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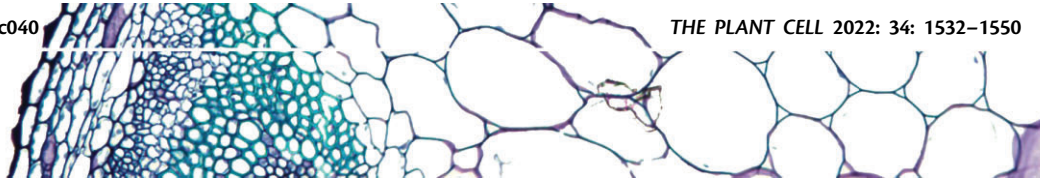
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Plant–microbe interactions in the apoplast: Communication at the plant cell wall

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Abstract

The apoplast is a continuous plant compartment that connects cells between tissues and organs and is one of the first sites of interaction between plants and microbes. The plant cell wall occupies most of the apoplast and is composed of polysaccharides and associated proteins and ions. This dynamic part of the cell constitutes an essential physical barrier and a source of nutrients for the microbe. At the same time, the plant cell wall serves important functions in the interkingdom detection, recognition, and response to other organisms. Thus, both plant and microbe modify the plant cell wall and its environment in versatile ways to benefit from the interaction. We discuss here crucial processes occurring at the plant cell wall during the contact and communication between microbe and plant. Finally, we argue that these local and dynamic changes need to be considered to fully understand plant–microbe interactions.

Introduction

The apoplast is the compartment of the plant between the plasma membrane and the external surface (Sattelmacher, 2001). This space contains the extracellular domains of plasma membrane proteins; cell wall (CW) polysaccharides, proteins, polyphenols, and ions; and water and air. The apoplast has essential roles in plant biology including photosynthesis, transpiration, water and nutrient uptake, and movement of signaling molecules (Figure 1). During plant colonization by all nonviral microbes, the apoplast is the space where the interaction is initially established and where the intruder lives for most, if not all, of its lifetime inside the host. The apoplast is, therefore, a site of intense activity as the interface for plant–microbe communication.

The interaction between microbes and plants ranges from mutualism to parasitism. Pathogens are further categorized, based on their different lifestyles in the host, as biotrophs,

necrotrophs, and hemibiotrophs, though there is some debate about the accuracy of these categories (Rajarammohan, 2021). Whatever the type of interaction, the microbe requires plant CW loosening and degradation in part for nutrition and in part to make space for growth (Kubicek et al., 2014). Some of these plant CW alterations caused by the intruder release CW fragments that are recognized by the host as damage-associated molecular patterns (DAMPs) through plasma membrane pattern recognition receptors (PRRs), which bind the released CW fragments (DeFalco and Zipfel, 2021; Figure 2A). Other PRRs recognize microbe-associated molecular patterns (MAMPs) like chitin oligomers released from fungal CWs by the action of plant apoplastic enzymes. MAMP and DAMP recognition by PRRs triggers plant pattern-triggered immunity (PTI) that results in important apoplast alterations acting as basal defenses, including apoplastic pH changes, Ca²⁺ release from the CW and

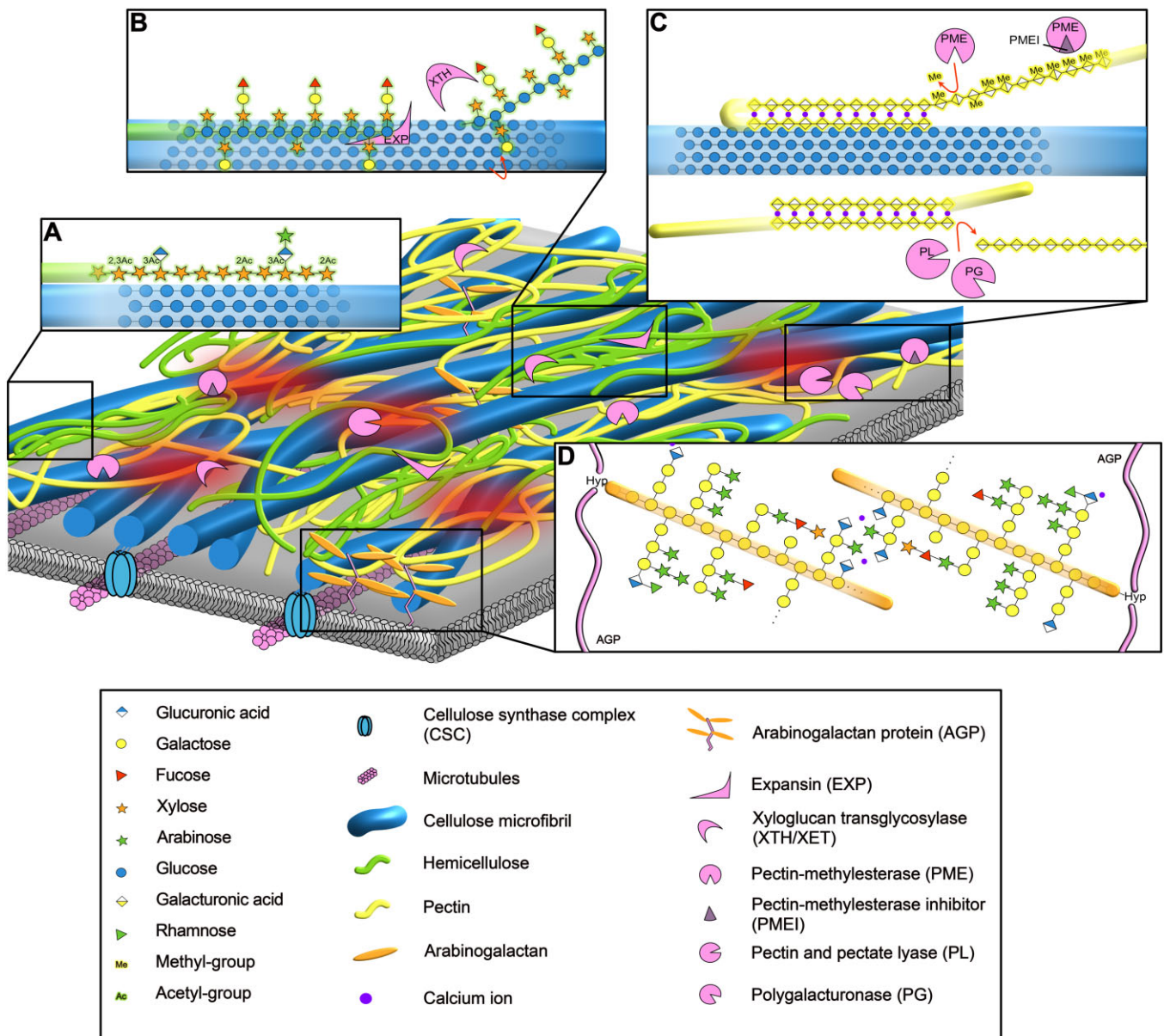


Figure 1 A structural model of the primary CW. Based on atomic force microscopic images of onion epidermal CWs (Cosgrove, 2014): cellulose microfibrils (blue fibrils) are shown embedded in a matrix of pectins (yellow chains), hemicellulose (green chains), arabinogalactan proteins (linear protein backbones are shown in pink with glycosylated hydroxyproline residues in orange), and other plant CW proteins (pink). Limited areas, called biomechanical hotspots (red shadows), are thought to contribute to CW mechanics disproportionately, and likely include sites of contact between cellulose and other molecules. The cellulose microfibrils are synthesized at the plasma membrane by cellulose synthase complexes tracking along microtubules, while the other polysaccharides are synthesized in the Golgi and assembled at the apoplast. A, Xylan is shown binding to the hydrophilic face of cellulose microfibrils via hydrogen bonding, in the same conformation as the glucan chains within cellulose. B, Xyloglucan binds to the hydrophobic face of cellulose based on molecular dynamics simulations, though details of this interaction require further investigation. This interaction is modified by EXP and XTH/XETs. EXPs are nonhydrolytic proteins that cause CW loosening through an unknown mechanism, most probably by separating hemicelluloses and cellulose that are interacting. An XTH has transglycosylated a xyloglucan chain onto a glucan chain of cellulose, forming a new covalent bond, highlighted in red. XTHs can also make xyloglucan–xyloglucan links, or hydrolyse xyloglucan, also (data not shown). C, HG is demethylated by PMEs that are inhibited by PMEIs, regulating the methylation status of the pectin. PME-demethylated regions of HG bind Ca²⁺ (fuchsia circles), forming dimerized egg-box structures, either intra- or intermolecularly. Ca²⁺-bound pectin seems to associate with cellulose, though the details of this interaction are not well understood. The size of demethylated HG is reduced by the cleavage of pectate and PLs and PGs. D, The glucuronic acid residues of arabinogalactan proteins can bind Ca²⁺, and this may enable dimerization.

influx to the cytosol, and production of reactive oxygen species (ROS). The signal transduction and activation of transcriptional responses to the intruder, amplified by various phytohormonal signals, leads to a complex defense reaction. The plant's response is specific to each infection, but includes programmed cell death, the secretion of antimicrobial peptides, pathogenesis-related (PR) proteins, and proteases into the apoplast, and structural modifications of the CW. The microbe must circumvent these apoplastic defenses to survive in the plant. To this end, microbes have evolved different mechanisms to minimize their detection by the host and to block the MAMP/DAMP-triggered defense.

For decades the study of plant responses to molecular pattern perception has received most of the attention in the field of plant resilience to biotic stress. In light of emerging methodologies, including high-resolution microscopy, structure-resolving techniques like solid-state nuclear magnetic resonance (NMR), and complex computational simulations, the architecture and mechanics of the plant CW are regaining their leading role in this area. Thus, in this review, we will avoid discussion of the details of DAMP/MAMP perception, the ensuing intracellular signaling pathways, and some downstream responses, which are well-reviewed elsewhere (Coaker, 2020; Zhou and Zhang, 2020; Bizuneh, 2021; DeFalco and Zipfel, 2021). Instead, we will focus on the plant CW as an active element in the interaction, describing how it is modified by the microbe, and reinforced by the plant, and how this relates with ion movement and changes in extracellular protein activity. This review will largely focus on pathogenic microbes and will not include an exhaustive comparison between mutualists and pathogens.

The plant CW

The plant CW is a heterogeneous mixture, mainly composed of polysaccharides (Burton et al., 2010). The properties of different CWs vary, even surrounding the same cell, due to interactions between CW components. To adapt to changing cellular and organ needs, CW properties can be modified by apoplastic proteins, changing ionic concentrations, and by deposition of new material. Here, we largely describe the composition of eudicot primary CWs, exemplified by the model plant *Arabidopsis thaliana* (Burton et al., 2010). However, the type and structure of polysaccharides, particularly hemicelluloses and pectins, varies phylogenetically, reviewed elsewhere previously (Scheller and Ulvskov, 2010). Within the same plant, CW composition and thickness varies in different tissues, such as the CWs of xylem vessels and tension wood, though this is outside the scope of this review (Burton et al., 2010; Gorshkova et al., 2015).

CW polysaccharides include cellulose, hemicelluloses, and pectins. The cellulose is synthesized at the plasma membrane by cellulose synthase complexes tracking over cortical microtubules (Figure 1), while pectins and hemicelluloses are synthesized in the Golgi (Paredes et al., 2006; Mohnen, 2008; Scheller and Ulvskov, 2010). During cellulose synthesis, the

β -1,4-glucan chains assemble into semi-crystalline microfibrils that form the structural base of the CW, contributing to its strength, tissue structure, and function (Somerville, 2006). Cellulose has been reported to bind hemicelluloses, facilitated by their structurally similar β -1,4-glycosidic bonds (Figure 1, A and B; Dick-Pérez et al., 2011; Simmons et al., 2016; Kang et al., 2019; Terrett et al., 2019). The composition of hemicelluloses is complex and varies in different phylogenetic groups, but hemicelluloses all share backbone β -1,4-glycosidic bonds, though some hemicelluloses have additional backbone glycosidic bonds (Scheller and Ulvskov, 2010). These interactions are thought to influence wall strength, supported by the developmental defects shown by many hemicellulose mutants (Scheller and Ulvskov, 2010; Grantham et al., 2017). The binding of hemicelluloses to cellulose microfibrils may prevent cellulose aggregation and enables cross-linking of microfibrils to each other or to different CW components, like the phenolic polymer lignin (Kang et al., 2019; Terrett et al., 2019). The prevention of cellulose aggregation could be important to maintain the orientation of microfibrils in the different lamellae of the wall, which may contribute to resistance to mechanical forces in different directions (Zhang et al., 2017). Any potential cross-linking between microfibrils or to other components, may prevent slippage of microfibrils, which is thought to contribute to cell expansion (Zhang et al., 2021c). The sites of interaction between cellulose and the hemicellulose xyloglucan, called "biomechanical hotspots" (Park and Cosgrove, 2012a), influence the biomechanical properties of the wall (Park and Cosgrove, 2012b) and are thought to be the target of expansins (Figure 1B), proteins which loosen the CW (Wang et al., 2013). The exact structure of the biomechanical hotspots is not fully understood. Endogenous xyloglucan transglycosylases (XTH/XETs, Figure 1B) also remodel xyloglucan and covalently link it to cellulose and other xyloglucans (Van Sandt et al., 2007; Wang et al., 2016). Similar remodeling activities have been identified for other hemicellulosic polysaccharides in some plants (Franková and Fry, 2021). The action of apoplastic CW-modifying proteins, like expansins and XTH/XETs, is regulated by pH (Sampedro and Cosgrove, 2005; Shi et al., 2015).

In contrast to the structurally similar cellulose and hemicelluloses, the other major polysaccharide component of plant CWs, especially in eudicots, are pectins. Pectins are mainly composed of homogalacturonan (HG), a backbone that can be decorated with different sugar branches, forming different pectic polysaccharides, including rhamnogalacturonan-II (Pellerin et al., 1996; Mohnen, 2008). HGs are secreted in an acetyl- and heavily methyl-esterified form. Once at the apoplast, they are demethylated by CW pectin methylsterases (PMEs) and deacetylated by pectin acetyl esterases (Pauly and Ramírez, 2018; Wu et al., 2018). PME activity is regulated by pectin-methylsterase inhibitors (PMEIs), among other actors, such as the proteases which can cleave the PME's auto-inhibitory domains (Bosch et al., 2005; Wormit and Usadel, 2018). PME activity is heavily

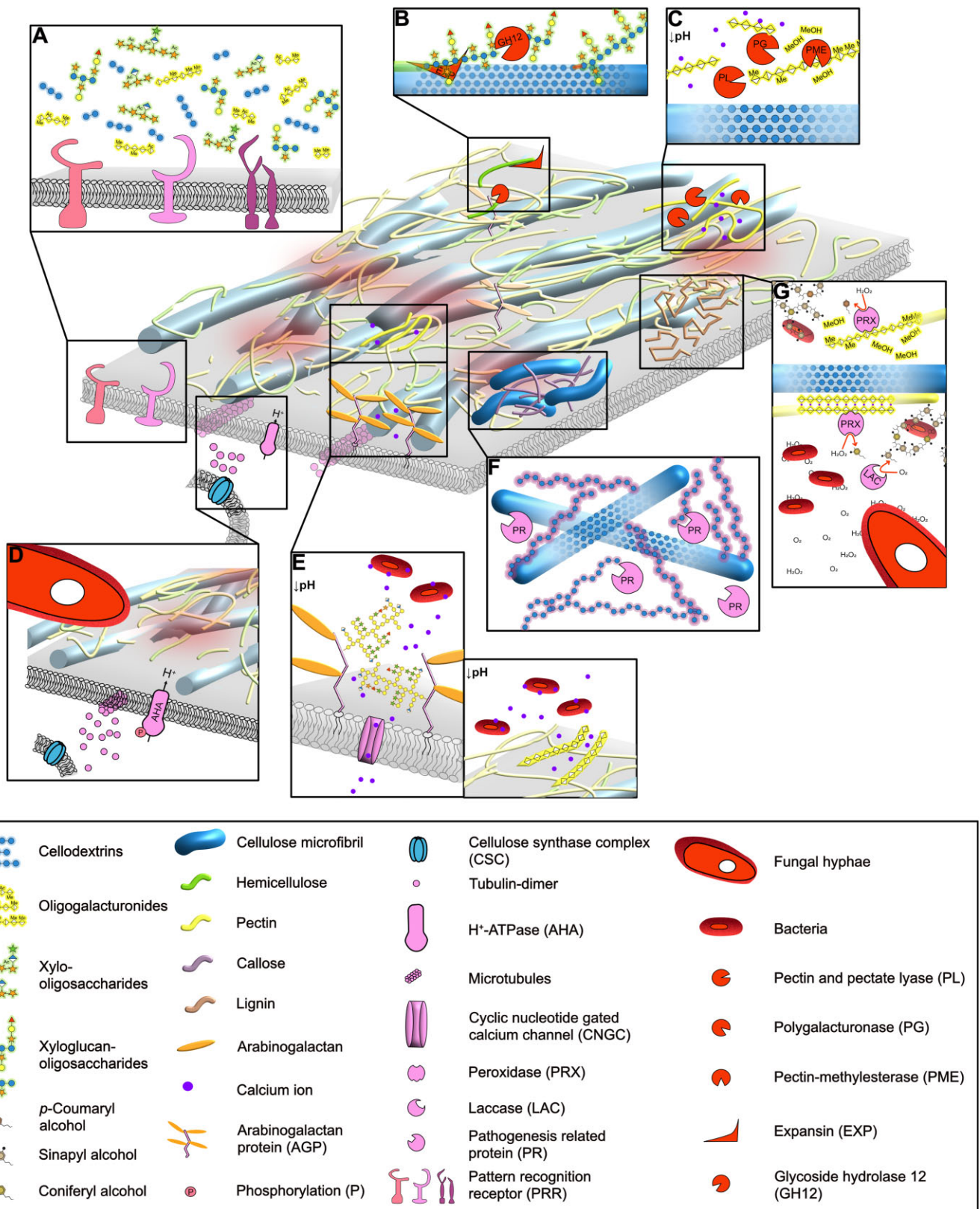


Figure 2 Modification of the plant CW environment upon microbial colonization. The polysaccharides of the primary CW represented in Figure 1 have been loosened and degraded by microbial CWDE and CW-modifying enzymes (red), and the CW ionic environment has been modified (A–E). The plant responds by synthesizing new CW material (F–G). For elements present in Figure 1, refer to its key. A, Plant CW polysaccharides become digested upon microbial enzymatic activities. Some of the resulting oligosaccharide fragments are detected as DAMPs by plasma membrane localized receptors that induce signaling cascades leading to defense reactions. Shown are confirmed DAMPs, such as cellobiose and OGs, and potential DAMPs, such as xyloglucan- and xylan-polysaccharides. B, Microbial xyloglucanases (GH12) and EXP cut the xyloglucan and loosen the

affected by pH, by altering the interaction of PMEIs and PMEs (Sénéchal et al., 2017; Pauly and Ramírez, 2018; Wu et al., 2018), and by changing the processivity of PMEs, which affects the formation of blocks of demethylated residues (Wormit and Usadel, 2018; Hocq et al., 2021). Demethylated regions of HG can bind Ca^{2+} , producing the so-called “egg-box” structures that form gels (Figure 1C; Jarvis and Apperley, 1995; Zdunek et al., 2021). The egg boxes are thought to enable dimerization of different pectin chains, with effects on the mechanical properties of the CW (Zdunek et al., 2021). The Ca^{2+} binding is affected in vitro by acetylation of HG, which might also affect the conformation of the backbone (Renard et al., 1999). Although their backbone has a different shape to that of hemicelluloses and cellulose, HG can also interact with cellulose (Wang et al., 2015; Figure 1C). The extent of this interaction and the rigidity of pectin correlates positively with demethylation (Phyo et al., 2017a). Consistent with this, the egg box HG seems to be closer to cellulose in space (pre-print Temple et al., 2021). The binding of Ca^{2+} , and thereby the conformation of HG, and its interaction with cellulose, is regulated by pH, as protonation of HG at low pHs stops the ionic interaction with Ca^{2+} (Phyo et al., 2019). On the other hand, HG demethylation may loosen the wall, allowing cell expansion. HG demethylation, observed in a band pattern in epidermal CWs (Haas et al., 2020), was predicted to allow expansion of those areas of the CW, leading to the formation of lobes in epidermal cells, though this model is controversial (Cosgrove and Anderson, 2020). The overexpression of polygalacturonases, enzymes that hydrolyse HG, some of which prefer demethylated HG as a substrate, also leads to increased cell expansion and decreased pectin–cellulose interactions, indicating that smaller pectins interact less with cellulose (Phyo et al., 2017b). Thus, pectin demethylation has been reported to both increase and decrease CW stiffness, depending on the experimental system used (Bou Daher et al., 2018; Altartouri et al., 2019; Wang et al., 2020a). In summary, while demethylation may enable cross-linking of HG chains and binding to cellulose, it also makes the HG more vulnerable to digestion by pectate lyases and

hydrolases that prefer charged pectin, which may explain contradictory effects on CW mechanics. Some of these different effects may arise from differences in the pattern of demethylation that is produced, which may make pectin more or less likely to chelate calcium or be cut by lyases and hydrolases (Wormit and Usadel, 2018).

Some pectins and the hemicellulose xylan have been reported to be covalently linked to arabinogalactan proteins (AGPs), though it is unclear how widespread the interaction is (Tan et al., 2013). AGPs sit at the interface between polysaccharide and protein, with a largely unfolded protein backbone that is heavily glycosylated (Figure 1D). The glucuronic acid (GlcA) residues at the end of AGP side-chains can bind to Ca^{2+} (Tryfona et al., 2012; Lampert and Várnai, 2013). Most classical AGPs are attached to the plasma membrane through a glycosylphosphatidylinositol anchor, but some are released into the wall.

CWs also contain the nonpolysaccharide polymers lignin and suberin. Lignin, a hydrophobic phenylpropanoid polymer (Ralph et al., 2004; Tobimatsu and Schuetz, 2019), can cross-link to other CW components (Terrett and Dupree, 2019), including polysaccharides and potentially proteins (Diehl and Brown, 2014; Preis et al., 2018). Pectin monomers are biosynthesized in the cytosol and polymerized in the apoplast by laccase and peroxidase proteins (Tobimatsu and Schuetz, 2019). The polymerization of lignin undergoes tight spatiotemporal control, normally found in select tissues, such as the xylem vessel, fiber cells, and the Casparian band, it can also be produced in response to pathogens (Lee et al., 2013; Barbosa et al., 2019). Suberin is a hydrophobic lipid-based polymer that can form part of the CWs of infected or wounded cells (Philippe et al., 2020).

We now have a reasonably detailed description of some of the major interactions arising between CW polysaccharides (Figure 1). However, a cohesive model of those interactions and their relationship to the emergent properties of the CW, and especially of whole cells or tissues, is still being developed. This is particularly relevant to plant–microbe interactions, where we need to understand how CW properties and structure relate to the development of disease.

Figure 2 (Continued)

xyloglucan–cellulose interactions, respectively. This may reduce cross-linking between microfibrils enabling separation/sliding of the cellulose microfibrils, which could be important for CW loosening. Other hemicelluloses are targeted by CWDEs from different CaZY families, not shown. C, Microbial PMEs remove methyl groups from HG, while pectate and PLs and PGs cut this polymer into smaller fragments. At low pH, or potentially small HG size, the HG loses the ability to bind Ca^{2+} ions, possibly reducing the interaction between HG and cellulose. D, Apoplast acidification through hyperactivation of the plant plasma membrane proton ATPases (AHAs) in response to *F. oxysporum* contact, leads to the depletion of cellulose synthase complexes from the plasma membrane and cortical microtubule depolymerization. This leads to a halt in cellulose synthesis and, may be a general response to pathogen infection, though has, thus far, only been observed in *F. oxysporum*. E, A drop in apoplastic pH leads to a release of Ca^{2+} ions from arabinogalactan proteins and HG, which could contribute importantly to the cytosolic Ca^{2+} peak detected in response to microbes. The liberated Ca^{2+} can be sequestered by bacterial extracellular polysaccharides, affecting the Ca^{2+} dynamics that are important for activating plant immunity. F, In response to some microbial attacks, the plant cell forms a papillae composed of cellulose, callose (purple chains), PRs, and secondary metabolites with antimicrobial properties. The papillae polysaccharides interact in unknown ways, though callose modifies the extensibility of cellulose gels in vitro. G, The plant cell reinforces its CW by lignification (light brown chains) through the activity of PRXs and LACs. PRXs binding to demethylated HG, which might help localize lignin formation at sites of CW damage. Some microbes get trapped in the newly formed lignin-network. Microbes can scavenge ROS through their extracellular polymeric substances. Many of the models shown are speculative, based on research in related contexts (C, D, F, and G) or the known activities of well-described enzymes (E and F).

Microbial modification of plant CW environment

CW polysaccharides

Microbes need to modify the plant CW to properly interact with the host. With this aim, they utilize noncatalytic proteins with important CW loosening effects, such as expansins and expansin-like proteins, looseningins, and swollenins, which were recently reviewed (Georgelis et al., 2015; Narváez-Barragán et al., 2020). Together with these proteins, intruders secrete an array of CW degrading enzymes (CWDEs) classified into families in the carbohydrate active enzyme (CaZY) database, based on their catalytic mechanism and sequence similarity: glycosyl hydrolase (GH), polysaccharide lyase (PL), carbohydrates esterase (CE), and auxiliary activity (AA) including lytic polysaccharide monooxygenase (LPMO; Lombard et al., 2014). The CWDEs remove substitutions, disrupt the interactions between polysaccharides, and break them into smaller fragments (Kubicek et al., 2014), thereby affecting the CW structure, though these effects are poorly understood (models of some potential structural changes are shown in Figure 2). The amount and variety of CWDEs secreted by pathogens correlates somewhat with their lifestyle and host (King et al., 2011; Zhao et al., 2013; Hane et al., 2020). In general, necrotrophs have a greater number of CaZY families in their genome than biotrophs (Kubicek et al., 2014). This is largely because necrotrophs kill host cells rather than using them as a continuous supply of primary metabolites, thus they must degrade and feed on the complex polymers of the CW (Hane et al., 2020). In contrast, many biotrophs and mutualistic microbes have a reduced number of CWDEs and may rely instead on endogenous plant CWDEs (Balestrini and Bonfante, 2014; Rich et al., 2014).

Pathogen CWDE mutants provide strong evidence that the degradation of specific polysaccharides is important for the development of disease. Some pathogens with reduced cellulase arsenals are impaired in virulence. For example, the absence of a single cellulase in the bacteria *Dickeya dadantii* and *Clavibacter michiganensis* decreased the severity of visible disease symptoms (Mäe et al., 1995; HWang et al., 2019). Knockdown of nine predicted cellulases, members of the GH6 and GH7 families, also reduced *Magnaporthe oryzae* virulence, potentially due to an increase in papillae formation or the diminished papillae-degradation capacity of the fungus (Van Vu et al., 2012). However, recent data show that *Fusarium oxysporum* with low cellulose-degradation capacity advance faster through the apoplast and are hypervirulent, but are impaired in saprophytic growth and reproduction (pre-print Gámez-Arjona et al., 2021). Thus, cellulose is an important structural barrier to the establishment of disease for some pathogens, while for others its degradation is mainly important for the saprophytic phase.

Hemicellulose and pectin degradation is also relevant for pathogenesis. Xyloglucan degradation seems to be important for the infection of some filamentous pathogens, as reported for *Phytophthora sojae* and *F. oxysporum* mutants, which

were considerably less virulent when lacking a single GH12 xyloglucanase (Figure 2B; Ma et al., 2015; Zhang et al., 2021b). In contrast, the hydrolytic activity of a *Botrytis cinerea* xyloglucanase is unimportant for its function in planta, though the enzyme induces cell death regardless of its activity (Zhu et al., 2017). Similarly, two *Verticillium dahliae* GH12 xyloglucanases also cause cell death in cotton (*Gossypium hirsutum*), reducing the virulence of the fungus, in the absence of these enzymes, the fungus becomes more virulent (Gui et al., 2017).

Other hemicelluloses are important for disease resistance and there are numerous reports of the importance of pathogen xylanases in the development of disease in Angiosperms. Xylanase mutants in the fungi *V. dahliae* (Wang et al., 2021a) and *M. oryzae* (Wu et al., 2016), the bacteria *Xanthomonas oryzae* (Rajeshwari et al., 2005), and the oomycete *Phytophthora parasitica* (Lai and Liou, 2018) have reductions in virulence. Xylanase activity is not always essential though, even for infection of plants with high xylan content, such as wheat, in *Fusarium graminearum* infection of wheat and soybean, deletion of a regulator of xylanase expression had little effect on symptoms, despite a drop in xylanase activity (Paccanaro et al., 2017). Demethylation of pectin by *F. graminearum* PMEs increases the percentage of symptomatic infected wheat spikelets (Sella et al., 2016). Mutations in a pectate lyase in *V. dahliae* (Yang et al., 2018), a polygalacturonase in *R. solanacearum* (among other examples; Huang and Allen, 1997, 2000; Basaran et al., 2007; Thilini Chethana et al., 2020), and in the newly discovered HG-specific LPMO in *Phytophthora infestans* compromise virulence (Figure 2B; Sabbadin et al., 2021). On the other hand, a *F. graminearum* polygalacturonase mutant has similar virulence in wheat and soybean to the wild-type fungus (Paccanaro et al., 2017). It is clear that some plant CW degradation is important for pathogenesis and mutualism, and most species require degradation of multiple polysaccharides, but the importance of degrading a particular CW component varies in different microbial species, exemplified by examples where CWDE mutants enhance or have no effect on virulence. The importance of CW degradation can be concealed by the degradation of other CW components; for instance, the importance of xylan and pectin degradation for *F. graminearum* is only apparent in a double mutant, which has lost both activities (Paccanaro et al., 2017). The function of various polysaccharides in plant defense are also understudied from the perspective of microbial CWDE mutants, especially that of mannans and arabinogalactans (Villa-Rivera et al., 2021). In some cases, the main difficulty is the challenge of working with certain plants, such as gymnosperms, which have a high mannan content (Scheller and Ulvskov, 2010).

Pathogens require CWDEs for effective establishment of disease; however, the products of the CWDE activity can be identified as DAMPs by the plant, activating immune responses. Oligogalacturonides (OGs) from HG; cello-oligosaccharides from cellulose, mixed-linkage glucan, and

xyloglucan; xylo-oligosaccharides from xylan; gluco-oligosaccharides from β -1,3-glucans similar to callose, as well as xyloglucan-oligosaccharides, have all been reported to activate PTI (Nothnagel et al., 1983; Souza et al., 2017; Claverie et al., 2018; Mélida et al., 2018, 2020; Yang et al., 2021). Oligosaccharides from different polymers induce different immune responses; xyloglucan-oligosaccharides and OGs both reduce disease severity from *B. cinerea* and *Hyaloperonospora arabidopsidis* infection, but only the OGs induced a ROS burst when applied to leaves (Claverie et al., 2018). Cello-oligosaccharides also did not induce a ROS burst in *Arabidopsis*, but did upregulate defense-gene transcription, e.g. WRKY30 (Souza et al., 2017).

Plants can decode oligosaccharides with exquisite precision. For instance, the addition of a galactose and fucose disaccharide to a seven-sugar xyloglucan-derived oligosaccharide enables it to inhibit auxin-induced elongation of etiolated pea (*Pisum sativum*) stems (York et al., 1984). These different oligosaccharides, derived from the same polymer, are potentially the products of different CaZymes. For example, GH30 xylanases produce longer xylo-oligosaccharides than GH11 xylanases, and the glucuronic acid substitution is found in a different position on these two xylo-oligosaccharides (Vrsanská et al., 2007). Plants and pathogens have differences in the CaZyme families in their genomes; for instance many fungi secrete GH12 xyloglucanases (Figure 2B) and many bacteria encode GH30 xylanases, neither of these GH families are present in the poplar (*Populus trichocarpa*) and *Arabidopsis* genomes (Kumar et al., 2019). Thus, plants might distinguish the CW degradation products derived from its own GHs during growth from those released by GHs from an intruder.

DAMP perception by PRRs is one of the most active areas of research in plant immunity and pathology and the topic of frequent reviews (Saijo et al., 2018; Hou et al., 2019; Lu and Tsuda, 2021). However, for most DAMPs, their PRR is unknown, and identifying such proteins will continue to be an important area of research, as we persevere in determining how specific but similar oligosaccharide structures generate different plant responses. This area is particularly complex, as PRRs are required to detect very specific structures, but also highly unrelated structures. For instance, the receptor CERK1, is involved in detecting short mixed linkage glucan (MLG) oligosaccharides and β -1,3-gluco-oligosaccharides, but not long β -1,3-gluco-oligosaccharides (Wanke et al., 2020; Yang et al., 2021). Despite this specificity in distinguishing different size similar structures, the *cerk1* mutant is affected in the detection of a variety of MAMPs, including chitin, lipopolysaccharides (LPS), and peptidoglycan (Desaki et al., 2018). Unexpectedly, CERK1 has been recently shown to be essential for the detection of mixed MLGs in *Arabidopsis*, rice (*Oryza sativa*) and barley (*Hordeum vulgare*), though this is controversial in *Arabidopsis* as different groups have shown opposite results in technically similar experiments (Barghahn et al., 2021; Rebaque et al., 2021; Yang et al., 2021). Interestingly, only monocots, not eudicots,

contain MLGs in their CWs (Little et al., 2018). A structurally similar MLG has been found in oomycete CWs, and thus the capacity to detect MLG-oligosaccharides may be important for eudicots to detect MAMPs from oomycetes rather than DAMPs from their own CWs (Rebaque et al., 2021).

To reduce DAMP-induced PTI, pathogens attempt to control the plant perception of polysaccharide DAMPs. With this aim, some microbes secrete proteins that sequester the DAMPs, blocking their binding to the corresponding PRRs, e.g. the *Ralstonia solanacearum* lectin that binds fucose containing xyloglucans (Kostlánová et al., 2005). Other pathogens have evolved CWDEs whose degradation products are not yet recognized as DAMPs by the plant, like the pectin LPMOs from oomycetes (Sabbadin et al., 2021). LPMOs are known for their contribution to lignocellulose deconstruction, based on their ability to degrade crystalline and recalcitrant polysaccharides. Thus, the oomycetes might have evolved a novel LPMO activity whose products are predicted to attenuate PTI, which could mimic the plant mechanism to mitigate its PTI, by producing oxidized OGs (Benedetti et al., 2018; Pontiggia et al., 2020). The novel role of pectin LPMOs in reducing defense activation is a speculative idea which will need to be investigated further.

In contrast to this idea of the immunity-evading function of oxidative polysaccharide degradation, the products of a cellulose-specific LPMO caused immune responses in *Arabidopsis*, some of which were stronger than to the widely accepted DAMP cellobiose (Zarattini et al., 2021). In addition, some pathogens express AA7 enzymes, which are thought to oxidize oligosaccharides, and may be important for reducing the immunogenic potential of pathogen generated DAMPs (Pontiggia et al., 2020; Haddad Momeni et al., 2021; Wang et al., 2021b). Interestingly, plants utilize AA7 enzymes to reduce the immune-activating capacity of DAMPs (Benedetti et al., 2018; Pontiggia et al., 2020). Future research on the homeostasis of DAMPs, by plant and pathogen, will continue to shape the field in the coming years. The negative effects of DAMP production can outweigh the advantages of structural disruption of the CW. Thus, the elimination of certain microbial CWDEs can increase their pathogenicity, presumably as a side-effect of reduced DAMP production. For instance, two *M. oryzae* mixed-linkage glucanase mutants have increased pathogenicity and, accordingly, the DAMPs produced by active versions of these proteins cause MAP kinase activation in the host (Yang et al., 2021).

Recently, it has been demonstrated that CWDEs can be MAMPs. Some catalytically inactive CWDE mutant proteins induce PTI, indicating that the enzymes themselves, and not just the DAMPs they generate, are recognized by the plant (Ma et al., 2015). Three Brassicaceae species have been shown to recognize three different short peptides derived from fungal, and potentially oomycete, polygalacturonases (Zhang et al., 2021a). Many other plant species did not recognize these polygalacturonases as MAMPs, suggesting that CWDE-derived MAMPs are highly specific to a few interactions. These peptides are buried in the hydrophobic core of

the polygalacturonases, suggesting the presence of plant proteases that digest the CWDEs and release these new MAMPs for recognition. Although the importance of extracellular proteases in plant immunity is well established (Wang et al., 2020b), their potential functions in releasing MAMPs from pathogen CWDEs remain to be fully investigated.

Microbial manipulation of the plant CW generates not only chemical but also mechanical signals (Bacete and Hamann, 2020). While CW loosening and cell separation are necessary to facilitate infection and make space for the growth of microbial cells or feeding structures (e.g. haustoria and arbuscules), the plant cell can perceive changes in the mechanical forces experienced by the plasma membrane and CW, as recently reviewed elsewhere (Codjoe et al., 2022). The mechanosensing can be important for generating an immune response, as mutants in some mechanosensitive proteins, such as the mechanosensitive channel of small conductance-like (MSL) plasma membrane channels, are affected in some downstream CW reinforcement responses and phytohormonal levels (Engelsdorf et al., 2018). The complex detection system evolved by plants integrates all these signals, activating an immune response that includes reinforcement of the CW, which will be discussed later.

Together with microbial mutants in CWDE and CW loosening proteins, plants impaired in the biosynthesis of certain CW components are used to understand CW-based disease resistance, recently reviewed elsewhere (Bacete et al., 2018). This approach has yielded important insights, especially into the interplay between CW structure, CW integrity monitoring, and phytohormone crosstalk. For instance, cellulose and pectin synthesis defects affect jasmonic, ethylene, and salicylic acid responses (among others), while hemicellulose synthesis defects can affect brassinosteroid and strigolactone responses (Bacete et al., 2018; Ramírez and Pauly, 2019; Menna et al., 2021). The responses can be highly specific even in mutants with defects in the same CW component. For example, different lignin synthesis mutants have little overlap in specific defense genes that are activated (Ha et al., 2021). Together with the study of plant CW mutants, the in planta expression of microbial CWDEs has revealed that structural changes of polysaccharides mediated by these enzymes, or the enzymes themselves are perceived by the plant (Swaminathan et al., 2021). For instance, the overexpression of fungal acetylsterases targeting pectin or xylan generates increases in defense gene expression. CW synthesis mutants with defects in pectin or xylan acetylation have resistance phenotypes, suggesting the importance of this polysaccharide structure (Manabe et al., 2011; Escudero et al., 2017). Despite these interesting discoveries, the interpretation of the structural roles of polysaccharides in the CW is complicated by the diverse hormonal and metabolic changes derived from CW modifications in these mutants (Hernández-Blanco et al., 2007; Menna et al., 2021). In addition, alterations in a certain CW component also affect the structure of the entire CW matrix (Huang et al., 2017; Park

and Cosgrove, 2012a). Thus, understanding the whole CW structure is essential to assess the effect of a certain mutation.

Apoplastic pH

Apoplast alkalization is reported as one of the first plant responses to MAMPs/DAMPs, together with a rise in cytosolic Ca^{2+} (Thor and Peiter, 2014; Moroz et al., 2017; Thor et al., 2020). The apoplast pH is mainly regulated by the activity of plasma membrane H^+ -ATPases (AHAs in Arabidopsis; Benschop et al., 2007; Nühse et al., 2007), channels that import H^+ to co-transport other molecules, and anion efflux (Jeworutzki et al., 2010; Lehmann et al., 2021). The exact molecular mechanism of the origin and consequences of this reduction of H^+ in the apoplast is still unknown but is required for plant defense against microbes, as shown in plants grown in acidic media (Yu et al., 2019). Therefore, to counteract the increase in pH, various microbes rely on apoplast acidification to colonize their host. Among them, the pathogenic fungi *Botrytis cinerea* and *Sclerotinia sclerotiorum* secrete citric acid and oxalic acid, respectively, in their hosts' apoplast (Bayram and Braus, 2012; Müller et al., 2018). Beneficial microbes also lower the apoplastic pH to establish their interactions, as reported for *Trichoderma atroviride* (Pelagio-Flores et al., 2017), where fungal and plant AHAs participate in the acidification of the apoplast (López-Coria et al., 2016; Pelagio-Flores et al., 2017).

On the other hand, some microbes benefit from an alkalized apoplast, which they trigger during infection. This is the case of various fruit-infecting microbes like *Colletotrichum spp.* and *Alternaria alternata* (Prusky et al., 2001; Alkan et al., 2013). However, the reality is more complex as the same pathogen can induce either acidification or alkalization during the process of host infection, and apoplast acidification also impacts plant defense (Kesten et al., 2019; Westphal et al., 2019). Those fruit pathogens seem to secrete small pH modulators that increase or decrease the environmental pH depending on the availability of carbon, with acidification occurring under carbon excess (Bi et al., 2016). Similarly, *F. oxysporum* has recently been reported to induce an immediate acidification of the apoplast (Kesten et al., 2019), followed by alkalization over time (Masachis et al., 2016; Kesten et al., 2019).

Fusarium spp. rely on an alkaline environment to infect the plants (Masachis et al., 2016; Wood et al., 2020), which they achieve by secreting small peptides that mimic plant rapid alkalization factors (RALFs; Masachis et al., 2016). Plant RALFs have been shown to bind to the CW-bound leucine-rich repeat extensins (LRXs), potentially influencing the CW properties (Mecchia et al., 2017; Fabrice et al., 2018; Herger et al., 2019). A similar interaction can be envisioned for the pathogen RALF-like which could alter the plant CW properties. The mechanism used by *F. oxysporum* to induce the initial apoplast acidification, how it modulates pH inside the root and how the molecular switch between acidification and alkalization occurs are unknown. In addition, the dramatic and immediate apoplastic pH drop observed upon

F. oxysporum contact impairs the cellulose synthesis machinery through the removal of CSCs from the plasma membrane and disassembly of the cortical microtubules, which influences the plant–fungal interaction (Figure 2D; Kesten et al., 2019; Menna et al., 2021). The changes in the apoplastic pH and their influence on the result of the plant–microbe interaction are time, organ, and even cell layer dependent. The complexity of apoplastic pH changes during plant–microbe interaction needs to be untangled with greater spatiotemporal resolution in different pathosystems. In addition, it will be essential to unravel the contribution of plant and pathogen proteins to these pH changes, at each stage of the interaction.

Apoplastic pH not only influences the development of disease, but it also has relevant effects on the plant CW, altering its physical and chemical properties. As mentioned above in “The plant CW”, the activity of many CW proteins is pH regulated, such as expansins, XTH/XETs, PMEs, and PMEIs (Figure 2C). Thus the drop in pH might enhance CW loosening by expansins, shift the balance between hydrolysis and cross-linking by transglycosylation or increase the processive generation of blocks of demethylated HG residues (Figure 2, A and B; McQueen-Mason et al., 1993; Hocq et al., 2021; Sampedro and Cosgrove, 2005). Also, the apoplastic pH influences the binding of cellulose and pectin (Figure 2C) nonenzymatically (Phyo et al., 2019). Thus, microbial modulation of apoplast pH might alter the activity of both plant and microbial CWDE and CW modifying proteins, and may modify polysaccharide interactions, which could enable a CW restructuring that favors colonization.

CW ions: Ca²⁺ and B

The detection of CW modification results in changes in cell signaling, particularly involving apoplastic ions. Among them, Ca²⁺ ions are some of the first actors in PTI, working as a secondary messenger that regulates the coordination of plant defense or adaptation to the presence of the microbe (Ranty et al., 2016; Zipfel and Oldroyd, 2017). Ca²⁺ is transported from the apoplast to the cytosol through plasma membrane-localized cyclic nucleotide-gated calcium channels at the plasma membrane, opened upon phosphorylation by active PRRs (He et al., 2019; Tian et al., 2019). In addition, Ca²⁺ can enter the cytosol from organelles, especially the vacuole (Hilleary et al., 2020). The participation of other channels and pumps in this Ca²⁺-influx and their contribution to microbe-triggered plant responses remains to be fully investigated. Once Ca²⁺ is inside the cytosol, the plant-specific family of Ca²⁺-dependent protein kinases (CDPKs) function as relays to decode Ca²⁺ signals. CDPKs have different affinities for Ca²⁺ and thereby the downstream signaling distinguishes between various Ca²⁺-stimuli, as reviewed before (Boudsocq and Sheen, 2013; Yip Delormel and Boudsocq, 2019).

Apoplastic Ca²⁺ interacts with plant CW components containing charged uronic acids (GlcA or GalA); i.e. demethylated-HG and AGPs, shaping the structure and rigidity of the CW, as discussed in the “The plant CW”

(Figure 1, C and D). This pH-sensitive pool of Ca²⁺ may be the origin of part of the Ca²⁺-influx from the apoplast and might have important amplificatory effects on microbe-induced Ca²⁺-signals (Figure 2E). Supporting this, the loss of AGP GlcA-residues impairs plant development and alters Ca²⁺-signaling in Arabidopsis in response to H₂O₂ treatment, but the effect of such mutants on Ca²⁺-signaling in the context of plant–microbe interactions has not been investigated (Lopez-Hernandez et al., 2020).

In addition to being a Ca²⁺ store, the Ca²⁺-binding by AGP might enable their pH-regulatable multimerization and/or cross-linking to other polysaccharides (Tryfona et al., 2012; Lampion and Várnai, 2013). If the Ca²⁺–AGP interaction contributes to mechanical stability of the plasma membrane and/or the CW, the pH changes may affect this property. The plasma membrane is an important mechanosensing part of the cell, containing haptosensitive channels, thus pH-induced Ca²⁺-release from CW polysaccharides may be amplified by the opening of these channels (Codjoe et al., 2022). Interestingly, classical AGPs (Schultz et al., 2002), tend to be upregulated in various pathosystems including bacterial and fungal hemibiotrophic vascular pathogens, such as *Fusarium* spp. and *Ralstonia* spp., and a fungal biotroph *Erysiphe necator* (Hu et al., 2008; Menna et al., 2021; Pimentel et al., 2021) but not in a bacterial biotrophic pathogen of brassicas, *Plasmiodiophora brassicae* (Badstöber et al., 2020). It is unknown how much of the internalized Ca²⁺ is soluble or CW bound in the apoplast and if the release of CW-bound Ca²⁺ alone is sufficient to trigger the Ca²⁺-peak and downstream signaling.

Microbes attempt to minimize plant Ca²⁺-influxes to establish their desired interaction with the host (Figure 2E). The bacterial CW component xanthan, a negatively charged polymer, is an efficient Ca²⁺ chelator in vitro (Aslam et al., 2008) that can suppress Arabidopsis immunity (Yun et al., 2006; Aslam et al., 2008). Ca²⁺ and other divalent cations play a substantial role in the attachment of *Rhizobium leguminosarum* to root hairs. The acidic extracellular polymeric substances (EPSs) of these bacteria chelate the apoplastic Ca²⁺, allowing for the gelification of EPSs that act as “glue” that attaches the microbes to the plant surface (Morris et al., 1989; Williams et al., 2008). Although not fully understood, Ca²⁺ plays a role in the attachment of *Agrobacterium tumefaciens* to roots and infection thereof (Matthysse, 2014). In addition to Ca²⁺-binding by microbial polysaccharides, a Ca²⁺-binding protein, rhicadhesin, participates in nonspecific attachment of bacteria to roots (Smit et al., 1992; Denny, 1995). In summary, the dampening of Ca²⁺-signaling seems to serve an important function in suppressing plant PTI in both pathogenic and mutualistic interactions.

Together with Ca²⁺, boron also has an important structural function in plant CWs. In the form of borate esters, boron interconnects RG-II (Ishii et al., 1999; Höfte and Voxeur, 2017) and might be involved in linking glycans of AGPs and extensins with each other (Tan et al., 2018). In

vitro, the stability of borate esters between AGPs/extensins is also regulated by pH. Boron deficiency leads to structural damage and limits plant growth by leading to a “swollen” CW (Wimmer and Eichert, 2013; Novaković et al., 2018). Recently, boron accumulation in the soil was shown to negatively impact microbial diversity, affecting bacteria more than fungi (Vera et al., 2021). Whether plant CW boron plays a direct role in plant–microbe interactions has not been studied so far, but the effects that boron insufficiency and overaccumulation have on the plant and the microbes in soil suggests that this molecule might influence the interactions.

Plant CW reinforcement for defense

CW polysaccharides

Modification and de novo synthesis of certain polysaccharides are part of the plant response to microbe colonization. Callose synthesis is especially important in the formation of papillae in response to biotrophic pathogens (Figure 2F) (Bellincampi et al., 2014; Wang et al., 2021b), while some fungi considered hemibiotrophs do not induce this plant defense, in some hosts (Carella et al., 2019; Menna et al., 2021a). The papillae contain additional components including cellulose, xylan, and antimicrobial peptides and metabolites (Wang et al., 2021a). It is not clear why callose might provide physical reinforcement to the CW, because in vitro mixtures suggest that callose reduces the stiffness of cellulose and increases ductility (Abou-Saleh et al., 2018). This callose-induced alteration in material behavior might be useful in preventing brittle breaks in the CW arising from the high pressure of appressoria. Due to the shape of the β -1,3 backbone of callose, it is unlikely to interact strongly with other CW components such as cellulose. It has also been suggested that callose fills pores in the CW, which might limit penetration of CWDEs or effectors into the CW (Eggert et al., 2014).

In addition, callose may have nonstructural roles. It could have a masking effect on the plant CW, especially against fungal pathogens. Fungal CWs contain β -1,3-glucans, and thus a high concentration of β -1,3-glucans from callose next to fungal hyphae may cause fungi to perceive the plant as “self” and downregulate virulence factor expression and/or secretion. The CW integrity and stress response component domain, reported to bind to polysaccharides including xylan and β -1,3-glucan, is found in fungal cell surface receptors that appear to be important for their development (Verna et al., 1997; Oide et al., 2019). In addition, the fungal CW integrity sensing pathway regulates the expression of genes, including secondary metabolite synthesis, required for fungal disease (Valiante, 2017). Thus, the direct sensing of β -1,3-glucans from callose may affect fungal behavior, though this speculative idea needs to be tested.

Together with the activation of the callose deposition machinery, several other plant polysaccharide synthesis gene families are transcriptionally upregulated in response to infections (Carella et al., 2019; Menna et al., 2021). Notably,

in some cases, the CW components that are affected have not been confirmed yet. For example, a liverwort increased the expression of two enzymes probably involved in the synthesis of xyloglucan and xylan in response to an oomycete (Carella et al., 2019). Enzymes with no predicted function are also upregulated in some infected plants, particularly of the cellulose synthase-like (CSL) Family. Arabidopsis roots infected with *F. oxysporum* increase the expression of a CSLE gene family member (Menna et al., 2021). Related CSLEs are also upregulated in Brassicas with clubroot disease and powdery mildew-infected grapes (Badstöber et al., 2020; Pimentel et al., 2021), while sweet orange (*Citrus sinensis*) upregulated a CSLB and a CSLE in response to a bacterium–virus co-infection (Fu et al., 2017). The expression of another CSL gene, AtCSLG2, increases in Arabidopsis attacked by *R. solanacearum* (Hu et al., 2008). The products of these CSLE, CSLB, and CSLG family members are not known, but other related CSL families have the capacity to synthesize mixed linkage glucans with β -1,3- and β -1,4-glycosidic bonds and mannans (Little et al., 2018). Mixed linkage glucans have not been reported to exist in eudicots, but these CSL subfamilies could synthesize specialized cellulose, mannans, callose, or a hitherto undiscovered polysaccharide, in response to pathogen infection. The overexpression of these enzymes, coupled with NMR, linkage and monosaccharide composition analysis will help us to discover their products and their role in plant defense.

Plant CW modifying proteins are also transcriptionally upregulated in response to pathogen infection, particularly CWDEs. For instance, in the interaction between *F. oxysporum* and Arabidopsis, the plant upregulates some pectate lyases, pectinases, methyl and acetyl esterases, and XTH/XETs (Menna et al., 2021). Cotton upregulates a pectinase during *V. dahliae* infection; a liverwort upregulates a predicted XTH/XET and an expansin when infected by an oomycete, and a plant XTH/XET is upregulated during *R. solanacearum* infection of Arabidopsis (Carella et al., 2019; Menna et al., 2021; Xiong et al., 2021). In principle, these endogenous enzymes have similar activities to the pathogen CWDEs, and thus can act as plant susceptibility factors, as reported for tomato (*Solanum lycopersicum*) polygalacturonases, expansins, and glucanases; an Arabidopsis expansin and an orange XTH (Flors et al., 2007; Cantu et al., 2009; Molina et al., 2021).

Plant CWDEs can also reinforce the host CW or boost the effectiveness of DAMPs, increasing the plant resistance. For example, the upregulation of an XTH in a resistant jute (*Corchorus trilocularis*) variety during infection with *Macrophomina phaseolina* may reinforce the CW by cross-linking (Sharmin et al., 2012). As pectin degradation relies on its degree of methylesterification, PME and PMEs influence the generation of OGs. In addition, PMEs have been reported to demethylate OGs, enhancing their capacity to activate defense responses (Sharmin et al., 2012; Xue et al., 2021). At the same time, the plant can also synthesize protease inhibitors to reduce the activity of its own and

the microbial CWDEs. Among them, PMEIs reduce the demethylation of pectins by PMEs, positively enhancing disease resistance (Lionetti et al., 2017; An et al., 2008; Liu et al., 2018). The contribution of plant CWDEs and their inhibitors to the plant response to microbes will need to be investigated further and more thoroughly linked to their specific biochemical activities, which will themselves likely be dynamic and regulated by pH and other apoplastic conditions (see the “Apoplastic pH” and “CW ions”).

ROS and lignin

Another essential element of plant apoplastic defense against microbes is the production of ROS by the action of plasma membrane-localized NADPH-oxidases, named respiratory burst oxidase homologs (RBOHs), and CW peroxidases (Torres, 2010; Daudi et al., 2012; Survila et al., 2016). ROS include highly reactive molecules including superoxide (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH^\cdot), and singlet oxygen (1O_2) (Apel and Hirt, 2004; Sharma et al., 2012; Janků et al., 2019). ROS act as toxic molecules to fight invading microbes and as signaling molecules to activate plant defense (Castro et al., 2021). In addition, ROS participate in physically blocking the intruder path by CW strengthening via the induction of callose synthesis genes and spatially restricted lignin deposition (Wang et al., 2021c).

Lignin is the product of the oxidative polymerization of three main monolignols, synthesized in the cytosol through the general phenylpropanoid biosynthetic pathway and secreted to the apoplast. Once at the CW, those monolignols are activated by the oxidation systems peroxidase/ H_2O_2 and/or laccase/ O_2 to be assembled into the final lignin polymers (Tobimatsu and Schuetz, 2019; Mnich et al., 2020). Lignification is a common response of plants to microbe infection (Figure 2G), starting with the triggering of the phenylpropanoid synthesis pathway (Ishihara et al., 2012; Galindo-González and Deyholos, 2016; Novo et al., 2017; Ferreira et al., 2017; Sabella et al., 2018). The monolignol polymerization can occur in highly restricted areas around pathogen cells, as shown in the Arabidopsis–*Pseudomonas syringae* pv *tomato* interaction, where localized lignification surrounding the bacteria reduced their movement (Lee et al., 2019). Consistently, more virulent bacteria strains possess effectors to suppress a strong ROS burst and lignification (Lee et al., 2019).

The highly contained formation of lignin seems to be a consequence of the precise localization and action of specific proteins. This event is well studied during the formation of the Casparian strip, where CASP proteins form complexes with peroxidases and RBOHs in small domains of the plasma membrane (Barbosa et al., 2019). The co-localization of peroxidases, and the RBOHs that produce their peroxide fuel, allows the formation of the thin strip of lignin (Barbosa et al., 2019; Rojas-Murcia et al., 2020). Pathogen-induced lignification may be analogous to Casparian strip formation. Indeed, the deposition of lignin around pathogenic bacteria in Arabidopsis depends on two CASP-like (CASPL) proteins

that localize in the plant plasma membrane surrounding the newly formed lignin (Lee et al., 2019). Binding to CASPLs is not the only mechanism for the specific localization of peroxidases and laccases within the CW (Hoffmann et al., 2020). Some peroxidases have been shown to bind to demethylated HG, and this can restrict them to specific regions of the CW (Figure 2G; Francoz et al., 2019; Shah et al., 2004). A similar mechanism can be envisioned during microbe-induced HG-demethylation, leading to the localization of certain peroxidases required for lignin formation to isolate the microbe and/or to protect the pectin regions that are more vulnerable to degradation by the intruder. This and other hypotheses remain to be tested, like the capacity of peroxidases to bind to other polysaccharide epitopes, or the possibility of laccases to have a similar polysaccharide-binding capacity.

Peroxidases also contribute to plant defense by cross-linking structural proteins in the CW, such as extensins and AGPs (Almagro et al., 2009; Mishler-Elmore et al., 2021), whose role in plant–microbe interactions was recently reviewed (Castilleux et al., 2018, 2021; Mishler-Elmore et al., 2021). In addition, other peroxidases synthesize ROS from the RBOH-derived H_2O_2 (Almagro et al., 2009; Tobimatsu and Schuetz, 2019). Thus, regulating peroxidase activity may be a mechanism for pathogens to reduce CW reinforcement and other plant defenses. This can be achieved by controlling apoplastic pH, as pH influences the activity of peroxidases and laccases (Pedreño et al., 1989; Nunes and Kunamneni, 2018). Moreover, the influence of pH on RBOHs, which provide the required ROS to peroxidases and laccases, is predicted but not fully understood. In addition, the influence of high proton concentration on the activity of ROS molecules remains to be shown.

Peroxidase activity can be further controlled by calcium ions; as it has been proposed that a drop in apoplastic Ca^{2+} may act as an off-switch for peroxidase activity (Plieth, 2012). Thus, when Ca^{2+} is rapidly internalized by the plant cells upon microbe attack, peroxidase activity could be limited (Hemetsberger et al., 2012). Some laccases include predicted calmodulin domains (Zhang et al., 2019), indicating that they may also be regulated by Ca^{2+} , though the exact role of these domains remains unknown. Lignin deposition and other ROS-dependent plant immune responses can also be minimized by the microbe through secretion of proteins that interfere with the host ROS-generating system, like the effector PEP1 of *Ustilago maydis* (Hemetsberger et al., 2012; Navarrete et al., 2021). Other microbes have evolved mechanisms to sequester ROS, such as the EPS of the bacteria *Azorhizobium caulinodans*, that sequesters H_2O_2 allowing the formation of root nodules in *Sesbiana rostrata* (Figure 2G; D’Haeze et al., 2004). The opportunistic fungal pathogen *Alternaria tenuissima* produces an EPS with a high potential for scavenging hydroxyl radicals and superoxide anions in vitro (Wang et al., 2019), though the in planta function remains to be tested. Recently, fungal endophytes and pathogens were shown to exploit a plant GH to release

a conserved oligosaccharide from their EPS, that acts as a ROS scavenger and subvert plant immune responses (Chandrasekar et al., 2021). In addition, acidification of the apoplast or the rhizosphere by microbes decreases the ROS generation potential of the plant (Yu et al., 2019).

Suberin

Together with lignin, suberin forms another layer of nonpolysaccharide protection against pathogen entrance into individual plant cells. It constitutes a hydrophobic barrier that naturally occurs in specialized tissues, such as seed coats, leaf epidermal cells, and periderm, or is specifically formed after wounding and microbe attack (Ranathunge et al., 2008; Philippe et al., 2020; Singh et al., 2021). Suberin monomers seem to be secreted through vesicular-tubular membrane structures that fuse to the plasma membrane and release their cargo (De Bellis et al., 2021). Once outside the cell, suberin becomes polymerized and forms a lamellar sheet between the plasma membrane and the CW (Philippe et al., 2020).

Suberization seems to be induced mainly by vascular pathogens to effectively limit their spread between vascular bundles and keep them contained in the already infected tissue (Robb et al., 1991; Kashyap et al., 2021b). In the interaction between *Vitis vinifera* and the vascular wilt pathogen *Phaeoaniella chlamydospora*, suberin deposition was shown to be active as a limiting factor for pathogen spread between xylem vessels (Pouzoulet et al., 2017). Similarly, the deposition of a ligno-suberin coating and tyramine-derived hydroxycinnamic acid amides have recently been reported to be required for tomato resistance to *R. solanacearum* (Kashyap et al., 2021a). Suberin deposition upon vascular pathogen infection is positively regulated by the transcription factor MYB41, whose promoter is specifically induced during stress conditions and its overexpression leads to ectopic suberization of various plant species and tissue types (Kosma et al., 2014; Vishwanath et al., 2015).

The regulation of suberin deposition in the context of plant–microbe interactions probably requires additional transcription regulators. The recently described MYBs that, together with MYB41, are sufficient to promote endodermal suberin deposition are interesting candidates to induce the same process upon biotic stress, but this role has to be confirmed (Shukla et al., 2021). Also, it will be important to understand suberin assembly in the wall, which is likely to occur through transesterification by enzymes similar to cutin synthases (Philippe et al., 2020). Moreover, the degradation of suberin by microbes is not well understood during plant colonization, and will also need to be investigated further, though various suberinases have been identified (Fernando et al., 1984).

Summary and perspectives

The plant CW is a dynamic, interactive part of the plant cell, whose properties change in response to the action of CW modifying enzymes, alterations in ionic composition, and the synthesis of new material. These changes are

particularly active in the context of plant–microbe interactions, where both organisms modify the plant CW and its environment and, at different time points, the same organism may reverse earlier changes.

Thus far, research in the field of plant CW role in host–microbe interaction has largely focused on the functional importance of individual CWDEs in causing disease, the role of CWD products as DAMPs, and the synthesis of new CW material as a defense response. These remain key areas of research; for instance, new CW-derived DAMPs have been identified whose receptor is unknown, many plasma membrane receptors have been reported to affect disease resistance but their ligands and/or exact role in plant defense have not been characterized. Proteomic technologies may be useful in this area, such as spatial proteomics and phosphoproteomics, to identify receptors and signaling components which respond to disease or to specific signals. Also, the coordination of plant response to its own CW-derived DAMPs and microbial-generated ones is an essential topic to be further explored. The dynamic and subcellular nature of plant CW-related changes, polysaccharide and ionic, mean that it is necessary to monitor interactions with higher temporal and spatial resolution, such as in different cell layers and cell areas. This should be possible by adapting to various pathosystems, the high-resolution microscopy, and new probes currently available or under-development in the plant biology field. We will also need to investigate the structural and mechanical changes in the plant CW during plant growth and in response to microbe colonization using cryo-electron microscopy, solid-state NMR and atomic force microscopy, among other techniques. Integrating such knowledge with computational simulations will enable us to analyze how plant CW structure and composition relates to mechanical properties. At the same time, it will be important to biochemically characterize individual members of large gene families (e.g. expansins, XTHs, and CSLs) to understand their functions in specific plant–microbe interactions. As an essential component of the plant cell with vital roles in plant–microbe interactions, it is extremely important to continue investigating how CW structure and composition relates to its properties, and how these are modified in response to environmental stress and coordinated with plant development.

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