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Mannans in primary and secondary plant cell walls†

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Abstract

A brief overview of the structure of mannans in plant cell walls and other organisms is presented. In particular, mannans, galactomannans and glucomannans in seed endosperm and vegetative tissues such as bulbs and tubers, galactoglucomannans (GGMs) in primary cell walls, and glucomannans and GGMs in secondary walls of hardwoods and softwoods are covered. Possible roles of mannans in primary plant cell walls other than as storage polysaccharides are discussed.

Keywords: galactomannans; galactoglucomannans; mannans; plant cell walls; polysaccharides

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Introduction

Mannans are widely distributed among living organisms. They are found as pure mannans (homomannans), galactomannans, glucomannans and galactoglucomannans. Also, cell walls from non-plant sources such as fungi or bacteria contain mannose-based polysaccharides. However, here the mannose residues are alpha-linked, whereas in the plant cell wall, mannose residues in polysaccharides are beta-linked. In yeast cell walls, including bakers' yeast (*Saccharomyces cerevisiae*) (Korn & Northcote, 1960), *Kluyveromyces lactis* (Raschke & Ballou, 1972) and *Candida utilis* (Ruszova et al., 2008), mixed linkage mannans containing (1→6) and (1→2)-linked α -mannosyl residues have been reported. Galactomannan has been isolated from cell walls of the fungus *Lineolate rhizophorae* (Giménez-Albian et al., 2007) and from the bacteria *Rahnella aquatilis* (Zdorovenko et al., 2006) with both containing (1→6) and (1→3)-linked α -mannosyl residues. Mannans from

the walls of the Chinese caterpillar fungus (*Cordyceps militaris*) consist of a (1→4)- α -D-mannose backbone branched at O-3 with side chains of (1→4)- α -D-glucose and (1→6)- β -D-galactose residues with β -D-galactose at the terminal position (Yu et al., 2009). From the edible mushrooms, *Auricularia auricula-judae*, (Sone et al., 1978) and *Tremella fuciformis* (Kakuta et al., 1979) heteromannans have been isolated in which the backbone is (1→3)- α -D-mannan. Lichen (*Thamnolia vermicularis* var. *subuliformis*) had a galactofuranosyl oligosaccharide linked to an (1→6)-linked α -manno-oligosaccharide (Omarsdottir et al., 2006). As the structures of the mannans from such organisms are generally unrelated to those of higher plant cell wall mannans, they will not be discussed further. It is noteworthy that the galactoglucomannan found in moss (*Fontinalis antipyretica*) has a backbone of (1→4)-linked β -mannose and glucose residues (Geddes & Wilkie,

Mannans in Wood

Galactoglucomannans are the major hemicellulose in softwoods (gymnosperms) followed by glucuronoxylan, whereas in hardwoods (angiosperms) glucomannans are a minor component and the major hemicellulose is glucuronoxylan (Timell, 1967). Softwoods have a range of compositions, but generally the mannose to glucose to galactose ratio is 3.5 – 4.5 : 1 : 0.5-1.1 (Willför et al., 2005a; 2008), although older literature favours a mannose to glucose to galactose ratio of 3 : 1 : 1 (Timell, 1967) (Figures 2b & c). In pine and spruce wood, GGM is not uniformly distributed in the cell walls, but is greatest near the lumen and least in the outer layer (Sjöström, 1993). The water-soluble O-acetyl-GGM from Norway spruce (*Picea abies*) has mannose to glucose to galactose ratio of 4 : 1 : 0.5, degree of acetylation of 0.3, with acetyl groups only at C-2 and C-3 of mannose (Willför et al., 2008). New Zealand-grown radiata pine (*Pinus radiata*) gave a similar ratio of 4.5 : 1 : 1.3 (Brasch, 1983) and 3.6 : 1 : 0.8 (McDonald et al., 1999) with O-acetyl groups only at the C-3 of mannose. The GGM from radiata pine contains regions of two or three contiguous glucose units as well as regions of manno-oligosaccharides (Tenkanen et al., 1997). The molecular weight of 30 to 60 kDa indicates that they are relatively small compared to other cell wall polysaccharides. The alkali-soluble GGM from the secondary cell walls of Norway spruce has been reported to have few side branches with a mannose to glucose to galactose of 33 : 8 : 1 (Capek et al., 2000) with branch points at O-6, O-3 and O-2 of mannose and O-6 and O-3 of glucose.

The ancient Chinese “fossil” conifer (*Metasequoia glyptostroboides*) contains distinctly less mannose than other gymnosperms and it is present in two different GGM forms (Wenda et al., 1990). One GGM has a mannose to glucose to galactose ratio of 1.5 : 1 : 1 that makes up 6.3% of the wood. The other has a mannose to glucose to galactose ratio of 5.3 : 3 : 1 that makes up 4.8% of the wood. Antibody labelling of glucomannans was observed only in the secondary walls of the differentiating tracheids of cypress (*Chamaecyparis obtusa*) wood (Maeda et al., 2000).

Water-soluble glucomannan from hardwoods had a mannose to glucose ratio of 2 : 1, with very small amounts of galactose, xylose and arabinose present for aspen (*Populus* spp.) and a mannose to glucose ratio of 2.1 – 2.4 : 1 for birch (*Betula* spp.) (Teleman et al., 2003). Both glucomannans are acetylated at O-2 and O-3 of mannose, with a degree of acetylation of 0.3. In the case of aspen, if it is a GGM and not a glucomannan, then the mannose to glucose to galactose ratio would be ~ 20 : 10 : 1 and in the case of birch, there would be even less galactose. Hornbeam (*Carpinus betulus*) wood has a glucomannan with a mannose to glucose ratio of 1.5 : 1 (Ebrigerová et al., 1972). Glucomannan makes up 5% of the secondary

wall of the poplar species, with a mannose to glucose ratio of 2 : 1 (Mellerowicz et al., 2001). An alkaline-soluble GGM has also been isolated from poplar (*Populus monilifera*), consisting of 1→4 linked β-D-mannopyranosyl and β-D-glucopyranosyl units in the backbone distributed at random, and (1→6)-β-D-galactopyranosyl units attached to mannose and glucose with a mannose to glucose to galactose ratio of 9.7 : 4.1 : 1 with a trace of xylose (Kubačková et al., 1992). Cottonwood (*Populus* spp.) had 2% (by dry weight) of mannan (Puls & Schuseil, 1993), equivalent to up to 5% GGM. Differences in the mannose to glucose ratio occur within a species depending on whether heartwood or sapwood was analysed, as shown in a survey of hardwoods (Willför et al., 2005b).

Interaction of Mannans with other Wall Polysaccharides

Mannans have long been known to be intimately associated with cellulose microfibrils and extensive treatment with strong alkali or other chaotropic agents is ineffective in removing them entirely from the cellulose microfibrils. They are commonly found in the cellulose residue after sequential extraction of walls. There is other evidence that mannans interact with cellulose. Ivory nut mannan was reported to be “crystallised” on cellulose microfibrils (Chanzy et al., 1978). Moreover, it has been shown the lower the number of galactose sidechains on a guar galactomannan, and the lower the acetyl groups, the higher was their affinity for bleached kraft paper (Hannuksela et al., 2002). Likewise, the lower the acetyl content, the more a glucomannan was adsorbed onto commercial cellulose (Laffend & Swenson, 1968). Neither the galactomannan locust bean gum nor xanthan gum (from the microorganism *Xanthomonas campestris*) will form a gel, but together they gel. Locust bean gum has been shown to adhere to microcrystalline cellulose (Mishima et al., 1998) and solid-state ¹³C NMR spectroscopy has confirmed that 70% of the mannosyl residues (but not the galactosyl residues) are bound to cellulose from softwood kraft pulp (Newman & Hemmingson, 1998). Schröder et al. (2004; 2006) reported that galactoglucomannan isolated from kiwifruit adhered to cellulose of filter paper, whereas storage glucomannans and galactomannans from seeds did not. Whitney et al. (1998) has also shown that the unsubstituted mannan portions of konjac glucomannan and the galactomannans (locust bean gum, guar and fenugreek (*Trigonella foenum-graecum*)) with low levels of galactose side chains interact with bacterial cellulose, as does glucomannan (mannose to glucose ratio 1.8 : 1) from beech (*Fagus crenata*) wood and other hemicelluloses, including xyloglucan. However, of all the hemicelluloses trialled, beech glucomannans showed the strongest affinity for bacterial cellulose, followed by xyloglucan and xylans, and with arabinogalactan having the least (Iwata et al., 1998).

Glucomannan-lignin-xylan complexes are thought to exist in spruce wood (Lawoko et al., 2005). Alternatively, mannan might associate with another hemicellulose such as xylan (Kerr & Fry, 2004; Rizk et al., 2000) and in lignified cell walls including wood, xylan interacts with lignin (Barakat et al., 2007).

This, along with other evidence, has led to the hypothesis that like xyloglucan and xylans, the glucomannans and the GGMs can act as cross-linking tethers between cellulose microfibrils and so contribute to the three-dimensional structure of the plant cell wall. This idea received a considerable boost from recent work in which an endo- β -mannanase from tomato fruit (Schröder et al., 2004; 2006) was shown to act not only as a hydrolase but also as a transglycosylase. Here, mannans such as GGM from kiwifruit as well as glucomannans or galactomannans were cleaved and attached to tritiated mannan-derived oligosaccharides in a transglycosylase reaction analogous to the action of the transglycosylase reaction xyloglucan transglucosylase/ hydrolase (XTH) (Nishitani & Tominaga, 1992; Fry et al., 1992; Farkas et al., 1992). The role of XTH is to continuously modify the xyloglucan-cellulose network during different stages of plant development by breaking and rejoining existing or newly synthesised xyloglucan molecules to existing xyloglucan (Thompson & Fry, 2001), thereby probably restoring and refining the xyloglucan-cellulose network during developmental processes. In this manner, endo- β -mannanase could cleave and lengthen glucomannan or GGM cross-links to allow cell expansion, or simply cleave the cross-links to contribute to softening of texture that occurs on ripening. Beyond the enzyme work, the evidence to support this hypothesis is sparse.

In wood, GGMs could strengthen cell walls by acting as cross-links from cellulose microfibrils to a hemicellulose-lignin complex.

The relatively small amount of glucomannan or GGM in primary cell walls does not negate their importance as cross-linking molecules. We have calculated with mung bean (*Vigna radiata*) hypocotyl cell walls that only 8% of the surface of the cellulose microfibrils is coated with adhering xyloglucan (Bootten et al., 2004). Nonetheless, the walls are perfectly functional and indeed a large number of cross-links are unnecessary. The fewer cross-links, the easier it would be to modify the walls during cell expansion and fruit ripening.

Conclusion

Mannans have been studied extensively in wood and considerably less in other species but their various roles have not been fully elucidated.

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