Phosphorylated RIN4 is perceived by the NLR receptor Resistance to *Pseudomonas syringae pv*. maculicola 1 (RPM1) to activate ETI responses (Chung et al., 2011; Liu et al., 2011).

Furthermore, BR-SIGNALING KINASE 1 (BSK1), a critical RLCK in the BR pathway, can positively regulate flg22-triggered immune response by associating with the FLS2 complex and subsequently activating MAPK cascade by phosphorylation (Figure 4) (Yan et al., 2018). In addition to BSK1, other members of the BSK subfamily also regulate plant immunity. For instance, BSK3 and BSK5 were reported to function together with several PRRs in response to bacterial elicitors (Xu et al., 2014; Majhi et al., 2019).

The role of RLCKs in plant growth and development

In addition to its role in plant immunity, BIK1 can directly associate and phosphorylate the BRI1 complex to negatively regulate the BR signaling (Lin et al., 2013a). In the presence of BR, BIK1 is released from the complex upon phosphorylation by BRI1 (Figure 4). On the other hand, in contrast with its negative role in regulating immunity, BSK1 plays a positive role in regulating the BR signaling (Tang et al., 2008). Together with RLCK CONSTITUTIVE DIFFERENTIAL GROWTH (CDG1), BSK1 positively governs plant growth and development by directly binding with BRI1 (Tang et al., 2008; Kim et al., 2011). Upon being phosphorylated by BRI1, BSK1 and CDG1 directly phosphorylate the phosphatase BSU1 (Figure 4) (Tang et al., 2008; Kim et al., 2011). Other BSK subfamily members such as BSK3 and BSK5 are also involved in BR signaling response (Tang et al., 2008; Sreeramulu et al., 2013). Sequentially, BSU1 dephosphorylates and deactivates BR INSENSITIVE 2 (BIN2). BIN2 further phosphorylates and inactivates the transcription factors BRASSINAZOLE-RESISTANT1 (BRZ1) and BRI1-EMS-SUPPRESSOR1 (BES1)/BZR2 responsible for the activation of BR-related genes (Chaiwanon et al., 2016; Kim and Russinova, 2020). Additionally, SHORT SUSPENSOR (SSP) or BSK12 was reported to be involved in embryo patterning. However, it is still unclear the receptor complex that SSP likely associates with to regulate plant growth and development (Bayer et al., 2009; Costa et al., 2014). Furthermore, another RLCK, known as CAST AWAY (CST), was reported to associate with HAE and BAK1 to inhibit floral organ abscission (Burr et al., 2011). Meanwhile, MARIS (MRI) and RIPK were found to regulate root hair growth and root development, respectively, in association with the FER receptor (Boisson-Dernier et al., 2015; Du et al., 2016; Liao et al., 2016).

INTRACELLULAR SIGNALING UPON ACTIVATION OF RLK, RLP, AND RLCK COMPLEXES

Phosphorylated RLCKs relay the signal transduction to convergent signaling hubs, including MAPK cascades, ROS production, cytosolic calcium (Ca^{2+}) influx, and activation of CALCIUM-DEPENDENT PROTEIN KINASES (CDPKs or CPKs) (Couto and Zipfel, 2016; He et al., 2018). In particular, the MAPK cascades are critical for regulating plant immunity and development. In general, three kinases compose the MAPK module: the MAPK kinase kinase (MAPKK or MEKK), the MAPK kinase (MAPKK or MKK), and the MAPK (MPK) (Meng and Zhang, 2013). This cascade is sequentially activated through phosphorylation events, resulting in the signal transduction to the next substrate (Figure 4) (Meng and Zhang, 2013).

In plant immunity, two parallel MAPK cascades are activated upon MAMP/DAMP perception. The first one comprises MEKK3 and MEKK5 (hereafter MEKK3/MEKK5); MKK4/MKK5; and MPK3/MPK6. The second one consists of MEKK1; MKK1/MKK2; and MPK4 (Meng and Zhang, 2013). For instance, the MAPK cascade activated in response to flg22 and elf18 include MEKK3/MEKK5-MKK4/MKK5-MPK3/MPK6 and MEKK1-MKK1/MKK2-MPK4 (Asai et al., 2002; Zipfel et al., 2006; Suarez-Rodriguez et al., 2007; Meng and Zhang, 2013; Bi et al., 2018; Sun et al., 2018). Meanwhile, the MAPK cascade downstream of chitin and CERK1 pathway consists of MEKK-MKK4/MKK5-MPK3/MPK6 (Miya et al., 2007; Meng and Zhang, 2013). Likewise, plant response to DAMPs leads to activation of WAK receptors that will transduce the signal through the MPK3/MPK6 cascade (Denoux et al., 2008; Galletti et al., 2011; Meng and Zhang, 2013). MAPK activation often leads to the expression of immune-related genes, ROS production, stomatal closure, ethylene production, and hypersensitive response (Meng and Zhang, 2013).

Besides its function in activating immunity, MAPK cascades are also crucial for signal transduction to regulate plant growth and development. For instance, the MAPK cascade comprising YDA-MKK4/MKK5-MPK3/MPK6 regulates stomatal patterning and development (Meng et al., 2015). Similarly, the above-mentioned MAPK cascade was reported to play a role downstream of the RLCK SSP to control embryo patterning (Costa et al., 2014). Moreover, the MKK4/MKK5-MPK3/MPK6 cascade is phosphorylated downstream of HAE and HSL2 receptors regulating floral organ abscission (Meng et al., 2016). However, the MAPKKK in this pathway is not known. Interestingly, the MAPK cascade seems not to be involved in the BR signaling; in fact, BR signaling mainly relies on RLCKs, phosphatases, and transcription factors to regulate plant development (Wang et al., 2014). The MAPK activation in plant development often leads to phosphorylation of transcription factors and enzymes that regulate the growth and development responses (He et al., 2018).

In addition to the MAPK cascade, the RESPIRATORY BURST OXIDASE HOMOLOGs (RBOHs), also known as NICOTINAMIDE ADENINE DINUCLEOTIDE PHOSPHATE (NADPH) oxidases, are the substrate for RLCKs to relay the signal transduction that results in the accumulation of ROS (Kärkönen and Kuchitsu, 2015). As reactive molecules, ROS are able to oxidize cellular components restricting their ability to function properly (Mittler et al., 2004). Thus, ROS levels require tight regulation to prevent cell damage due to excessive ROS production (Lee et al., 2020). In *Arabidopsis*, plasma membrane-resident RBOHD is mainly responsible for ROS burst upon MAMP perception (Torres et al., 2002; Wang et al., 2020b). The PRRs FLS2, EFR, PEPR1, LYK5, and CERK1, upon the perception of their cognate ligands, phosphorylate BIK1, which subsequently phosphorylates RBOHD resulting in ROS production (Figure 4) (Kimura et al., 2017). Moreover, upon the perception of eATP by the DORN1 receptor, RBOHD is also phosphorylated, leading to stomatal closure and an increase of ROS burst (Chen et al., 2017). ROS also function in controlling plant growth and development. For instance, ROS positively regulates root meristem development via BR signaling (Lv et al., 2018; Tian et al., 2018). Further, the ROS oxidative state can also expedite the cell division of embryonic roots (de Simone et al., 2017). Further, the accumulation of ROS regulates cell expansion and elongation of roots in *Arabidopsis* (Foreman et al., 2003).

One of the plant responses to a variety of stimuli is an increase of the concentration of the cytosolic free Ca^{2+}, which leads to two opposite reactions: calcium inflow and calcium outflow (Tuteja and Mahajan, 2007). The calcium ion influx can be perceived by Ca^{2+}-sensors that subsequently activate CDPKs (Tuteja and Mahajan, 2007; Boudsocq and Sheen, 2013). CDPKs can decode the calcium signals into phosphorylation reactions to subsequently relay the signal to trigger plant response to a stimulus (Boudsocq and Sheen, 2013). The flg22-FLS2 complex was reported to activate CPK4, CPK5, CPK6, and CPK11 that afterward positively regulate the expression of immune-related genes (Boudsocq et al., 2010). However, CPK28 was found to negatively regulate plant immunity by phosphorylation of BIK1, limiting the amount of BIK1 available for PTI activation (Monaghan et al., 2014). Moreover, CDPKs also regulate ROS burst through phosphorylation; namely, CPK5 was reported to positively control ROS activation after flg22 perception (Boudsocq et al., 2010; Dubiella et al., 2013). CDPKs also function in plant development. For instance, several CDPKs were reported to regulate pollen tube growth in *Arabidopsis* (Myers et al., 2009). Differing from its role in immunity, CPK28 plays a positive role in vascular development and stem elongation (Matschi et al., 2013). Nonetheless, the mechanism behind the CDPK regulation of immunity and development is not well understood. Recent studies have provided new insights into calcium signaling. For instance, upon MAMP perception, the Ca^{2+} channel, OSCA1.3, regulates stomatal closure, and subsequently, it is regulated by BIK1, leading to an increase of Ca^{2+} influx (Thor et al., 2020). In addition, the CYCLIC NUCLEOTIDE-GATED CHANNEL 2 (CNGC2) and CNGC4 were reported to be essential in the formation of a functional calcium channel, that after MAMP perception, is phosphorylated by BIK1, resulting in an increase of calcium in the cytoplasm (Tian et al., 2019).

CONCLUDING REMARKS

In the past decade, remarkable advances have been made to reveal the critical role of the plant cell surface receptors in regulating plant immunity, growth, and development. Despite the fact that the functions of a large body of RLKs and RLPs await to be ascertained, many RLKs and RLPs have been uncovered to play novel sentinel roles in perceiving diverse endogenous and exogenous signals through the binding of specific ligands by their extracellular domains; however, the cognate ligands for most RLKs and RLPs remain to be identified.

The signals perceived by the RLK and RLP complexes are relayed to the downstream signaling modules that further transduce the signaling to activate and coordinate distinct physiological responses. Interestingly, layered crosstalk via convergent and shared components occurs in plant immunity, growth, and development. For instance, the SERK family proteins act as shared co-regulatory receptors for numerous RLKs and RLPs to modulate growth and development processes and immune response to different microbial elicitors. The mechanism underlying SERKs' versatility to function in multiple signaling processes is yet to be understood. It also remains unknown how the SERK family has evolved in plants and whether the functional conservation of SERKs exists in early evolved plant species. Furthermore, RLCKs, which are emerging as signaling nodes that link RLK and RLP complex activation to downstream signaling, are also shared components in different receptor-mediated signaling pathways. The pathways activated by RLKs and RLPs lead to the phosphorylation of RLCKs, which relay specific intracellular outputs through phosphorylation and activation of signaling components, including MAPK cascades (Luo et al., 2020; Bi et al., 2018; Liang and Zhou, 2018). Yet, identifying the full spectrum of RLCK substrates is needed for a better understanding of cell surface signaling in plants.

Recent studies have indicated that the plasma membrane is compartmentalized into microdomains that harbor RLKs and their associated signaling components to promote rapid and optimized response to different stimuli (Bücherl et al., 2017; Ott, 2017; Jaillais and Ott, 2020). It would be interesting to examine the composition and dynamics of the microdomains containing RLK and RLP complexes with shared components in response to various stimuli in plant immunity, growth, and development.

Future studies employing multidisciplinary approaches are necessary to elucidate the components needed to activate the different RLK- and RLP-receptor complexes and signaling transduction to specific downstream modules. This information is crucial to understand how diverse RLK and RLP signaling pathways coordinate plant growth, development, and immune responses in different biological contexts such as under biotic stress, where activation of defense responses usually leads to restriction of plant growth (Lozano-Durán and Zipfel, 2015; Ortiz-Morea et al., 2020). Considering the important roles of RLKs and RLPs in plant growth and immune responses, it is expected that RLK- and RLP-receptor complex activation is subjected to tight regulation under pathogen attacks and their coordinated actions collectively modulate the growth-defense trade-off. Functional characterization of plasma membrane-resident RLKs and RLPs perceiving diverse environmental and endogenous cues will be continuously a burgeoning area of investigation and offer insight into strategic development for improved crop resilience.

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