

## Xylogalacturonan exists in cell walls from various tissues of *Arabidopsis thaliana*

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### Abstract

Evidence is presented for the presence of xylogalacturonan (XGA) in *Arabidopsis thaliana*. This evidence was obtained by extraction of pectin from the seeds, root, stem, young leaves and mature leaves of *A. thaliana*, followed by treatment of these pectin extracts with xylogalacturonan hydrolase (XGH). Upon enzymatic treatment, XGA oligosaccharides were primarily produced from pectin extracts obtained from the young and mature leaves and to a lesser extent from those originating from the stem of *A. thaliana*. The oligosaccharide GalA<sub>3</sub>Xyl was predominantly formed from these pectin extracts. No XGA oligosaccharides were detected in digests of pectin extracts from the seeds and roots.

A low number of XGA oligosaccharides was obtained from pectins of *A. thaliana*. This indicates a uniform distribution of xylose in XGA from *A. thaliana*. The predominant production of GalA<sub>3</sub>Xyl, as well as the release of linear GalA oligosaccharides pointed to a lower degree of xylose substitution in XGA from *A. thaliana* than in XGA from apple and potato.

The estimated amount of XGA accounted for approximately 2.5%, 7% and 6% (w/w) of the total carbohydrate in the pectin fraction of the stem, young leaves and mature leaves, respectively.

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### 1. Introduction

Primary cell walls are the major textural components of plant-derived foods. The most important polysaccharides

that account for 90–100% of the structural polymers of these cell walls are cellulose, hemicellulose and pectin (Albersheim et al., 1996).

Cellulose is comprised of β-(1 → 4)-linked D-glucan while hemicelluloses primarily consists of xyloglucan and arabinoxylan (Albersheim et al., 1996). Pectin is a heteropolysaccharide, which contains α-(1 → 4)-linked D-galacturonic acid chains (also known as the smooth regions of pectins) and the branched polysaccharides rhamnogalacturonan I, rhamnogalacturonan II, and xylogalacturonan (referred to as the “hairy” regions) (Benen et al., 2002; Schols and Voragen, 1996; Vincken et al., 2003).

**Abbreviations:** MALDI-TOF MS, matrix assisted laser desorption ionization time of flight mass spectrometry; HPAEC, high performance anion exchange chromatography; PAD, pulsed amperometric detection; XGH, xylogalacturonan hydrolase; XGA, xylogalacturonan; CWM, cell wall material; CWM-s, saponified cell wall material; RG-I, rhamnogalacturonan I; AIR, alcohol insoluble residue; UA, uronic acid.

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The cellulose–hemicellulose network is embedded in a matrix of pectic polysaccharides, which form a hydrated and crosslinked three-dimensional network (Gibeaut and Carpita, 1994; Knox, 2002).

Xylogalacturonan (XGA) is a chain of  $\alpha$ -(1 → 4)-linked D-galacturonic acid, which is substituted with  $\beta$ -D-xylose at the O-3 position. It is suggested that this biopolymer is a side chain of RG-I (rhamnogalacturonan I) in the “hairy” regions of pectin (Vincken et al., 2003).

The presence of XGA in plants has been reported in storage tissues or reproductive organs such as in cell walls of peas, soybeans, watermelons, apples, pears, onions, potato's, pine pollen, and cotton seeds (Albersheim et al., 1996; Le Goff et al., 2001; Nakamura et al., 2002; Schols et al., 1995; Thibault and Ralet, 2001; Vincken et al., 2003; Voragen et al., 2001; Zandleven et al., 2006; Huisman et al., 1999). Its presence has also been reported in exudates from trees, such as gum tragacanth from the *Astragalus species* (Aspinall and Baillie, 1963).

Previous studies demonstrated that leaf primary cell walls of *A. thaliana* contain homogalacturonan, RG-I, RG-II, xylan, xyloglucan and cellulose (Zablackis et al., 1995). These polymeric structures were also suggested to be present in cell walls of the stem of this plant species (Gardner et al., 2002). Additionally, mannan polysaccharides have also been reported in the cell walls of leaves and stem of *A. thaliana* (Handford et al., 2003).

So far, the presence of other polysaccharides, such as XGA, has not been demonstrated in *A. thaliana* (Zablackis et al., 1995), although it has been suggested that this polymer exists in root caps of this plant species. This was based on immunocytochemical analysis using an LM8 antibody that was raised against pea XGA (Willats et al., 2004). Also Gardner et al. (2002) mentioned XGA as a probable xylose-containing polysaccharide in the stem of *A. thaliana*; however this was only based on the sugar composition of the alcohol insoluble residue (AIR) of the stems.

Recently, a gene (At5g33290) expected to encode a  $\beta$ -xylosyl transferase was identified in *A. thaliana*. Pectin isolated from a T-DNA insertion line having a T-DNA insertion in this particular gene was found to contain less xylose compared to the wild type (Sørensen et al., unpublished data). We therefore hypothesized that pectin from *A. thaliana* may contain regions of XGA. To investigate this, pec-

tin was extracted from cell wall material, prepared from the seeds, roots, young leaves and mature leaves of *A. thaliana*. The pectin fractions were analysed for their sugar composition and subsequently treated with xylogalacturonan hydrolase (XGH) to determine the presence of XGA. The enzyme XGH is known to degrade the galacturonic acid backbone and has a requirement for xylosylation (Beldman et al., 2003). Based on the action of XGH towards a XGA derived from gum tragacanth (XGA-29; Zandleven et al., 2005) and XGA from the saponified modified “hairy” regions of apple and potato (Zandleven et al., 2006), this enzyme has a preference to cleave between two xylosylated galacturonic acid units as deduced from the high production of the di-saccharide GalAXyl. XGH can also act between two GalA residues of which only one is xylosylated as shown from the production of XGA oligosaccharides which have no xylose substitution at the non-reducing end or at the reducing end.

Based on the obtained XGA hydrolysis products from the pectin fractions of *A. thaliana*, some structural characteristics of XGA from this species are hypothesized. Also the amount of XGA liberated from these pectin fractions was estimated.

## 2. Results

### 2.1. Analysis of CWM

CWM was prepared from the seeds, roots, stem, young leaves and mature leaves of *A. thaliana*. In line with other reports (Zablackis et al., 1995), polysaccharides possibly lost during some of the preparation steps (i.e. starch and protein removal) were not considered as cell wall components.

These CWM was saponified to ensure full removal of methyl- and acetyl esters, which could interfere with subsequent enzymatic treatment. The sugar composition of the saponified CWM (CWM-s) samples is shown in Table 1. All the samples contained high amounts of glucose and significant amounts of xylose, which suggests the presence of cellulose, and possibly xylan and/or xyloglucan. The presence of these polysaccharides was indicated in cell walls of *A. thaliana* leaves before (Zablackis et al., 1995).

Table 1  
Sugar composition (mol%) and total carbohydrate content (w/w %) of CWM-s from mature leaves, young leaves, stem, root and seeds of *A. thaliana*

	Rha (mol%)	Fuc (mol%)	Ara (mol%)	Xyl (mol%)	Man (mol%)	Gal (mol%)	Glc (mol%)	UA (mol%)	Total carbohydrate (w/w%)
Mature leaves	3	1	8	9	5	7	33	35	49
Young leaves	2	1	7	8	6	8	37	33	47
Stem	1	0	6	20	7	5	43	19	57
Root	2	1	18	14	4	7	35	20	52
Seeds	8	1	18	8	3	11	27	25	20

The total carbohydrate content was calculated from GC and AUA data.

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