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The state of cell wall pectin monitored by wall associated kinases: A model

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The Wall Associated Kinases (WAKs) bind to both cross-linked polymers of pectin in the plant cell wall, but have a higher affinity for smaller fragmented pectins that are generated upon pathogen attack or wounding. WAKs are required for cell expansion during normal seedling development and this involves pectin binding and a signal transduction pathway involving MPK3 and invertase induction. Alternatively WAKs bind pathogen generated pectin fragments to activate a distinct MPK6 dependent stress response. Evidence is provided for a model for how newly generated pectin fragments compete for longer pectins to alter the WAK dependent responses.

Keywords: Arabidopsis, cell wall, plant defense, receptors, signaling

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The cell walls of angiosperms are composed of a complex arrangement of cellulose, hemicellulose and pectin. The pectins can be selectively and locally modified to be cross-linked into a structural network that can have dramatic effects on cell enlargement,[1-3] but numerous pathogens and mechanical disruptions fragment this pectin network, leading often to a plant stress response.[4-6] The Wall Associated Kinases (WAKs) are receptor kinases that bind pectin in the cell wall, and span the plasma membrane to place a serine/threonine kinase in the cytoplasm.[7-16] A number of studies have shown that WAKs are required for cell expansion during development, but also mediate a pectin fragment induced stress response.[12,16,17] How these receptors can be involved in 2 distinct responses is not well understood, but the key perhaps lies in that WAKs bind to long polymers of pectin cross-linked in the cell wall of unchallenged plants, but also to pectin fragments or oligogalacturonides (OGs) generated by wounding or pathogens as they invade.[12,18] What has been missing is a model for how WAKs might distinguish the 2 pectin states so as to trigger expansion versus a stress response. We proposed a model where newly generated OGs compete with native pectin for WAKs, and activate alternate signal transduction pathways.[13]

Background

Plant cell walls arise through a complex, developmentally regulated coordination of synthesis, turnover, and interactions between protein and carbohydrates.[12] Screens for mutants in developmental processes have not surprisingly then revealed numerous alleles of cell wall biosynthesis genes, and conversely mutations in cell wall function have identified alleles in genes normally associated with a variety of metabolic and developmental pathways.[21] These genes include receptor kinases such as *THE1*,*FER, HERK*, ANX, and *RLP44* and have been termed cell wall sensors.[19-26] Of the "wall sensors" only WAKs, also receptor kinases, are known to bind to a cell wall component, pectin.

Pectin is first made as methyl esterified α1–4 D-galacturonic acid in the golgi, secreted,[1,3,27] and then modified and cross-linked in the extracellular space. Localized activity of Pectin Methylesterases (PME) expose an oxygen to bind calcium that mediates a crosslinking. It is thought that regulation of the location and extent of PME activity can influence wall structure and directionality of loosening thereby influencing cell growth.[24] Because WAKs bind to pectin they long

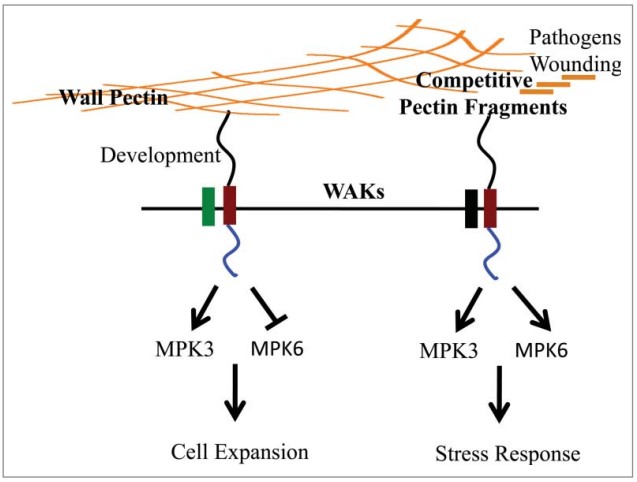

Figure 1. (**A**) Model for Pectin and OG (pectin fragment) Activation of 2 Responses through WAK. Orange lines represent cell wall pectin, cross-linked or fragmented by pathogens or wounding. OGs outcompete longer polymers for activation of a WAK (red boxes) dependent stress response. WAKs are predicted to associate with co-receptors (green or black) to mediate different responses. In the absence of pathogen, WAKs monitor cell wall pectin and are required for cell expansion. See text for details.

have been candidates for the pectin and thus wall sensors for both expansion and pathogen disturbances. WAKs are bound to native pectins in plants[10,12,13,16] but *in vitro* binding assays demonstrate that WAKs have a higher binding of de-esterified over esterified pectins,[9,28,29] and have a preference (competition assays) for short OGs of degree of polymerization.[9-15] Pathogens tend to target de-esterified pectins. During seedling growth, WAKs are required for cell expansion and have been shown to be involved in the pectin activation of MPK3 and a vacuolar invertase that can increase turgor driven expansion.[9,10,12] But WAKs are also required for a response to pathogen, are necessary for the OG stress response[14] and bind and trigger a response to OGs in a transient assay.[17] This stress response appears to have a distinct signaling pathway and includes a ROS burst, MPK6 activity, and the EDS1 and PAD4 dependent activation of numerous genes, including the *ca*. 1000 fold induction of a downstream target gene *FADlox* which serves as a robust indicator.[13,14]

A Model

We recently showed that a dominant *WAK2* allele *WAK2*^{cTAP} whose encoded protein requires a functional pectin binding domain and an active kinase induces a constitutive stress response.[13,14] But importantly, this *WAK* allele is suppressed by a null allele of a pectin methyl esterase, *pme3*.[13] This provides genetic evidence that WAKs are sensing the de-esterified form of pectin, consistent with the higher affinity *in vitro* of WAKs for de-esterified over esterified pectin. But we also found that the *pme3/pme3* mutant plant is more responsive to OGs than WT plants. One explanation is that since WAK is bound less tightly to esterified pectin in the mutant, then more is available to receive incoming OGs. Collectively the data are consistent with a model (**Fig. 1**) where OGs are competing with native pectin for WAKs, and this provides a mechanism for WAKs to distinguish pectins, and activate alternate pathways.

Future Questions

The question now remains as to how the 2 different types of pectins can trigger one receptor to activate different paths. It is possible that part of the mechanism lies in the heterogeneity of the WAK family, as there are 5 WAKs tightly clustered in a 30 KB Arabidopsis locus.[30] But it is also possible that WAKs associate with different co-receptors to distinguish the pectin, and these receptor complexes have different downstream partners. Analysis of the components of the 2 pathways should help to answer this next question.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

References

1. Somerville C, Bauer S, Brininstool G, Facette M, Hamann T, Milne J, Osborne E, Paredez A, Persson S, Raab T, et al. Toward a systems approach to understanding plant cell walls. Science 2004; 306:2206-11; PMID:15618507; http://dx.doi.org/10.1126/science.1102765
2. Kohorn BD. Plasma membrane-cell wall contacts. Plant Physiol 2009; 124:31-8; http://dx.doi.org/10.1104/pp.124.1.31
3. Caffall KH, Mohnen D. The structure, function, and biosynthesis of plant cell wall pectic polysaccharides. Carbohydr Res 2009; 344:1879-900; PMID:19616198; http://dx.doi.org/10.1016/j.carres.2009.05.021
4. Mohnen, D. Pectin structure and biosynthesis. Curr Opin Plant Biol 2008 11, 266-277; PMID:18486536; http://dx.doi.org/10.1016/j.pbi.2008.03.006
5. Wolf S, Mouille G, Pelloux J. Homogalacturonan methyl-esterification and plant development. Mol Plant 2009; 2:851-60; PMID:19825662; http://dx.doi.org/10.1093/mp/ssp066
6. Peaucelle A, Braybrook S, Höfte H. Cell wall mechanics and growth control in plants: the role of pectins revisited. Front Plant Sci 2012; 3:121; PMID:22685449; http://dx.doi.org/10.3389/fpls.2012.00121
7. He ZH, Fujiki M, Kohorn BD. A cell wall-associated, receptor-like protein kinase. J Biol Chem 1996; 271:19789-93; PMID:8702686; http://dx.doi.org/10.1074/jbc.271.33.19789
8. Kohorn BD. WAKs; cell wall associated kinases. Curr Opin Cell Biol 2001; 13:529-33; PMID:11544019; http://dx.doi.org/10.1016/S0955-0674(00)00247-7
9. Kohorn BD, Johansen S, Shishido A, Todorova T, Martinez R, Defeo E, Obregon P. Pectin activation of MAP kinase and gene expression is WAK2 dependent. Plant J 2009; 60:974-82; PMID:19737363; http://dx.doi.org/10.1111/j.1365-313X.2009.04016.x
10. Kohorn BD, Kobayashi M, Johansen S, Friedman HP, Fischer A, Byers N. Wall-associated kinase 1 (WAK1) is crosslinked in endomembranes, and transport to the cell surface requires correct cell-wall synthesis. J Cell Sci 2006; 119:2282-90; PMID:16723734; http://dx.doi.org/10.1242/jcs.02968
11. Kohorn BD, Kobayashi M, Johansen S, Riese J, Huang LF, Koch K, Fu S, Dotson A, Byers N. An Arabidopsis cell wall-associated kinase required for invertase activity and cell growth. Plant J 2006; 46:307-16; PMID:16623892; http://dx.doi.org/10.1111/j.1365-313X.2006.02695.x
12. Kohorn BD, Kohorn SL. The cell wall-associated kinases, WAKs, as pectin receptors. Front Plant Sci 2012; 3:88; PMID:22639672; http://dx.doi.org/10.3389/fpls.2012.00088
13. Kohorn BD, Kohorn SL, Saba NJ, Martinez VM. Requirement for pectin methyl esterase and preference for fragmented over native pectins for wall-associated kinase-activated, EDS1/PAD4-dependent stress response in Arabidopsis. J Biol Chem 2014; 289, 18978-86; http://dx.doi.org/10.1074/jbc.M114.567545
14. Kohorn BD, Kohorn SL, Todorova T, Baptiste G, Stansky K, McCullough M. A dominant allele of

Arabidopsis pectin-binding wall-associated kinase induces a stress response suppressed by MPK6 but not MPK3 mutations. Mol Plant 2012; 5:841-51; PMID:22155845; http://dx.doi.org/10.1093/mp/ssr096
15. Kohorn BD, Lane S, Smith TA. An Arabidopsis serine/threonine kinase homologue with an epidermal growth factor repeat selected in yeast for its specificity for a thylakoid membrane protein. Proc Natl Acad Sci USA 1992; 89:10989-92; PMID:1438303; http://dx.doi.org/10.1073/pnas.89.22.10989
16. Wagner TA, Kohorn BD. Wall-associated kinases are expressed throughout plant development and are required for cell expansion. Plant Cell 2001; 13, 303-18; PMID:11226187; http://dx.doi.org/10.1105/tpc.13.2.303
17. Brutus, A, Sicilia F, Macone A, Cervone F, De Lorenzo G. A domain swap approach reveals a role of the plant wall-associated kinase 1 (WAK1) as a receptor of oligogalacturonides Proc Natl Acad Sci USA 2010; 107:9452-7; PMID:20439716; http://dx.doi.org/10.1073/pnas.1000675107
18. Ferrari S, Savatin DV, Sicilia F, Gramegna G, Cervone F, Lorenzo GD. Oligogalacturonides: plant damage-associated molecular patterns and regulators of growth and development. Front Plant Sci 2013; 4:49; PMID:23493833; http://dx.doi.org/10.3389/fpls.2013.00049
19. Hematy K, Höfte H. Novel receptor kinases involved in growth regulation. Curr Opin Plant Biol 2008; 11:321-8; PMID:18395489; http://dx.doi.org/10.1016/j.pbi.2008.02.008
20. Hematy K, Sado PE, Van Tuinen A, Rochange S, Desnos T, Balzergue S, Pelletier S, Renou JP, Höfte H. A receptor-like kinase mediates the response of Arabidopsis cells to the inhibition of cellulose synthesis. Curr Biol 2007; 17:922-31; PMID:17540573; http://dx.doi.org/10.1016/j.cub.2007.05.018
21. Wolf S, Mravec J, Greiner S, Mouille G, Höfte H. Plant cell wall homeostasis is mediated by brassinosteroid feedback signaling. Curr Biol 2012; 22:1732-7; PMID:22885061; http://dx.doi.org/10.1016/j.cub.2012.07.036
22. Guo H, Ye H, Li L, Yin Y. A family of receptor-like kinases are regulated by BES1 and involved in plant growth in Arabidopsis thaliana. Plant Signal Behav 2009; 4:784-6; PMID:19820315; http://dx.doi.org/10.4161/psb.4.8.9231
23. Miyazaki S, Murata T, Sakurai-Ozato N, Kubo M, Demura T, Fukuda H, Hasebe M. ANXUR1 and 2, sister genes to FERONIA/SIRENE, are male factors for coordinated fertilization. Curr Biol 2009; 19:1327-31; PMID:19646876; http://dx.doi.org/10.1016/j.cub.2009.06.064
24. Wolf S, Höfte H. Growth control: a saga of cell walls, ROS, and peptide receptors. Plant Cell 2014; 26:1848-56; PMID:24808052; http://dx.doi.org/10.1105/tpc.114.125518
25. Wolf S, van der Does D, Ladwig F, Sticht C, Kolbeck A, Schurholz AK, Augustin S, Keinath N, Rausch T, Greiner S, et al. A receptor-like protein mediates the response to pectin modification by activating brassinosteroid signaling. Proc Natl Acad Sci USA 2014; 111:15261-6; PMID:25288746; http://dx.doi.org/10.1073/pnas.1322979111
26. Haruta M, Sabat G, Stecker K, Minkoff BB, Sussman MR. A peptide hormone and its receptor protein kinase regulate plant cell expansion. Science 2014; 343:408-11; PMID:24458638; http://dx.doi.org/10.1126/science.1244454
27. Harholt J, Suttangkakul A, Vibe Scheller H. Biosynthesis of pectin. Plant Physiol 2010; 153:384-95; PMID:20427466; http://dx.doi.org/10.1104/pp.110.156588
28. Decreux A, Messiaen J. Wall-associated kinase WAK1 interacts with cell wall pectins in a calcium-induced conformation. Plant Cell Physiol 2005; 46:268-78; PMID:15769808; http://dx.doi.org/10.1093/pcp/pci026
29. Decreux A, Thomas A, Spies B, Brasseur R, Van Cutsem P, Messiaen J. In vitro characterization of the homogalacturonan-binding domain of the wall-associated kinase WAK1 using site-directed mutagenesis. Phytochemistry 2006; 67:1068-79; PMID:16631829; http://dx.doi.org/10.1016/j.phytochem.2006.03.009
30. He ZH, Cheeseman I, He D, Kohorn BD. A cluster of five cell wall-associated receptor kinase genes, Wak1-5, are expressed in specific organs of Arabidopsis. Plant Mol Biol 1999; 39:1189-96; PMID:10380805; http://dx.doi.org/10.1023/A:1006197318246
31. Kohorn BD, Kohorn SL, Saba NJ, Meco Martinez V. Requirement for pectin methyl esterase and preference for fragmented over native pectins for Wall Associated Kinase Activated, EDS1/PAD4 dependent stress response in Arabidopsis. J Biol Chem 2014; 289:18978-86; PMID:24855660; http://dx.doi.org/10.1074/jbc.M114.567545