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The function of the plant cell wall in plant–microbe interactions

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ABSTRACT

The plant cell wall is an interface of plant–microbe interactions. The ability of microbes to decompose cell wall polysaccharides contributes to microbial pathogenicity. Plants have evolved mechanisms to prevent cell wall degradation. However, the role of the cell wall in plant–microbe interactions is not well understood. Here, we discuss four functions of the plant cell wall—physical defence, storage of antimicrobial compounds, production of cell wall-derived elicitors, and provision of carbon sources—in the context of plant–microbe interactions. In addition, we discuss the four families of cell surface receptors associated with plant cell walls (malectin-like receptor kinase family, wall-associated kinase family, leucine-rich repeat receptor-like kinase family, and lysin motif receptor-like kinase family) that have been the subject of several important studies in recent years. This review summarises the findings on both plant cell wall and plant immunity, improving our understanding and may provide impetus to various researchers.

1. Introduction

Plants constantly interact with microbes in their natural environment. These interactions may be beneficial or detrimental (Imam et al., 2016) and are a cause/consequence of plant–microbe co-evolution (Morgan et al., 2005), a phenomenon that has existed since before plant terrestrialisation (Ramanan et al., 2016). During this process, plants acquired a remarkably complex and robust cell wall to prevent the entry of intruders. Beyond its role as a protective barrier, plants recognise cell wall perturbations and degradation products and elicit immune responses. Therefore, the plant cell wall is not only a passive structural component but also an essential medium for communication with the surrounding environment.

A complete architectural model of the plant cell wall has not yet been established, owing to its structural complexity (Cosgrove, 2014; Fry, 2011; Keegstra et al., 1973). Researchers have not yet identified the group of enzymes that synthesise the complex structural polysaccharides. For instance, at least 67 types of glycosyltransferases are required for pectin biosynthesis, only less than half of which have been biochemically and genetically characterised (Mohnen, 2008). Therefore, plant cell walls remain underexplored. Plant–microbe interactions are also increasingly being studied. Plants recognise microbe-derived substances that are common in a broad range of microorganisms called microbe-associated molecular patterns (MAMPs) and induce defence responses (pattern-triggered immunity: PTI) to protect themselves (Chisholm et al., 2006; Jones and Dangl, 2006). Pathogenic microbes release various effector proteins to evade PTI. During plant–microbe interactions, plants sense molecules (damage-associated molecular patterns: DAMPs) produced in response to cell destruction to amplify defence responses (Tanaka and Heil, 2021). Technical advancements in omics approaches can provide information on the global alterations in genes, proteins, and metabolites in plants and microorganisms that occur due to their interaction with each other in specific experimental models (e.g. interactions between Arabidopsis and *Pseudomonas syringae*) (Garcia-Seco et al., 2017; Nobori et al., 2018; Zhang et al., 2019). Further studies are expected to reveal the biological significance of plant microbiomes and molecular mechanisms underlying the plant holobiont (collection of the host plant and its interacting species).

The contribution of the plant cell wall to plant immunity has long been recognised (Albersheim et al., 1969; Edwards and Ayres, 1981; Hammerschmidt et al., 1984; Vance et al., 1976). Both these research fields have developed separately due to their complexity, thereby resulting in insufficient integrated knowledge. For example, models of cell wall reorganisation during a microbial response are rarely discussed, with some exceptions such as papilla formation and hemicellulose cross-linking (Underwood, 2012; Malinovsky et al., 2014).

This review focuses on the role of plant cell walls in plant immunity, aiming to build a basis for further integrated research. In particular, we

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summarise important discoveries that unveil the mechanisms by which plant cell wall components and cell wall-related cell surface receptors contribute to immunity.

2. Plant cell wall components modulate susceptibility and resistance to microbes

Plant cell walls are structurally and functionally divided into primary and secondary cell walls (Cosgrove and Jarvis, 2012). The primary cell wall is synthesised during cell growth and is highly extensible (Cosgrove, 2005). After the cell expands and reaches the required size, the secondary cell wall is synthesised by pushing the primary cell wall outwards. The synthesis of these two types of cell walls is strictly regulated by distinct genetic networks (Hyde et al., 2018; Rao and Dixon, 2018; Sakamoto et al., 2018). Furthermore, the two cell wall types differ in their composition. The primary cell wall is composed of cellulose, hemicellulose (especially xyloglucan and mannan), and pectin (Cosgrove, 2005). While the secondary cell wall of gymnosperms and angiosperms is composed of cellulose, hemicellulose (especially xylan), and lignin (Zhong and Ye, 2014). The presence of lignin, a phenolic polymer, in the secondary cell wall makes it hard, thick, and poorly extensible (Zhong et al., 2019). The components of both cell wall types are interconnected by hydrogen bonds and stacking interactions (Lima et al., 2004; Park and Cosgrove, 2015). These physical interactions play at least four roles in plant–microbial interactions: they provide a physical barrier, produce antimicrobial compounds, induce immunity by detecting polysaccharide degradants, and supply a carbon source to symbiotic microbes. Here, we discuss these four functions and the cell wall components that mediate them.

2.1. Physical barrier

To obtain nutrients from plants, pathogenic microbes need to break through plant cell walls. The pathogens use various carbohydrate-active enzymes to degrade plant cell walls (Kubicek et al., 2014; Lyu et al., 2015; Zerillo et al., 2013; Zheng et al., 2013). Loss of such hydrolytic enzymes results in decreased virulence of *Botrytis cinerea* in tomatoes (Have et al., 1998), *A. thaliana* and grapevine (Valette-Collet et al., 2007), *Alternaria citri* in citrus (Isshiki et al., 2001), *Nectria hematococca* in pea (Rogers et al., 2000), *Claviceps purpurea* in rye (Oeser et al., 2002), and *Aspergillus flavus* in cotton (Shieh et al., 1997). The alterations in plant cell wall composition caused by genetic mutations change its resistance/susceptibility to plant pathogens. In *Arabidopsis*, many cell wall mutants show varying resistance/susceptibility to the necrotrophic fungus *Plectosphaerella cucumerina*, the vascular bacterium *Ralstonia pseudosolanacearum*, and the biotrophic oomycete *Hyaloperonospora arabidopsidis* (Molina et al., 2021).

Plants are known to thicken their cell wall in response to microbial invasion, particularly at the sites of microbial penetration (Fig. 1a) (Gadaleta et al., 2019; Schulze-Lefert, 2004; Underwood, 2012). For example, lignin biosynthesis genes are upregulated and ectopic lignin deposition occurs when plants sense a pathogenic challenge (Bhuiyan et al., 2009; Eynck et al., 2012; Miedes et al., 2014; Wan et al., 2021; Xu et al., 2011). Elicitor-induced lignin deposition is controlled by the transcription factor MYB15 in *Arabidopsis* (Chezem et al., 2017). MYB15 also promotes the synthesis of the antimicrobial molecule coumarin, whose synthesis is similar to that of lignin (Chezem et al., 2017). The role of MYB15 was confirmed using 1 μM flg22 (part of bacterial flagellin) treatment and the colony forming unit under *P. syringae* DC3000. However, another study assessed MYB15 pathway activation (Kim et al., 2020) using *P. syringae* DC3000 carrying a virulent and avirulent effector (*AvrRpm1*). Interestingly, the activation of *MYB15* and its downstream genes was observed with avirulent strain but not virulent strain treatment, suggesting that the MYB15 pathway activation depends on effector-triggered immunity. Similarly, the *myb15* mutant deficient in two of the four phenylalanine ammonia-lyase genes involved in the biosynthesis of anthocyanin pigments and lignin showed decreased resistance to *P. syringae*, although its salicylic acid (SA) content was similar to that in wild-type plants (Huang et al., 2010). Differences in lignin synthesis between crop varieties are also known to affect resistance; tomato varieties resistant to *Ralstonia solanacearum* can rapidly accumulate lignin upon infection, whereas non-resistant varieties cannot (Mandal et al., 2011). In contrast, there are known cases in which inhibition of lignin synthesis, achieved by downregulation of hydroxycinnamoyl CoA: shikimate hydroxycinnamoyl transferase (HCT) or a type III cell wall-bound peroxidase and loss of function of cinnamoyl CoA reductase 1 (CCR1), leads to a constitutive defence response that enhances pathogen resistance in *Arabidopsis* (Gallego-Giraldo et al., 2011, 2020; Ramírez et al., 2011).

Mutations in cellulose synthase (CESA) often result in the hyperactivation of the immune response network involving cell wall integrity sensors (Caño-Delgado et al., 2003; Ellis et al., 2002; Hématy et al., 2007). The *cesa4*, *cesa7*, and *cesa8 Arabidopsis* mutants exhibit resistance to *P. syringae*, *B. cinerea*, *Plectosphaerella cucumerina*, and *R. solanacearum* (Hernández-Blanco et al., 2007). A forward genetic screening for aberrant lignification patterns in the phloroglucinol-stained primary roots isolates the ectopic lignifying *Arabidopsis* mutant *eli1*, which contains a point mutation in *CESA3*, that induces a defence response mediated by jasmonic acid (JA) and ethylene pathways (Caño-Delgado et al., 2003; Ellis et al., 2002). These findings suggest that some mutants previously isolated with defective cell wall synthesis (e.g. *murus*: *mur1-11* and *irregular xylem*: *irx1-15*) may exhibit secondary effects via hormone cross-talk.

Similar to lignin, callose (β-1,3-glucan) is also used as a cell wall reinforcement, especially in the papillae to counteract pathogens penetrating using cellulase against β-1,4-glucan (Voigt, 2014). There are 12 callose synthases (CALSs) in *Arabidopsis* that are highly sub-functionalised (Verma and Hong, 2001). Of these, *CALS12/GSL5* (*GLUCAN SYNTHASE-LIKE 5*) is responsible for papillary callose formation (Ellinger and Voigt, 2014). The T-DNA insertion line of *CALS12/GSL5* (*cals12/gsl5*) fails to accumulate both wound callose and papillary callose (Jacobs et al., 2003). Although the *cals12/gsl5* mutant cannot deposit callose at sites of attempted penetration, it is known as *powdery mildew resistant 4* (*pmr4*) due to its resistant phenotype to powdery mildew. The *cals12/gsl5/pmr4* mutant shows hyperactivation of defence-associated genes, especially those involved in SA signalling (Nishimura et al., 2003; Vogel and Somerville, 2000). In contrast, the overexpression of *CALS12/GSL5/PMR4* induces papillae thickening and blocks haustoria formation by both adapted and non-adapted powdery mildew without induction of either SA- or JA-dependent pathways and without hampering plant growth (Ellinger et al., 2013).

2.2. Reservoir of antimicrobial molecules

Plants secrete various enzymatic and non-enzymatic antimicrobials into the apoplast (Fig. 1b). In *Arabidopsis*, the secretion of tryptophan-derived secondary metabolites, such as that of camalexin into the apoplastic space, is regulated by the ATP-binding cassette (ABC) transporters AtABCG36/PLEIOTROPIC DRUG RESISTANCE8 (PDR8)/PENETRATION3 (PEN3) and AtABCG40/PDR12 (He et al., 2019). ABC transporters are also involved in the secretion of antifungal diterpene in tobacco (Crouzet et al., 2013; Jasiński et al., 2001). To prevent fungal growth, plants secrete hydrolases, such as chitinase, into the apoplast to degrade fungal cell walls (Martínez-Cruz et al., 2021). Fungi also decompose plant cell walls using various hydrolases such as polygalacturonase. To prevent this, plants use polygalacturonase-inhibiting proteins (PGIPs) that prevent pectin degradation. In *Arabidopsis*, antisense suppression of *PGIP1* reduces resistance, whereas overexpression of *PGIP1* and *PGIP2* increases resistance to *B. cinerea* (Ferrari et al., 2003, 2006).

High-reactivity molecules are also produced in response to pathogen recognition. Reactive oxygen species (ROS; e.g. superoxide radicals) and

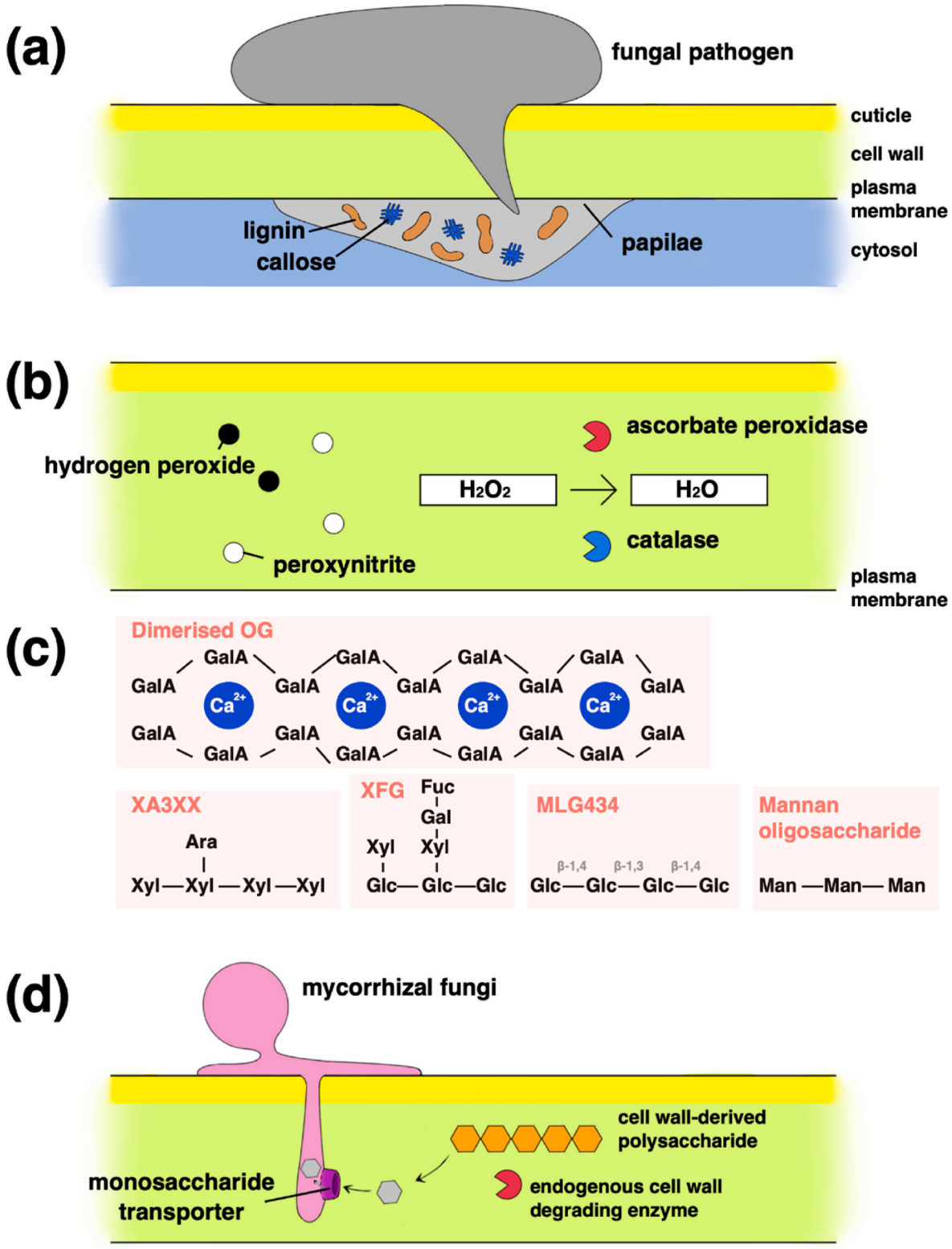

Fig. 1. Four functions of the plant cell wall in plant–microbe interactions. (a) physical barrier (e.g. in leaf), (b) reservoir of antimicrobial compounds (e.g. in root), (c) cell wall-derived elicitors, and (d) carbon source (the structure in pink indicates mycorrhiza and its hypha).

reactive nitrogen species (RNS; e.g. nitric oxide and peroxynitrite) are used as key defence molecules (García-Olmedo et al., 2001). Superoxide is produced in the apoplast by NADPH oxidases, referred to as respiratory burst oxidase homologues (RBOHs), localised in the plasma membrane and converted to hydrogen peroxide by superoxide dismutase (SOD). ROS not only directly attack pathogens but also act as a second messenger to activate defence pathways (Castro et al., 2021). Hydrogen peroxide is involved in papilla formation by serving as a substrate for peroxidase that catalyses the cross-linking of phenolic compounds (Brown et al., 1998). Enzymes such as catalase and ascorbate oxidase are responsible for scavenging cellular ROS that damage plants (Farvardin et al., 2020).

2.3. Cell wall-derived elicitors

Various plant cell wall-derived oligosaccharides function as DAMPs (Fig. 1c, Table 1) to induce immune responses (Vorwerk et al., 2004). For instance, pectin degradants like α-1,4 oligogalacturonides (OGs) trigger ROS accumulation, callose deposition, induction of defence-related genes, and alteration of secondary metabolites (Aziz et al., 2007; Denoux et al., 2008; Galletti et al., 2008, 2011; Gamir et al., 2021). These responses are signalled via the cell surface receptors, wall-associated kinases (WAKs) (Kohorn, 2001). Similar to flg22, the induction of defence-related genes to OGs in *Arabidopsis* is fast and transient (Denoux et al., 2008). Cellulose-derived oligosaccharides (composed of β-1,4 linkages) and callose/fungal cell wall-derived oligosaccharides (composed of β-1,3 linkages) are also elicitors that enhance pathogen resistance (Aziz et al., 2007; Johnson et al., 2018; Locci et al., 2019; Mélida et al., 2018; Souza et al., 2017). Recently, several studies have reported that oligosaccharides derived from hemicellulose, including arabinoxylan oligosaccharides, mixed-linkage glucan (MLG: β-1,3/1,4-glucan) oligosaccharides, xyloglucan oligosaccharides, and mannan oligosaccharides, induce immune responses. XA3XX (3^3-α-L-arabinofuranosyl-xylotetraose), the digestion product of wheat arabinoxylan by glycoside hydrolase (GH) family 11 xylanases, induces PTI in wheat (Mélida et al., 2020). The digestion products of MLG, the major hemicellulose in the grass family (Vega-Sanchez et al., 2013), stimulate the same pathway as that of chitooligosaccharide-induced immunity in both monocots and eudicots (Rebaque et al., 2021; Yang et al., 2021). Although fucosylated-xyloglucan and galactoglucomannan digestion products induce PTI and contribute to pathogen resistance (Claverie et al., 2018; Zang et al., 2019), their receptors have not yet been identified.

Pathogens have developed mechanisms to avoid PTI (Wolf, 2022). For example, the necrotrophic fungus *B. cinerea* produces most OGs by β-elimination catalysed by pectin lyases instead of hydrolases, thus

Table 1
Summary of plant cell wall-derived elicitors.

Cell wall-derived elicitor[a]	Origin	Receptor	Downstream pathway	Observed response	Function	Reference
α-1,4 oligogalacturonide (DP[b]>8)	Pectin	WAKs	MPK3, MPK6	ROS[j] accumulation, callose deposition, induction of defence-related genes, hormones, and secondary metabolites	Resistance to *Botrytis cinerea*	Aziz et al. (2007); Denoux et al. (2008); Gamir et al. (2021); Galletti et al. (2008); Galletti et al. (2011)
β-1,3-glucan oligosaccharide (DP = 6)	Callose/fungal cell wall	CERK1, LYK4, LYK5	MPK3, MPK6, MPK4/11	ROS accumulation, elevation of cytoplasmic Ca^{2+}, induction of defence-related genes	Resistance to *Plectosphaerella cucumerina* and *Hyaloperonospora arabidopsidis*	Mélida et al. (2018)
β-1,4-glucan oligosaccharide (DP = 2)	Cellulose/ fungal cell wall		MPK3, MPK6	Elevation of cytoplasmic Ca^{2+}, induction of defence-related genes	Resistance to *Pseudomonas syringae* pv. *tomato* DC3000	Locci et al. (2019); Souza et al. (2017)
β-1,4-glucan oligosaccharide (DP = 3–9)	Cellulose/ fungal cell wall	Not determined but BAK1-independent	MPK3	ROS accumulation, elevation of cytoplasmic Ca^{2+}, increase in β-1,3 gluncanase and chitinase activity	Resistance to *Botrytis cinerea*	Aziz et al. (2007); Johnson et al. (2018)
Arabinoxylan oligosaccharide (XA3XX[c])	Xylan	Not determined but CERK1 and BAK1-independent	MPK3, MPK6	ROS accumulation, elevation of cytoplasmic Ca^{2+}, induction of defence-related genes	Resistance to *Pseudomonas syringae* pv. *tomato* DC3000 and *Sclerotinia sclerotiorum*	Mélida et al. (2020)
Mixed-linkage glucan oligosaccharide (DP = 3–4, MLG43[d], MLG34[e], MLG434[f], MLG344[g], MLG443[h])	Mixed-linkage glucan/cell wall from oomycete	CERK1, LYK4, LYK5	MPK3, MPK6	ROS accumulation, elevation of cytoplasmic Ca^{2+}, induction of defence-related genes	Resistance to *Pseudomonas syringae* pv. *tomato* DC3000, *Sclerotinia sclerotiorum*, *Botrytis cinerea,* and *Magnaporthe oryzae*	Rebaque et al. (2021); Yang et al. (2021)
Xyloglucan oligosaccharide (DP = 7, XFG[i])	Xyloglucan		MPK3, MPK6	Callose deposition, induction of defence-related genes, phytoalexin accumulation	Resistance to *Botrytis cinerea* and *Hyaloperonospora arabidopsidis*	Claverie et al. (2018)
Mannan oligosaccharide (DP = 2–6, possibly α-Gal side chain containing)	Mannan		MPK6, MPK12	ROS, nitric oxide, phytoalexin accumulation, elevation of cytoplasmic Ca^{2+}, stomata closure	Resistance to *Xanthomonas oryzae* and *Phytophthora nicotianae*	Zang et al. (2019)

[a] Chitin oligosaccharides are abbreviated from the table because of their different origins.
[b] DP: Degree of polymerisation.
[c] XA3XX: 3^3-α-L-arabinofuranosyl-xylotetraose.
[d] MLG43: Glc-β-1,4-Glc-β-1,3-Glc.
[e] MLG34: Glc-β-1,3-Glc-β-1,4-Glc.
[f] MLG434: Glc-β-1,4-Glc-β-1,3-Glc-β-1,4-Glc.
[g] MLG344: Glc-β-1,3-Glc-β-1,4-Glc-β-1,4-Glc.
[h] MLG443: Glc-β-1,4-Glc-β-1,4-Glc-β-1,3-Glc.
[i] X: Xyl-α-1,6-Glc, F: Fuc-α-1,2-Gal-β-1,2-Xyl-α-1,6-Glc, G: Glc.
[j] ROS: reactive oxygen species.

avoiding the production of OGs that are recognised by plants (Voxeur et al., 2019). Plants have a large number of carbohydrate-active enzymes that serve various functions, including adaptation to environmental stresses (Ishida and Yokoyama, 2022). Interestingly, these GH families are often different from that of microorganisms, implying a mechanism for avoiding self-elicitation owing to the difference in substrate and product specificities. For instance, in the case of xyloglucanase, fungi use GH7 and 12, but plants use GH16. Similarly, bacteria use GH10, 11, and 30 xylanases, but plants only possess GH10 xylanase (Dora et al., 2022; Kumar et al., 2019; Yokoyama, 2020). In the case of glucuronoxylan degradation, GH10 xylanase produces relatively shorter oligos such as Me-GlcA-Xyl3 (degree of polymerisation: DP = 4) and Me-GlcA-Xyl4 (DP = 5), whereas GH30 xylanase produces a broader size of products represented as $(Xyl)_n$-GlcA-Xyl (DP = n+2) (Puchart et al., 2019). The genome of the ectomycorrhizal fungus *Laccaria bicolor* loses a large number of carbohydrate-active enzymes for plant cell wall degradation (Martin et al., 2008). This may be necessary to avoid damaging the host plant while evading plant immunity without producing OG elicitors.

2.4. Carbon source

Plants and arbuscular mycorrhizal fungi exchange at least carbohydrates and nitrogen with each other (Fellbaum et al., 2012). The main form of carbohydrate exchanged is sucrose, a product of photosynthesis, which is transported to the biotrophic interface through sucrose transporters (SWEETs) (Manck-Götzenberger and Requena, 2016). Plants also produce carbohydrates by breaking down their own cell walls in response to fungi (Balestrini and Bonfante, 2014). For instance, xyloglucan endotransglucosylase/hydrolase is upregulated in *Medicago truncatula* during mycorrhizal infection (Maldonado-Mendoza et al., 2005). Similarly, the expression of the β-xylosidase/α-arabinosidase-like gene in tomatoes is strongly induced during arbuscule formation (Fiorilli et al., 2009). Mycorrhiza takes up various types of monosaccharides via monosaccharide transporters (MST). MST2 of the arbuscular mycorrhizal *Rhizophagus* sp. imports glucose, mannose, galactose, xylose, glucuronic acid, and galacturonic acid *in vitro*. Symbiosis with *M. truncatula* is inhibited by host-induced gene silencing of MST2 (Helber et al., 2011). Thus, cell wall polysaccharides function as a factor in facilitating symbiosis (Fig. 1d). However, the need for cell wall degradation in symbiosis remains to be elucidated.

2.5. Key open questions

Although there is a correlation between lignin content and plant resistance, the precise mechanisms by which lignin prevents microbial growth remains to be elucidated. It may manifest its effect by triggering basal immunity in plants against pathogen invasion or might be one of the pleiotropic effects in cell death for containment. The use of plant cell wall degradation products by pathogenic microbes also remains to be elucidated. Furthermore, determining whether and how endogenous plant GHs do not cause immune activation warrants further research.

3. Cell wall integrity sensing

Arabidopsis thaliana has more than 600 receptor-like kinases (RLKs) that are the primary cell surface receptors. These receptors are grouped into 12 families (de Azevedo Manhães et al., 2021), of which four have a strong relationship with the plant cell wall under biotic stress: malectin-like receptor kinases (MLKs), WAKs, leucine-rich repeat receptor-like kinases (LRR-RLKs), and lysin motif receptor-like kinases (LysM-RLKs) (Table 2). These receptors are required for both plant immunity and development (de Azevedo Manhães et al., 2021; Shiu et al., 2004), but their function (immunity response vs. growth and development) is not mutually exclusive because of the interconnection and convergence of their downstream pathways (Ma et al., 2016; Tang et al., 2017). RLKs are thought to bind ligands (mainly oligosaccharides, peptides, and hormonal molecules) via extracellular domains and transduce signals to downstream cascades through the activity of their intracellular kinase domain. Some ligand-binding receptors lack the intracellular kinase domain and form a complex with co-receptors with kinase activity to activate signalling pathways (Xi et al., 2019). This section presents the functions of the cell wall-related RLK families and highlights key advances.

3.1. Malectin-like receptor kinase family

MLKs, also known as the *Catharanthus roseus* (Madagascar periwinkle) receptor-like kinase (*Cr*RLKs) family, include 17 genes in *A. thaliana*. Fifteen of these genes (*THESEUS 1* (*THE1*), *HERCULES1* and *2* (*HERK1*, *2*), *FERONIA* (*FER*), *ANXUR1* and *2* (*ANX1*, 2), *BUDDHA'S PAPER SEAL1* and *2* (*BUPS1*, *2*), *CURVY1* (*CVY1*), *MEDOS1* to *MEDOS4* (*MDS1* to *MDS4*), *ANJEA* (*ANJ*), and *ERULUS* (*ERU*)), required for development and growth, have been partially characterised (Table 2) (Bai et al., 2014; Feng et al., 2019; Gachomo et al., 2014; Galindo-Trigo et al., 2020; Ge et al., 2017; Guo et al., 2009; Kwon et al., 2018; Lindner et al., 2012; Miyazaki et al., 2009; Muro et al., 2018; Nibau and Cheung, 2011; Richter et al., 2018; Schoenaers et al., 2017). The ligands of MLKs are small peptides called rapid alkalinisation factors (RALFs) and have been identified based on the direct interaction between some MLKs and RALFs (Ge et al., 2017; Murphy and De Smet, 2014). The cell wall-related MLKs THE1 and FER are discussed in the following paragraphs.

THE1 is believed to monitor cell wall integrity (Gigli-Bisceglia et al., 2020). This hypothesis is based on the observation that the *the1* mutant partially restores the decreased elongation of dark-grown hypocotyls of the cellulose synthase mutant, *prc1* (*procuste1*), which has a mutation in *CESA6* (Fagard et al., 2000; Hématy et al., 2007). In the *prc1 the1* double mutant, cellulose synthesis remains defective, but ectopic lignin accumulation, ROS production, and *the1*-dependent differential gene expression are strongly suppressed. In addition, the *the1* mutant is insensitive to pharmacologically-induced inhibition of cellulose biosynthesis (Denness et al., 2011). Screening of RALF-insensitive mutants based on RALF-induced root shortening revealed that *the1* is less responsive to RALF34 supplementation. The RALF34-THE1 pathway contributes to extracellular alkalinisation (the pH of RALF34-treated *Arabidopsis* plants is approximately 0.4 units higher than that of mock treatment or RALF34-treated *the1*) (Gonneau et al., 2018). When the apoplast becomes acidic, cell wall reorganising enzymes become more active, leading to cell wall loosening and cell expansion (Merz et al., 2017). The RALF34-THE1 pathway inhibits this process, partly explaining the growth inhibition effect of RALF34 treatment.

FER is the most ubiquitous and highly expressed MLK in *A. thaliana* (Lindner et al., 2012). Several functions of FER, including polar growth (Duan et al., 2010; Haruta et al., 2014), localisation of synergid cell proteins (Escobar-Restrepo et al., 2007), resistance to light-dependent oxidative stress (Shin et al., 2021), response to mechanical stress (Shih et al., 2014), and facilitation of root–microbiota interaction under low-phosphate conditions (Tang et al., 2022), have been reported. Therefore, FER may mediate various cellular signalling pathways by interacting with different ligands. In the *fer* mutant, both cell stretch-induced Ca^{2+} signals and upregulation of touch-inducible genes are impaired, suggesting that the *fer* mutant cannot detect mechanical stimuli (Shih et al., 2014). The auto-phosphorylation activity of FER has been demonstrated *in vivo* (Escobar-Restrepo et al., 2007), but its kinase activity is not required for the mechanical stress response (Shih et al., 2014). Like THE1, the RALF-FER complex triggers alkalinisation of the apoplast, which is facilitated by the inhibition of the H^+-ATPase (Haruta et al., 2014). Furthermore, *Fusarium oxysporum* releases endogenous RALF in tomato, which induces host alkalinisation and increases its virulence (Masachis et al., 2016).

Immunity-related functions of the RALF-FER pathway have been

Table 2
Summary of cell wall-related receptor-like kinases (RLKs).

Family	Gene	Species	Ligand	Interaction partner	Function	Reference
MLK (MALECTIN-LIKE RECEPTOR KINASES)	*THE*(*THESEUS*)*1*	*Arabidopsis thaliana*	RALF(RAPID ALKALIZATION FACTOR)34		Cell wall integrity sensing	Gonneau et al. (2018); Hématy et al. (2007)
	HERK(*HERKULES*)*1, 2*	*Arabidopsis thaliana*			Cell elongation, pollen tube reception	Galindo-Trigo et al. (2020); Guo et al. (2009)
	FER(*FERONIA*)	*Arabidopsis thaliana*	RALF1, 23, 34		Mechanical force sensing, low Pi response, relocalisation of synergid cell protein, resistance to photo-oxidative stress	Duan et al. (2010); Escobar-Restrepo et al. (2007); Haruta et al. (2014); Shih et al. (2014); Shin et al. (2021); Song et al. (2021); Masachis et al. (2016); Tang et al. (2022)
	ANX(*ANXUR*)*1, 2*	*Arabidopsis thaliana*	RALF4, 19, 34	BUPS1, 2	Pollen tube growth	Miyazaki et al. (2009); Muro et al. (2018)
	BUPS(*BHUDDA'S PAPER SEAL*)*1, 2*	*Arabidopsis thaliana*	RALF4, 19, 34	ANX1, 2	Pollen tube growth	Ge et al., (2017), Feng et al., (2019)
	CVY(*CURVY*)*1*	*Arabidopsis thaliana*			Cell morphogenesis, growth phase transition	Gachomo et al. (2014)
	MDS(*MEDOS*)*14*	*Arabidopsis thaliana*			Affects sensitivity to Ni^{2+}, Cd^{2+}, Zn^{2+}	Richter et al. (2018)
	ANJ(*ANJEA*)	*Arabidopsis thaliana*			Pollen tube reception	Galindo-Trigo et al. (2020)
	ERU(*ERULUS*)	*Arabidopsis thaliana*			Polar growth, maintenance of cytosolic Ca^{2+} concentration, NH_4^+ sensing	Kwon et al. (2018); Schoenaers et al. (2017)
WAK (WALL-ASSOCIATED KINASES)	*WAK1, 2, 4, 5*	*Arabidopsis thaliana*	Oligogalacturonides		Range of immunity response	Brutus et al. (2010); Gadaleta et al. (2019)
	WAKL(*WAK-LIKE*)*10*	*Arabidopsis thaliana*			Resistance to *Pseudomonas syringae* pv. *tomato* DC3000	Bot et al. (2019)
	WAKL22	*Arabidopsis thaliana*			Resistance to three *Fusarium* species	Diener and Ausubel (2005)
	OsWAK1, 14, 91, 92, 112d	*Oryza sativa*		OsRFP(RING FINGER PROTEIN) 1	Resistance to *Magnaporthe oryzae*	Delteil et al. (2016); Li et al. (2009)
	RcWAK4	*Rosa chinensis*			Resistance to *Botrytis cinerea*	Liu et al. (2021)
	GhWAKL	*Gossypium hirsutum*		DnaJ	Resistance to *Verticillium dahliae*	Feng et al. (2021)
	Rlm(*RESISTANCE TO LEPTOSPHAERIA MACULANS*)*9*)	*Brassica napus*	AvrLm5-9		Resistance to *Leptosphaeria maculans*	Larkan et al. (2020)
	LepR(*LEPTOSPHAERIA RESISTANCE*)*3*)	*Brassica napus*	AvrLm1		Resistance to *Leptosphaeria maculans*	Larkan et al. (2013), Larkan et al. (2015)
	ZmWAK1	*Zea mays*			Resistance to *Exserohilum turcicum*	Yang et al. (2019)
	Htn(*HISTATIN*)*1*	*Zea mays*			Resistance to *Exserohilum turcicum*	Hurni et al. (2015)
LRR-RLK (LEUCINE-RICH REPEAT-RECEPTOR-LIKE KINASES)[c]	*RLP*(*RECEPTOR-LIKE PROTEIN*)*42*	*Arabidopsis thaliana*	Polygalacturonase		Resistance to *Botrytis cinerea* and *Aspergillus niger*	Zhang et al. (2014)
	LeEIX(*ETHYLENE-INDUCING XYLANASE*) *1, 2*	*Solanum lycopersicum*	Xylanase		Resistance to *Trichoderma* spp.	Bar et al. (2010)
	FEI1, 2	*Arabidopsis thaliana*		SOS(SALT OVERLY SENSITIVE)5?	Cellulose synthesis regulation in mucilage	Harpaz-Saad et al. (2011); Xu et al. (2008)
	CARD(*CANNOT RESPOND TO DMBQ*)*1*	*Arabidopsis thaliana*	DMBQ (dimethoxybenzoquinone)?		Resistance to *Pseudomonas syringae* pv. *tomato* DC3000 cor^-, host plant sensing by parasitic plants	Laohavisit et al. (2020)
LysM-RLK (LYSIN MOTIF RECEPTOR-LIKE KINASES)	*LYK*(*LYSIN MOTIF RECEPTOR KINASE*)*15*	*Arabidopsis thaliana*	Chitin oligosaccharides	CERK1, BAK(BRI1-ASSOCIATED RECEPTOR KINASE)1, BKK (BAK1-LIKE 1)1	Range of immunity response	Brotman et al. (2012); Cao et al. (2014); Giovannoni et al. (2021); Paparella et al. (2014); Wan et al. (2008)
	LYM(*LYSM DOMAIN GPI-ANCHORED PROTEIN*)*1, 3*	*Arabidopsis thaliana*	Peptide glycan	CERK1?	Resistance to *Pseudomonas syringae* pv. *tomato* DC3000	Willmann et al. (2011)
	MdCERK(*CHITIN ELICITOR RECEPTOR KINASE*)*1, 2*	*Malus domestica*			Resistance to *Botryosphaeria dothidea* and *Glomerella cingulate*	Chen et al. (2020)

(*continued on next page*)

Table 2 (*continued*)

Family	Gene	Species	Ligand	Interaction partner	Function	Reference
	OsCERK1	*Oryza sativa*	MLG(mixed-linkage glucan) oligosaccharides	OsCEBiP	Range of immunity response	Yang et al. (2021)
	OsCEBiP(CHITIN OLIGOSACCHARIDE ELICITOR-BINDING PROTEIN)	*Oryza sativa*	Chitin oligosaccharides	OsCERK1	Range of immunity response	Shimizu et al. (2010)
	OsLYP(LYSIN MOTIF-CONTAINING PROTEIN) 4, 6	*Oryza sativa*	Peptide glycan, Chitin oligosaccharides		Resistance to *Xanthomonas oryzae* and *Magnaporthe oryzae*	Liu et al. (2012)

reported (Song et al., 2021; Tang et al., 2022). In the roots of the *fer* mutant, basal ROS level is reduced due to the loss of the control of NADPH oxidase activity through a small GTPase Rho of plants 2 (ROP2). Consequently, beneficial *Pseudomonas* is enriched in the rhizosphere. This phenomenon is also observed in both the wild-type and RALF23-overexpressed lines with RALF23 (negative regulator of FER) supplementation (Song et al., 2021). Under low-phosphorus conditions, the master transcription factor PHOSPHATE STARVATION RESPONSE 1 (PHR1) is activated via the dissociation of its suppressor (Puga et al., 2014). PHR1 binds to the cis-regulatory element, PHR1-binding sequence (P1BS), and facilitates the expression of its downstream genes (Bustos et al., 2010). Several RALFs (RALF1, 4, 22, 23, 33, and 34) that contain P1BS in their promoters are transcriptionally upregulated by PHR1. After the processing of a 138-aa protein with subtilisin-like serine protease, 51-aa mature cytosolic RALF peptides are released into the apoplast (Srivastava et al., 2009). The RALF-FER complex inhibits the interaction of the flagellin receptor FLAGELLIN-SENSING 2 (FLS2) and EF-Tu receptor (EFR) with their co-receptor BRI1-associated receptor kinase (BAK1) (Stegmann et al., 2017). Owing to the inactivation of PTI, plants allow the colonisation of beneficial endophytic bacteria, which leads to better phosphate uptake (Tang et al., 2022).

3.2. Wall-associated kinase family

There are five members of the WAK family and at least 22 WAK-like genes (*WAKLs*) in *A. thaliana*. These receptors detect OGs in a Ca^{2+}-dependent manner (Decreux and Messiaen, 2005; Kohorn and Kohorn, 2012; X. Wu et al., 2020). Pectin has multiple domains — homogalacturonan (HG), rhamnogalacturonan I (RG-I), rhamnogalacturonan II (RG-II), arabinan, and xylogalacturonan—formed by different combinations of sugars and different linkages (Dehors et al., 2019). These are synthesised in the Golgi apparatus, especially the HG backbone is synthesised in a highly methylesterified form. After being trafficked to the apoplast, apoplastic pectin methylesterase (PME) removes the methyl ester group from the galacturonic acid moiety of HG. De-methylesterified HG dimerises via a Ca^{2+} cross-link, known as the egg-box conformation (Mohnen, 2008) (Fig. 1c). Degradation of HG by polygalacturonase produces de-methylesterified OGs (DP > 9) and such degradants can be the primary substrate of WAKs for the induction of an immune response (Côté and Hahn, 1994; Decreux and Messiaen, 2005). Among the various structural forms of OGs, the OG-dimer has a high affinity for WAK1 (Cabrera et al., 2008), explaining the requirement of Ca^{2+} for sensing.

Transgenic *Arabidopsis* plants expressing the constitutively activated form of WAK2 (*CA-WAK2*) exhibit severe dwarfism. This phenotype is rescued by a mutation in pectin methylesterases (*PME3*). In the *pme3* and *CA-WAK2 pme3* mutants, most of the OGs are monomeric, which is the unbound form for the WAK2 receptor (Kohorn et al., 2014). In contrast, overexpression of a PME in strawberry plants enhances their resistance to *B. cinerea* (Osorio et al., 2008), suggesting a hyperactivation of the WAK pathway. This is in accordance with the studies reporting that *wak* mutants exhibit reduced resistance to fungal pathogens (Table 2) (Bot et al., 2019; Brutus et al., 2010; Delteil et al., 2016; Gadaleta et al., 2019; Hurni et al., 2015; Li et al., 2009; Liu et al., 2021; Yang et al., 2019). These observations highlight the role of pectin degradants as DAMPs through the recognition of WAKs. Interestingly, ROS production is suppressed in the *wak1 wak2 wak3 wak4 wak5* quintuple *Arabidopsis* mutant upon recognition of not only OGs but also flg22 or chitin. In contrast, the expression of *WRKY54* induced by flg22 or chitin was not abolished in the *wak* quintuple mutant (Kohorn et al., 2021). WAKs may functionally interact with RLKs for MAMP-induced activation of NADPH oxidase. WAKs stimulate the mitogen-activated protein kinase 3 (MPK3) and MPK6 cascades (Andreasson and Ellis, 2010; Galletti et al., 2011; Mattei et al., 2016; Moscatiello et al., 2006; Wang et al., 2020). Although *CA-WAK2 mpk6* plants restore dwarfism, the *CA-WAK2 mpk3* plants do not, indicating that only MPK6, and not MPK3, is involved in the same pathway as WAK2 (Kohorn et al., 2012, 2016).

In addition to WAKs, WAKLs function as receptors of OGs (Table 2). The *wakl* mutants show reduced resistance to *F. oxysporum* (Diener and Ausubel, 2005; Feng et al., 2021). In *Brassica napus*, a specific *WAKL* has been isolated as a resistance gene against the fungal pathogen *Leptosphaeria maculans* (Larkan et al., 2013, 2015, 2020).

3.3. Leucine-rich repeat receptor-like kinase family

The LRR-RLK family is comprised of 226 genes in *A. thaliana* and forms an extensive family of RLKs (Ngou et al., 2022). LRRs have evolved to recognise various ligands (Furumizu et al., 2021). For instance, LRR-RLKs FLS2 and EFR in Arabidopsis recognise peptides derived from bacterial conserved proteins to induce PTI and function as a sensor for the enemy's invasion (Boller and Felix, 2009). Receptor-like protein 42 (RLP42) recognises not only peptides but also fungal polygalacturonase (Table 2) (Zhang et al., 2014). Similarly, fungal ethylene-inducing xylanase triggers an immune response by binding to tomato LRR-RLKs LeEix1 and LeEix2 (Bar et al., 2010; Ron and Avni, 2004). The pathways downstream of LRR-RLKs involved in PTI have been well-investigated, and multiple such pathways result in Ca^{2+} influx into the cytosol, ROS production, and callose and lignin deposition (Malinovsky et al., 2014; Segonzac and Zipfel, 2011).

An example of plant cell wall-related LRR-RLKs includes FEI1 and FEI2. The *fei1 fei2* double mutant shows shorter roots, root-tip swelling, and lignin deposition under 4.5% sucrose or 50 mM NaCl conditions, perhaps due to cell wall stress. A cellulose synthesis inhibitor isoxaben induces a similar phenotype in wild-type roots at 10 nM but is effective at 2 nM in the *fei1 fei2* double mutant. Under high sucrose or NaCl conditions, the effect becomes stronger in wild-type plants and hypersensitivity to isoxaben is observed in *prc1*, suggesting that the *fei1 fei2* phenotypes are derived from a defect in cellulose biosynthesis. The incorporation of labelled glucose to cell wall fractions at high sucrose conditions is reduced in *fei1 fei2* mutant root tips (Xu et al., 2008). A similar root-tip phenotype is observed in the case of mutations in genes encoding other cell wall structural proteins, namely, arabinogalactan-protein SALT OVERLY SENSITIVE 5 (SOS5) and arabinogalactan-protein COBRA (COB) (Roudier et al., 2005; Shi et al., 2003). The *fei1 fei2 sos5* triple mutant exhibits the same growth phenotype as the *fei1 fei2* mutant, whereas the *fei1 fei2 cob* triple mutant shows a more severe phenotype, indicating that FEI1, FEI2, and SOS5

are part of the same pathway, whereas COB is involved in a different pathway (Xu et al., 2008). In addition, *fei2* and *sos5* mutants show depleted seed coat mucilage due to cellulose reduction (Harpaz-Saad et al., 2011) but the *fei1 fei2 sos5* triple mutant does not (Basu et al., 2016). A similar phenotype was observed in the *cesa5* mutant, suggesting that these three genes are involved in cellulose synthesis through a linear genetic pathway (Harpaz-Saad et al., 2011). These findings suggest that some LRR-RLKs influence cellulose synthesis by affecting structural proteins in the cell wall. However, potential ligands and downstream pathways of these LRR-RLKs remain elusive.

Parasitic plants form haustoria by recognising host-derived quinones such as 2,6-dimethoxy-1,4-benzoquinone (DMBQ). Recently, DMBQ was shown to increase cellular Ca^{2+}, activate MAP kinases, and promote defence-related gene expression in nonparasitic *Arabidopsis* plants (Laohavisit et al., 2020). Analysis of DMBQ-insensitive *Arabidopsis* mutants revealed an LRR-RLK (subfamily VIII-1) named CANNOT RESPOND TO DMBQ 1 (CARD1), also known as HPCA1, which is the causal gene for impairment of H_2O_2-induced Ca^{2+} signalling (F. Wu et al., 2020). The *card1* mutants exhibit decreased resistance and loss of stomatal closure in response to *P. syringae* pv. *tomato* DC3000 strain that is unable to produce coronatine, and pre-treatment with DMBQ confers resistance against the bacterial pathogen. DMBQ-induced elevation of Ca^{2+} concentration is also observed in the roots of a parasitic plant *Phtheirospermum japonicum* and *CARD1* homologues of *Phtheirospermum japonicum* and *Striga asiatica*, which is also a parasitic plant, complement the loss of Ca^{2+} spiking phenotype in *Arabidopsis card1*. Although the direct binding of quinones to CARD1 has not yet been demonstrated, it plays a crucial role in the perception or signal transduction of quinones derived from the plants themselves or pathogenic microbes. In plants, DMBQ is possibly produced by the oxidation of phenolic compounds such as syringic acid synthesised from monolignol sinapyl alcohol, which is a precursor molecule for the biosynthesis of lignin (Boerjan et al., 2003). Thus, not only cell wall breakdown but also cell wall precursors might be used as a DAMP or signalling molecule.

3.4. Lysin motif receptor-like kinase family

LysM-RLKs were initially known as receptors for chitin oligosaccharides derived from the fungal cell wall (Buendia et al., 2018; Kaku et al., 2006). In *A. thaliana*, five genes have been identified for synthesizing LysM-RLKs (Wan et al., 2012). In addition, ten other genes from the public database TAIR (https://www.arabidopsis.org/index.jsp) were classified as LysM domain-containing proteins (LYP), which lack the kinase domain. Genetic analysis revealed that LysM-containing receptor-like kinase 5 (LYK5) is the primary chitin oligosaccharide receptor. LYK5 forms a complex with the co-receptor CERK1 in a ligand-inducible manner (Cao et al., 2014). Mutations and overexpression of LYKs/LYPs lead to changes in microbial resistance (Table 2) (Brotman et al., 2012; Chen et al., 2020; Giovannoni et al., 2021; Liu et al., 2012; Paparella et al., 2014; Shimizu et al., 2010; Wan et al., 2008; Willmann et al., 2011). In addition to chitin oligosaccharides, structurally similar molecules, such as lipo-chito oligosaccharides known as nodulation factors and fungal peptide glycans, are also recognised by LysM-RLKs (Buist et al., 2008; Limpens et al., 2003).

Recently, OsCERK1 was identified as the receptor of MLG-derived oligosaccharides in rice (Yang et al., 2021). The ligand oligosaccharides (MLG43 and MLG443; please refer to the legend in Table 2 for nomenclature) are produced by GH12 endoglucanases of the fungal pathogen *Magnaporthe oryzae*. The MLG-derived oligosaccharides induce heterodimerisation of OsCERK1 and OsCEBiP, similar to the LYK5-CERK1 interaction (Yang et al., 2021). The OsCERK1-OsCEBiP pathway activates the MPK3/MPK6 cascade and promotes ROS accumulation (Yang et al., 2021). In *Arabidopsis*, structurally diverse MLG-derived oligosaccharides, including MLG34, MLG434, and MLG344, can activate PTI (Rebaque et al., 2021). Furthermore, the MPK3 and MPK6 signals induced by MLG43 treatment are partially reduced in both the *cerk1* mutant and the *lyk4 lyk5* double mutant (Rebaque et al., 2021). This indicates that MLG43 triggers an immune response via multiple LysM-RLKs. Transcriptome analysis revealed that several genes upregulated by MLG43 and chitohexaose treatments are common but do not overlap completely (Rebaque et al., 2021). Thus, MLG43 and chitohexaose are recognised by the common receptors, or downstream pathways of different LysM-RLKs are convergent.

Plant cell walls deploy various enzymes to degrade pathogen cell walls. To enhance pathogen resistance, plants induce the expression of chitinase (Collinge et al., 1993; Gupta et al., 2013; Rawat et al., 2017). Chitinase from a fern (*Pteris ryukyuensis*) contains a LysM domain as the carbohydrate-binding module to enhance its chitinase activity (Ohnuma et al., 2008). However, pathogens mimic LysM domain utilisation. Fungal pathogens secrete LysM-containing effector proteins to escape host recognition of chitin oligomers in the interface between plants and microbes (Kombrink and Thomma, 2013).

3.5. Key open questions

The most important question remaining is which factors reflect cell wall integrity. Considering WAKs, the direct interaction of cell wall components may determine cell wall integrity. However, it is unlikely to happen in crystalline cellulose or polymerised phenolic compounds. How different RALFs have different effects on MLKs is also unclear. Furthermore, how cell wall integrity-dependent signal is separated by other stimuli such as mechanical stress or drought stress remains to be clarified and is crucial in understanding the processing of external stimuli to optimise the growth-defence trade-off.

4. Conclusion

Plant–microbe interactions are closely related to cell wall function. Plants and microbes undergo an arms race, competing for plant cell wall reinforcement and degradation. This can sometimes terminate one geological age; for example, one theory suggests that the end of the Carboniferous Period is marked by the fungal acquisition of the lignin-degrading enzyme peroxidases (Floudas et al., 2012). The fundamental functions of the cell wall covered in this review include physical defence, storage of antimicrobial substances, production of DAMPs, and provision of carbon sources. These functions contribute significantly to microbial resistance or the promotion of plant–microbe symbiosis. In addition, the MLK, WAK, LRR-RLK, and LysM-RLK are cell surface receptors that monitor cell wall status and responses to pathogens. Some of these receptors recognise cell wall-derived products directly or indirectly and help plants adapt to the environment mediated by large-scale transcriptional alterations. In the future, the mechanisms of cell wall reorganisation over time in response to microbes will need to be elucidated. Furthermore, understanding the seamless link between the three elements, namely the cell wall, cell surface receptors, and intracellular response, is important.

CRediT authorship contribution statement

Konan Ishida: Conceptualization, Visualization, Project administration, Writing – original draft, Writing - review & editing, Funding acquisition. **Yoshiteru Noutoshi:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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