STRUCTURE AND FUNCTION OF PLANT ARABINOGALACTAN-PROTEINS

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Proteoglycans, glycoproteins and peptidoglycans are hybrid molecules in which the saccharide and peptide components are linked covalently.

In proteoglycans the polypeptide chain is substituted by covalently linked polysaccharide chains, whereas in glycoproteins the polypeptide chains bear covalently linked oligosaccharides. In the peptidoglycans polysaccharide chains are substituted by oligopeptides which may be covalently cross-linked.

The plant arabinogalactan-proteins are proteoglycans.† Their distribution is shown in Table 1. In these ubiquitous plant macromolecules the polysaccharide portions are β-galactopyranose polymers to which are attached mono- or oligosaccharide substituents composed of D-galactopyranose and L-arabinofuranose residues. Other monosaccharides may also be present in the peripheral substituents, depending on the source e.g. L-rhamnopyranose, L-arabinopyranose, D-glucuronic acid and D-galacturonic acid and their 4-0-methyl derivatives, D-xylopyranose, L-fucopyranose and D-mannopyranose.

Table 1. *Distribution of arabinogalactan-proteins*

Mosses;
coniferous woods;
gums, saps and exudates of angiosperms;
organs such as seeds, leaves, roots and fruits;
media of various tissues in culture.

Typically the polysaccharide portion has a multi-branched organization involving 1,3-, 1,6- and 1,3,6- linked β-galactopyranosyl residues as shown in the accompanying formula (Figure 1).

Analytical data for selected examples, summarized in Table 2, show that the arabinogalactan-proteins are a heterogenous group of molecules with molecular sizes ranging from 16,000 to over two million. The larch arabinogalactan is exceptional in not having a protein component but is classified with the arabinogalactan-proteins since it is an arabino-3,6-galactan with a structure typical of the arabinogalactan-proteins. The protein content of arabinogalactan-proteins is variable and typically, but not universally, they have an appreciable hydroxyproline component.

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†A fuller account of the chemistry, biochemistry, origins and functions of plant arabinogalactan-proteins is given in Clarke, A.E., R.L. Anderson and B.A. Stone, Phytochemistry 17 (No. 12) (1978).

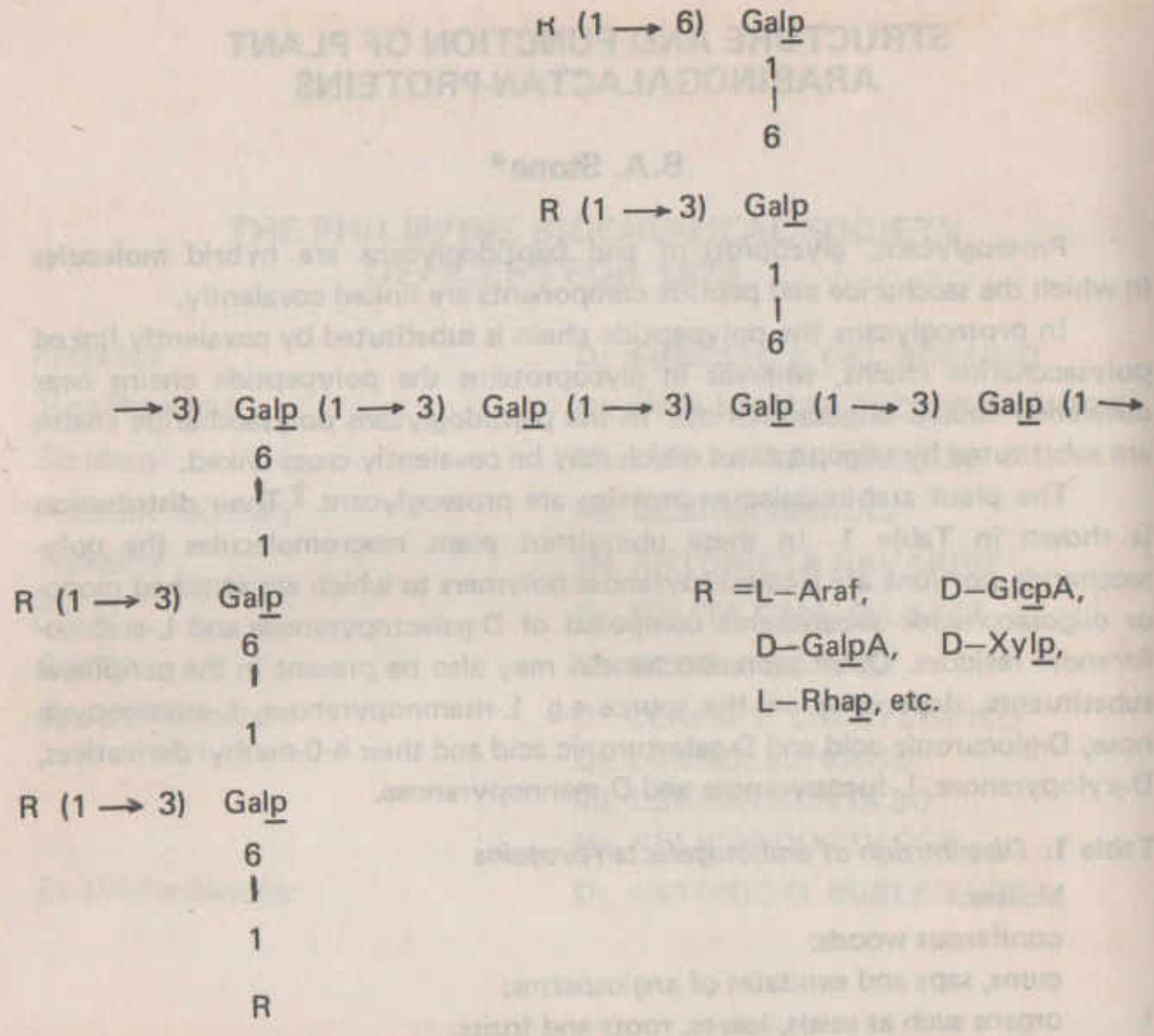


Figure 1. Typical polysaccharide structure of plant arabinogalactan-proteins.

The arabinogalactan-proteins may be distinguished from the arabinose- and galactose-containing glycoproteins found in cell walls and as soluble cytoplasmic components in potato tubers (potato lectin). In these molecules the polypeptide backbone is substituted by short arabinose oligosaccharides and by single galactosyl residues.

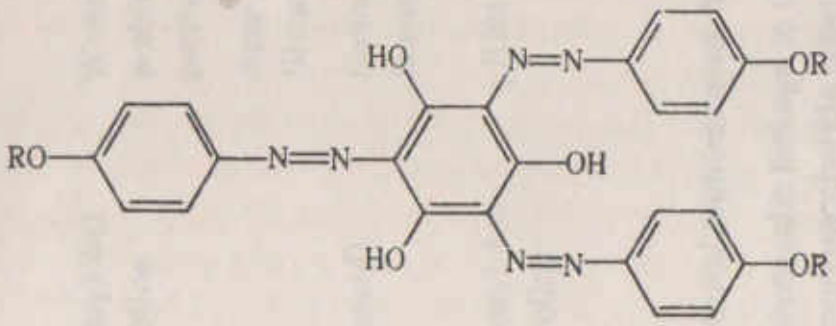
The chemistry of the covalent linkages between the saccharide and polypeptide portions of arabinogalactan-proteins and glycoproteins has been investigated in a few cases and the nature of the linkages, which are confined to glycosides of hydroxyproline and serine is summarized in Table 3.

Typically the arabinogalactan-proteins are readily soluble in water. Solutions of larch arabinogalactan, even at high concentrations, are not viscous. However, the exudate gums often give highly viscous solutions. Their high viscosity relates partly to the peripheral uronic acid residues which are ionized at neutral pHs and partly to the molecular architecture of their polysaccharide backbones. Those with highly branched molecules being less viscous than those with extended molecular conformations. The exudate gums are secreted as sticky fluids which harden to glassy solids as they dry.

Table 2. *Analytical data for selected arabinogalactan-proteins.*

Source	Protein (%)	Hydroxyproline (% total amino acids)	MW x 10^{-5}
Larch wood	?	–	0.16 (5-30%) 1.0 (70-90%)
Rye grass endosperm cultures	5	14.8	2.3
Exudate gums	0.13-34.3	+	0.47-40
Maple sap	9.4	12.7	2 fractions from Sephadex G-100
Rape seed	11	11.6	1.26
Wheat endosperm	8	16.7	0.2
Cannabis leaves			
South Africa			
Fract. B	25	6.3	0.42 & 1.25
Thailand			
Fract. B	25	0	0.42 & 1.25
Style mucilage	3	< 0.9	1.5-4.0

The biological functions of the arabinogalactan-proteins may be as diverse as their structures. Definitive information is lacking in all but a few cases. A prerequisite to the understanding of their function is the description of their location at the tissue, cellular and subcellular levels. To this end studies have been assisted by the availability of the Yariv artificial antigens whose basic structure is shown below.



These glycoside azo dyes have been shown to interact with arabinogalactan-proteins to give coloured and insoluble complexes. The specificity requirements for the interaction are shown in Table 4. Using these dyes as indicators it has been shown that arabinogalactan-proteins have a very wide phylo genetic distribution in plants and in histochemical tests their tissue, cell, and in some cases, sub-cellular locations have been defined (Table 5). At present

their localization at the ultrastructural level has not been possible. The interaction of the arabinogalactan portion of arabinogalactan-proteins with certain carbohydrate-binding molecules such as *Tridacna maxima* lectin or the J-539 myeloma protein which are specific for galactosyl residues, offers another method for their localization in tissues.

Apart from the demonstrated ability of the style mucilage to contribute carbohydrate for the growth of the invading pollen tube the functional roles of arabinogalactan-proteins remain essentially a matter for speculation. A number of possibilities based on known structural features and physico-chemical behavior of the molecules are summarized in Table 6. However a great deal more experimental evidence will need to be gathered before such speculations concerning their roles can be accepted or rejected.

Table 3. *Proposed carbohydrate-protein linkages in plant proteoglycans and glyco-proteins containing arabinose and galactose.*

Linkage Type	Proteoglycan Source	Anomeric Configuration	Glycoprotein Source	Anomeric Configuration
Galactopyranosyl-4-0 hydroxyproline	Wheat endosperm arabinogalactan-peptide	β	*Chlamydomonas* cell wall protein	?
	Acer culture filtrate	?		
Galactopyranosyl-0-serine	*Cannabis sativa* leaves	?	Cell wall glyco-protein (extensin)	?
			Potato lectin	∝
Arabinofuranosyl 4-0-hydroxyproline	Rice bran proteoglycan	∝	Cell wall glycoprotein (extensin)	∝
			Potato lectin	β

Table 4. *Structural requirements for Yariv artificial antigen – arabinogalactan- protein interaction.*

1) the glycosidic linkage to the phenyl ring must be in the β configuration.
2) the monosaccharide substituents must be D-glycosyl enantiomorphs.
3) the C(O)2 of the glycosyl substituent must have the same configuration as in D-glucopyranose.
4) tri-substituted and di-substituted Yariv antigens interact, mono-substituted derivatives are inactive.
5) the azo-and glycosyloxy-groups must be in 1:4 relationship to the phenyl ring.

Table 5. *Tissue, cell and sub-cellular locations of arabinogalactan-proteins.*

Cell type	Location	Species
Xylem and ray cells	Intracellular	*Larix* spp.
Endosperm	Intracellular vesicles	Rye grass
Aleurone	Plasma membrane-cell wall interface	Cereal seeds
Cotyledons -parenchyma	Intercellular spaces	Jack bean Lima bean
	Periphery of cyto-plasm	Pigeon pea
Petioles and leaves		
-secretory cells & phloem	Intracellular	*Hedera helix*
-central pith parenchyma	Intracellular vesicles	*Hedera helix*
-phloem	Plasma membrane and inner face of wall	*Zantedischia*
-aerenchyma		*Alocasia* spp.
Reproductive tissues		
-stigma	Papillae surfaces	
-stylar canal	Contents	*Gladiolus*
-pollen grains	Periphery of cyto-plasm	
Leaf (cultured cells)	Protoplast surfaces	*Nicotiana, Petunia, Triticum,* etc.
Xylem	Sap	Sugar maple
Fruits, trunks, leaves	Exudates	*Citrus* spp. fruits *Acacia* spp. trunks *Welwitchia* leaves

Table 6. *Possible functions of arabinogalactan-proteins.*

Possible Function		Relevant structural feature or physico-chemical property
Nutritional – secretory cells in style canal		
Protective – anti-freeze in wood (*Larix*)		high solubility high water holding capacity
– blocking of wounds (gum exudates)		
– resistance to localized desiccation		
Binding of small molecules		
– flavanol glucosides		ability to bind glycosides e.g. Yariv antigens
Binding of large molecules		
– Adhesion	– cell-cell "stick"	lectin and other carbohydrate binding interactions, adhesive properties of exudate gums and other arabinogalactan-proteins, coacervate formation, backbone interactions, charged surfaces.
	– pollen grain capture	
– Recognition	– specificity in cell-cell interactions	specific side chain structures as binding sites for lectin interactions.
	– cell-microorganism interactions	