

## Arabinogalactan proteins – Multifunctional glycoproteins of the plant cell wall

Yingxuan Ma<sup>a</sup>, Kim Johnson<sup>b,\*</sup>

<sup>a</sup> Key Laboratory of Forest Genetics & Biotechnology of Ministry of Education, Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing, Jiangsu 210037, China

<sup>b</sup> La Trobe Institute for Sustainable Agriculture & Food, Department of Animal, Plant and Soil Sciences, AgriBio Building, La Trobe University, Bundoora, VIC 3086, Australia

### ARTICLE INFO

#### Keywords:

Arabinogalactan-protein  
Plant cell wall  
Glycoprotein  
Plant development  
Signalling

### ABSTRACT

Arabinogalactan-proteins (AGPs) are cell wall glycoproteins that make up a relatively small component of the extracellular matrix of plants yet have significant influence on wall mechanics and signalling. Present in walls of algae, bryophytes and angiosperms, AGPs have a wide range of functional roles, from signalling, cell expansion and division, embryogenesis, responses to abiotic and biotic stress, plant growth and development. AGPs interact with and influence wall matrix components and plasma membrane proteins to regulate developmental pathways and growth responses, yet the exact mechanisms remain elusive. Comprising a large gene family that is highly diverse, from minimally to highly glycosylated members, varying in their glycan heterogeneity, can be plasma membrane bound or secreted into the extracellular matrix, have members that are highly tissue specific to those with constitutive expression; all these factors have made it extremely challenging to categorise AGPs many qualities and roles. Here we attempt to define some key features of AGPs and their biological functions.

### Introduction

Arabinogalactan-proteins (AGPs) are glycoproteins predicted to be present in the walls of all plant and algal species and have intrigued and challenged cell wall and developmental biologists for decades. In addition to their roles regulating many aspects of plant development, AGPs have industrial and health applications including as gums in food products and pre-biotics in the human gut, respectively. While the definition of AGPs has come to cover a broad range of glycosylated protein molecules, they share the feature of large type II arabinogalactan (AG) glycan chains O-linked to Hydroxyproline (Hyp) in the protein backbone (Fig. 1). AGPs include a N-terminal signal sequence directing them into the endoplasmic reticulum (ER) for post-translational processing and many also include a signal at the C-terminus for addition of a glycosylphosphatidyl inositol (GPI) anchor. GPI-anchors can associate with specific membrane domains proposed to influence trafficking of AGPs through the ER and Golgi and delivery to the cell surface to attach the protein to the outer leaflet of the plasma membrane (PM) facing the wall (Fig. 1) (Muniz and Riezman, 2016). Sequences encoding AGPs have regions with an amino acid bias for proline (P), alanine (A), serine

(S) and threonine (T), or 'PAST' that occur in a clustered, non-contiguous manner, for example SPATTP, termed AG glycomotifs (Fig. 1). The proline residues are converted to hydroxyproline (Hyp, O) by prolyl 4-hydroxylases that act as sites for addition of the first galactose (Gal), by Hyp-O-galactosyltransferases (Hyp-O-GalTs) in the ER-Golgi and then further extended by a series of glycosyltransferases in the Golgi Apparatus (Silva et al., 2020; Fig. 1). AG glycans consist of a backbone of  $\beta$ -1,3 linked Gal with  $\beta$ -1,6 linked Gal sidechains substituted with  $\alpha$ -L-Arabinose (Ara)f and this core structure appears to be remarkably stable across different plant species (Strasser et al., 2021, Tryfona et al., 2012). What has been shown to vary are the branch types and sugars on the  $\beta$ -1,6 linked Gal sidechains, and can include Ara, rhamnose (Rha), Gal, fucose (Fuc) and glucuronic acid (GlcA) depending on the species and tissue type, in variable ratios (Strasser et al., 2021, Tryfona et al., 2012). A key tool for isolating AGPs is  $\beta$ -Yariv reagent which can precipitate with AGPs and has enabled characterisation of glycan structures (Strasser et al., 2021, Tryfona et al., 2012). The physico-chemical properties of many AGPs, and therefore functions and interactions, will be significantly influenced by the large glycan structures. In seed plants, Araf is the major terminal sugar and the neutral/

*Abbreviations:* AGP, Arabinogalactan protein; AG, Arabinogalactan; GPI, glycosylphosphatidyl inositol; RG-I, rhamnolacturonan-I; ER, endoplasmic reticulum.

\* Corresponding author.

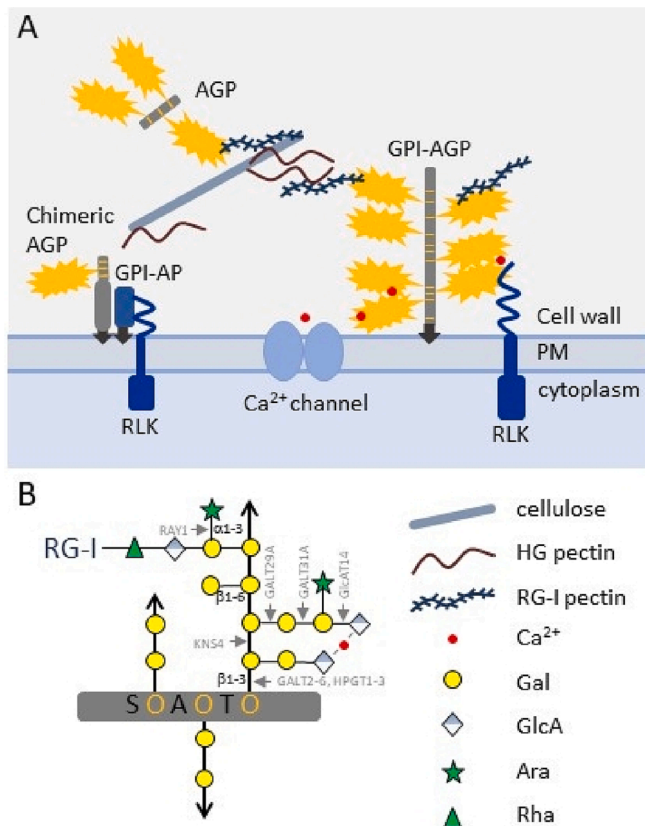
E-mail address: [k.johnson@latrobe.edu.au](mailto:k.johnson@latrobe.edu.au) (K. Johnson).

<https://doi.org/10.1016/j.tcs.2023.100102>

Received 30 January 2023; Received in revised form 14 February 2023; Accepted 15 February 2023

Available online 17 February 2023

2468-2330/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).



**Fig. 1.** Arabinogalactan proteins (AGPs) are highly diverse glycoproteins in the plant extracellular matrix. **(A)** Schematic representation of AGP locations and interactions with cell wall structural components and signalling pathways. AGP can be either secreted into cell walls or located at the plasma membrane (PM) via glycosylphosphatidylinositol (GPI)-anchor (arrow). Arabinogalactan (AG) glycan chains (orange) can interact with pectin rhamnogalacturonan-I (RG-I) and form larger complexes with wall polysaccharides. AGPs, including GPI-anchored AGPs (GPI-AGPs) located at the PM-cell wall interface, have potential to bind calcium via AG glycans. Signalling pathways may be activated by calcium release, for example in response to changes in pH, and transport of calcium into the cytoplasm via calcium channels or by interaction of AGPs with PM localised receptor-like kinases (RLKs). Chimeric AGPs may interact with other GPI-anchored proteins (GPI-AP) and form larger cell wall sensing complexes with RLKs. **(B)** Schematic representation of AG glycan structures. AG glycomotifs consist of clustered, non-contiguous hydroxyproline (O) residues such as the SO, AO, TO, and VO repeats in the protein backbone and direct addition of O-linked type II arabinogalactan polysaccharides. AG glycans consist of a backbone of  $\beta$ -(1-3)-linked galactose (Gal) and  $\beta$ -(1-6)-linked Gal as sidechains, with terminal sugars that can include arabinose (Ara), glucuronic acid (GlcA) and rhamnose (Rha). Glycosyltransferases responsible for AG biosynthesis include galactosyltransferase 2-6 (GALT2-6) and Hyp-O-galactosyltransferases 1-3 (HPGT1-3) responsible for initiation of AG glycan synthesis, KNS4/UPEX1 for elongation of  $\beta$ -(1-3)-Gal backbone, GALT29A and GALT31A for  $\beta$ -(1-6)-Gal addition, REDUCED ARABINOSE YARIV1 (RAY1) for  $\alpha$ -(1-3)-Ara addition and glycosyltransferase 14 members that add Me-GlcA. AG glycan can covalently interact with pectin RG-I via Rha and associate with calcium via GlcA residues. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

polar characteristics make the AGPs highly hydrophilic and influences water holding, adhesion and emulsification properties. Using antibody labelling to different AG glycan epitopes, it is clear that branches and terminal residues can vary greatly, likely on different AGP molecules and certainly between different tissue types and species (Silva et al., 2020). Terminal sugars, such as methylated sugars and uronic acids can generate a less hydrophilic surface and introduce negative charges, respectively. AGP structures have likely evolved specific adaptations to

environment and developmental/tissue contexts. For example, algal AGPs have a large amount of 3-O-methyl-hexose but less Ara or Gal as shown in  $\beta$ -Yariv extracted AGPs from *Ulva Lactuca* (Prerovska et al., 2021). Bryophyte and fern AGPs have been found to have a high content of Rha and methylated Rha at the periphery leading to a less polar surface and potentially mediate hydrophobic interactions that modulate cell wall properties during water stress (Pfeifer et al., 2022). In *Arabidopsis*, covalent linkages between Rha on AGPs and galacturonic acid on rhamnogalacturonan-I (RG-I) pectin are strongly associated with the cell wall and proposed to function in maintaining a functional wall structure through pectin crosslinking (Tan et al., 2013, Tan et al., 2023). The degree of glucuronidation on *Arabidopsis* AGPs is associated with the calcium binding and influences signalling and salt tolerance (Lopez-Hernandez et al., 2020). In seagrass AGPs, a high proportion of methylated GlcA is thought to introduce negative charges that associate calcium at the exclusion of sodium as an adaptation to the marine environment (Pfeifer et al., 2020). The glycans of AGPs and their heterogeneity are important not only to their roles interacting with different wall components but also for acting in signalling pathways. For example, the terminal 4-Me-GlcA- $\beta$ -1,6-Gal disaccharide is necessary and sufficient to act as a signal in an ovular methyl-glucuronosyl arabinogalactan (AMOR) in *Torenia fournieri* to regulate pollen tube competency to ovular (Mizukami et al., 2016). What remains unclear is the regulation of these specific glycan epitopes and on what AGP molecules they occur.

The AGPs superfamily is hugely diverse and includes highly glycosylated molecules, such as 'classical' AGPs and AG-peptides that have protein backbones that are PAST-rich (>45 %) and glycosylation makes up to 90 % of the total mass. Study of such AGPs from gum arabic suggest an ellipsoid morphology and ability to self-aggregate (Renard et al., 2012). AGPs also include multidomain, moderately glycosylated proteins, where the AG glycans are just one of the features that contribute to function. The AG glycomotif region may occur as little as once in 'non-classical' AGPs which include other protein regions; such as histidine (H)- or cysteine (C)-rich regions. Hybrid AGPs include other hydroxyproline-rich glycoprotein motifs such as SPPPP found in extensins (Ma et al., 2018). In recent bioinformatics studies of the AGP superfamily, AG glycomotifs were found to be associated with 9 AGP subgroups and there are likely more (Ma et al., 2017, Johnson et al., 2017). Chimeric AGPs include a recognised PFAM domain and over 12 types of have been identified, although in many, glycosylation has not been confirmed (Ma et al., 2017, Johnson et al., 2017). A study of one of the most well recognised chimeric AGPs, the Fasciclin-like AGP (FLA) family, found AG glycomotif regions and other domains of the protein, such as fasciclin domain type, are strongly associated, suggesting functional specificity (Shafee et al., 2020). Many AGPs have also been found to have distinct expression profiles, for example, exclusively in pollen or cells with secondary cell walls (Silva et al., 2020). Members of this intriguing family are therefore likely to have become specialised for their roles in the extracellular matrix of plant cells, playing a myriad of functions in reproduction, development, responses to abiotic and biotic stresses (Silva et al., 2020). In the following sections we briefly outline a few key areas where AGPs have functional importance as structural wall integrators and cell surface 'hubs' in signalling pathways.

## AGPs and the wall matrix

During growth, development and in response to the environment, the wall is highly dynamic to maintain structural integrity and cellular functions, including cell-cell communication, adhesion and expansion. There are numerous AGP members in any given tissue and analysis of knockout lines of individual AGPs often shows no obvious phenotype (Ma et al., 2018). Mutants in multiple AGP members or the glycosyltransferases involved in AG glycan synthesis have been generated to overcome redundancy. These studies have shown the importance of AGPs for maintenance of wall structure. For example, mutant

combinations of the eight Hyp-O-GalTs in *Arabidopsis* showed AGP roles in maintenance of both primary and secondary walls during growth and development, including in root cell expansion, stem biomechanics, seed coat differentiation and pollen formation (Kaur et al., 2022). Many AGPs are specific to floral reproductive structures and include classical AGPs, AG peptides and FLAs (Ma et al., 2018). Under-glycosylation and/or reduction of AGPs has been shown to strongly impact male reproduction. Mutation of KNS4/UPEX1, which encodes a  $\beta$ -1,3-galactosyltransferase responsible for AG glycan synthesis, impacts pollen exine development (Suzuki et al., 2017), the *agp6agp11* double mutant showed compromised pollen grain development (Coimbra et al., 2009) and investigation of *galt2galt5galt7galt8galt9* quintuple mutants showed severe disruption of pollen wall development in exine and intine layers (Kaur et al., 2022). AGPs are proposed to act as a molecular scaffold, required for correct assembly of polysaccharides during pollen development.

AGPs have also been shown to be important for maintenance of other complex polysaccharide structures, such as mucilage. Severe seed mucilage phenotypes were found when glycosyltransferase 14 members were disrupted, the enzymes that add Me-GlcA to AG glycans (Ajayi et al., 2021). The *glat14a-1glat14c-1* mutants show loss of adherent mucilage and significant alterations in cellulose ray formation and seed coat morphology (Ajayi et al., 2021). Mutation of *fla4/sos5* also show lower seed mucilage adherence (Griffiths et al., 2014). AGPs are components of root mucilage, secreted by cells sloughed off from the root cap that provides physical and biological protection. AGPs, along with pectins, are thought to contribute to mucilage hydration and lubrication of the root tip, as well as influencing the interactions of root associated, cap-derived cells with root-infecting pathogens, influencing growth, binding, and trapping of pathogenic and beneficial microbes, including bacteria and oomycetes (Driouich et al., 2021).

A question remains as to how AGPs support cell wall structure and adhesion. In cultured cells of *Arabidopsis*, the majority of AGP was shown to be covalently linked with RG-I glycans, in a 2:1 (RG-I to AGP) ratio (Tan et al., 2023) and the AGP APAP1 has been shown to link to RG-I and arabinoxylan that form a larger complex (Tan et al., 2013). AGPs are proposed to be part of tightly associated cell wall polysaccharide complexes through covalent and non-covalent interactions that contribute to the mechanical properties required for cell functions, as well as providing important links between the wall and plasma membrane for signalling.

## AGPs and signalling

AGPs have long been implicated in signalling pathways yet their structural complexity and lack of identified direct signalling partners has made understanding the mechanisms extremely challenging. AGPs may influence signalling indirectly, via changes in wall properties, or directly by acting as co-receptors at the PM (Fig. 1). AGPs influence on signalling pathways via wall changes was shown in *hpgt1,2,3* triple mutants that showed a reduction in cellulose, accumulation of pectin and disrupted plasmodesmata structure (Okawa et al., 2022). Mutants showed stomatal patterning defects that are proposed to result from increased symplastic transport of signalling molecules, such as the transcription factor SPEECHLESS, through larger plasmodesmata cavities (Okawa et al., 2022). Involvement of AGPs in embryo development in brown algae and gametophore cell wall development in the moss *Physcomitrium patens* suggest signalling roles were established early in evolution (Teh et al., 2022, Herve et al., 2016). AGPs with transmembrane domains, SLEEPING BEAUTY (SB) and SB-like (SBL), redundantly and specifically act to delay the timing of juvenile bud initiation in *P. patens* by modifying cell wall properties (Teh et al., 2022). SB was shown to regulate the transcription of class C auxin response factor (ARF) *PpARFC2* that in turn acts as a transcriptional repressor of cell wall remodelling genes (Teh et al., 2022). The factors that SB directly interact with at the PM remain unclear. Cross-over of AGPs with hormone signalling pathways

likely fine-tunes growth and developmental in feedback loops involving the cell wall. An AGP peptide, AGP21 has been identified as acting in brassinosteroid (BR) pathways that regulate root hair development in *Arabidopsis* (Borassi et al., 2020). AGP21 is positively regulated by the transcription factor BRASSINAZOLE RESISTANT 1 (BZR1) activated by BR signalling. Disruption of AGP21, in mutant lines or by mutation of AG glycomotifs, mimics  $\beta$ -Yariv treatment and leads to defective root hair development by altering expression of the root hair repressor *GLABRA 2* (Borassi et al., 2020). No direct physical interaction of AGP21 with BR co-receptors at the PM was detected however given the challenges of detecting glycan-protein interactions this possibility cannot be excluded (Borassi et al., 2020).

A proposed chemical interaction of AGPs with calcium (Lampert and Varnai, 2013) was supported by study of *glat14a,b,d,e* mutants in *Arabidopsis* (Lopez-Hernandez et al., 2020). Loss of GlcA in AGPs resulted in reduced calcium binding and mutant phenotypes showed they are essential for signalling processes required for normal growth and development (Lopez-Hernandez et al., 2020). The binding and release of calcium by AGPs is proposed to contribute to apoplastic calcium levels and influence cellular signalling. The signalling components involved remain unclear and could involve plasma membrane  $H^+$ -ATPases, calcium channels and receptor-like kinases (Lopez-Hernandez et al., 2020).

There remain gaps in our understanding of the role of AGPs in these complex feedback loops, including identification of the signalling partners of AGPs, the connections between cell wall polysaccharides, AGPs and cell surface receptors and the dynamics involved in responding to cellular and external cues.

## Conclusions and open questions

Our understanding about AGP glycan structures, synthesis and molecular functions has greatly advanced in recent years. AGPs are now recognised as playing roles in regulating both cell wall structural integrity and cell wall signalling and opens multiple avenues for exploring functional mechanisms and potential applications. Understanding AGPs role in the wall has potential to improve crop tolerance to salt stress and resilience to more variable climates such as low and high temperatures (Kutsuno et al., 2022, Liu et al., 2022). The role of AGPs in regulating development of reproductive organs and pollination could contribute to overcoming barriers of crossing or self-incompatibility (Zhou et al., 2022). These potential applications of AGPs encourage further investigation of some key outstanding questions: Are AGPs acting as a structural scaffold, signalling ligand or both? What polysaccharides are AGPs interacting with in different wall contexts? Do AGPs directly interact with signalling partners and what are they? In which sub-cellular compartment(s) are AGPs active? What structures contribute to AGP functions? Where and how is the degree and specificity of AG glycosylation regulated? Can efficient genome editing tools overcome genetic redundancy to understand roles of multiple, related members? These questions will keep researchers investigating AGPs for decades to come.

## CRedit authorship contribution statement

**Yingxuan Ma:** Writing – original draft, Writing – review & editing.  
**Kim Johnson:** Writing – original draft, Writing – review & editing, Visualization.

## 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.

## References

- Ajayi, O.O., Held, M.A., Showalter, A.M., 2021. Two beta-glucuronosyltransferases involved in the biosynthesis of type II arabinogalactans function in mucilage polysaccharide matrix organization in *Arabidopsis thaliana*. *BMC Plant Biol.* 21, 245.
- Borassi, C., Gloazzo Dorosz, J., Ricardi, M.M., Carignani Sardoy, M., Pol Fachin, L., Marzol, E., Mangano, S., Rodriguez Garcia, D.R., Martinez Pacheco, J., Rondon Guerrero, Y.D.C., Velasquez, S.M., Villavicencio, B., Ciancia, M., Seifert, G., Verli, H., Estevez, J.M., 2020. A cell surface arabinogalactan-peptide influences root hair cell fate. *New Phytol.* 227, 732–743.
- Coimbra, S., Costa, M., Jones, B., Mendes, M.A., Pereira, L.G., 2009. Pollen grain development is compromised in *Arabidopsis* agp6 agp11 null mutants. *J. Exp. Bot.* 60, 3133–3142.
- Driouch, A., Gaudry, A., Pawlak, B., Moore, J.P., 2021. Root cap-derived cells and mucilage: a protective network at the root tip. *Protoplasma* 258, 1179–1185.
- Griffiths, J.S., Tsai, A.Y., Xue, H., Voiniciuc, C., Sola, K., Seifert, G.J., Mansfield, S.D., Haughn, G.W., 2014. SALT-OVERLY SENSITIVE5 Mediates *Arabidopsis* Seed Coat Mucilage Adherence and Organization through Pectins. *Plant Physiol.* 165, 991–1004.
- Herve, C., Simeon, A., Jam, M., Cassin, A., Johnson, K.L., Salmean, A.A., Willats, W.G., Doblin, M.S., Bacic, A., Kloareg, B., 2016. Arabinogalactan proteins have deep roots in eukaryotes: identification of genes and epitopes in brown algae and their role in *Fucus serratus* embryo development. *New Phytol.* 209, 1428–1441.
- Johnson, K.L., Cassin, A.M., Lonsdale, A., Bacic, A., Doblin, M.S., Schultz, C.J., 2017. Pipeline to identify hydroxyproline-rich glycoproteins. *Plant Physiol.* 174, 886–903.
- Kaur, D., Moreira, D., Coimbra, S., Showalter, A.M., 2022. Hydroxyproline-O-Galactosyltransferases Synthesizing Type II Arabinogalactans Are Essential for Male Gametophytic Development in *Arabidopsis*. *Front. Plant Sci.* 13, 935413.
- Kutsuno, T., Chowhan, S., Kotake, T., Takahashi, D., 2022. Temporal cell wall changes during cold acclimation and deacclimation and their potential involvement in freezing tolerance and growth. *Physiol. Plant.* e13837.
- Lampert, D.T., Varnai, P., 2013. Periplasmic arabinogalactan glycoproteins act as a calcium capacitor that regulates plant growth and development. *New Phytol.* 197, 58–64.
- Liu, J., Meng, J., Chen, H., Li, X., Su, Z., Chen, C., Ning, T., He, Z., Dai, L., Xu, C., 2022. Different responses of banana classical AGP genes and cell wall AGP components to low-temperature between chilling sensitive and tolerant cultivars. *Plant Cell Rep.* 41 (8), 1693–1706.
- Lopez-Hernandez, F., Tryfona, T., Rizza, A., Yu, X.L., Harris, M.O.B., Webb, A.R., Kotake, T., Dupree, P., 2020. Calcium Binding by Arabinogalactan Polysaccharides Is Important for Normal Plant Development. *Plant Cell* 32, 3346–3369.
- Ma, Y., Yan, C., Li, H., Wu, W., Liu, Y., Wang, Y., Chen, Q., Ma, H., 2017. Bioinformatics Prediction and Evolution Analysis of Arabinogalactan Proteins in the Plant Kingdom. *Front. Plant Sci.* 8, 66.
- Ma, Y., Zeng, W., Bacic, A., Johnson, K., 2018. AGPs through time and space. *Annu. Plant Rev.* 767–804.
- Mizukami, A.G., Inatsugi, R., Jiao, J., Kotake, T., Kuwata, K., Ootani, K., Okuda, S., Sankaranarayanan, S., Sato, Y., Maruyama, D., Iwai, H., Garenaux, E., Sato, C., Kitajima, K., Tsumuraya, Y., Mori, H., Yamaguchi, J., Itami, K., Sasaki, N., Higashiyama, T., 2016. The AMOR Arabinogalactan Sugar Chain Induces Pollen-Tube Competency to Respond to Ovular Guidance. *Curr. Biol.* 26, 1091–1097.
- Muniz, M., Riezman, H., 2016. Trafficking of glycosylphosphatidylinositol anchored proteins from the endoplasmic reticulum to the cell surface. *J. Lipid Res.* 57, 352–360.
- Okawa, R., Hayashi, Y., Yamashita, Y., Matsubayashi, Y., Ogawa-Ohnishi, M., 2023. Arabinogalactan protein polysaccharide chains are required for normal biogenesis of plasmodesmata. *Plant J.* 113 (3), 493–503.
- Pfeifer, L., Shafee, T., Johnson, K.L., Bacic, A., Classen, B., 2020. Arabinogalactan-proteins of *Zostera marina* L. contain unique glycan structures and provide insight into adaptation processes to saline environments. *Sci. Rep.* 10, 8232.
- Pfeifer, L., Mueller, K.K., Classen, B., 2022. The cell wall of hornworts and liverworts: innovations in early land plant evolution? *J. Exp. Bot.* 73, 4454–4472.
- Prerovska, T., Henke, S., Bleha, R., Spiwok, V., Gillarova, S., Yvin, J.C., Ferrieres, V., Nguema-Ona, E., Lipovova, P., 2021. Arabinogalactan-like Glycoproteins from Ulva lactuca (Chlorophyta) Show Unique Features Compared to Land Plants AGPs. *J. Phycol.* 57, 619–635.
- Renard, D., Garnier, C., Lapp, A., Schmitt, C., Sanchez, C., 2012. Structure of arabinogalactan-protein from *Acacia* gum: from porous ellipsoids to supramolecular architectures. *Carbohydr. Polym.* 90, 322–332.
- Shafee, T., Bacic, A., Johnson, K., Wilke, C., 2020. Evolution of sequence-diverse inordered regions in a protein family: order within the chaos. *Mol. Biol. Evol.* 37 (8), 2155–2172.
- Silva, J., Ferraz, R., Dupree, P., Showalter, A.M., Coimbra, S., 2020. Three Decades of Advances in Arabinogalactan-Protein Biosynthesis. *Front. Plant Sci.* 11, 610377.
- Strasser, R., Seifert, G., Doblin, M.S., Johnson, K.L., Ruprecht, C., Pfrengle, F., Bacic, A., Estevez, J.M., 2021. Cracking the “Sugar Code”: A snapshot of N- and O-glycosylation pathways and functions in plants cells. *Front. Plant Sci.* 12, 640919.
- Suzuki, T., Narciso, J.O., Zeng, W., Van De Meene, A., Yasutomi, M., Takemura, S., Lampugnani, E.R., Doblin, M.S., Bacic, A., Ishiguro, S., 2017. KNS4/UPEX1: A Type II Arabinogalactan beta-(1,3)-Galactosyltransferase Required for Pollen Exine Development. *Plant Physiol.* 173, 183–205.
- Tan, L., Eberhard, S., Pattathil, S., Warder, C., Glushka, J., Yuan, C., Hao, Z., Zhu, X., Avci, U., Miller, J.S., Baldwin, D., Pham, C., Orlando, R., Darvill, A., Hahn, M.G., Kieliszewski, M.J., Mohnen, D., 2013. An *Arabidopsis* cell wall proteoglycan consists of pectin and arabinoxylan covalently linked to an arabinogalactan protein. *Plant Cell* 25, 270–287.
- Tan, L., Zhang, L., Black, I., Glushka, J., Urbanowicz, B., Heiss, C., Azadi, P., 2023. Most of the rhamnogalacturonan-I from cultured *Arabidopsis* cell walls is covalently linked to arabinogalactan-protein. *Carbohydr. Polym.* 301, 120340.
- Teh, O.K., Singh, P., Ren, J., Huang, L.T., Ariyaratne, M., Salamon, B.P., Wang, Y., Kotake, T., Fujita, T., 2022. Surface-localized glycoproteins act through class C ARFs to fine-tune gametophore initiation in *Physcomitrium patens*. *Development* 149.
- Tryfona, T., Liang, H.C., Kotake, T., Tsumuraya, Y., Stephens, E., Dupree, P., 2012. Structural characterization of *Arabidopsis* leaf arabinogalactan polysaccharides. *Plant Physiol.* 160, 653–666.
- Zhou, D., Zou, T., Zhang, K., Xiong, P., Zhou, F., Chen, H., Li, G., Zheng, K., Han, Y., Peng, K., Zhang, X., Yang, S., Deng, Q., Wang, S., Zhu, J., Liang, Y., Sun, C., Yu, X., Liu, H., Wang, L., Li, P., Li, S., 2022. DEAPI encodes a fasciclin-like arabinogalactan protein required for male fertility in rice. *J. Integr. Plant Biol.* 64, 1430–1447.