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Structure of Plant Cell Walls

XI. GLUCURONOARABINOXYLAN, A SECOND HEMICELLULOSE IN THE PRIMARY CELL WALLS OF SUSPENSION-CULTURED SYCAMORE CELLS[1]

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ABSTRACT

The isolation, purification, and partial characterization of a glucuronoarabinoxylan, a previously unobserved component of the primary cell walls of dicotyledonous plants, are described. The glucuronoarabinoxylan constitutes approximately 5% of the primary walls of suspension-cultured sycamore cells. This glucuronoarabinoxylan possesses many of the structural characteristics of analogous polysaccharides that have been isolated from the primary and secondary cell walls of monocots as well as from the secondary cell walls of dicots. The glucuronoarabinoxylan of primary dicot cell walls has a linear β-1,4-linked D-xylopyranosyl backbone with both neutral and acidic sidechains attached at intervals along its length. The acidic sidechains are terminated with glucuronosyl or 4-*O*-methyl glucuronosyl residues, whereas the neutral sidechains are composed of arabinosyl and/or xylosyl residues.

The complete structure of any higher plant cell wall has not been elucidated. The primary cell walls of suspension-cultured sycamore cells have been studied more than any other. These walls are composed of about 34% pectin, 24% hemicellulose, 23% cellulose, and 19% hydroxyproline-rich glycoprotein (21).

A xyloglucan was the only hemicellulose detected in the primary cell walls of suspension-cultured sycamore cells (11) or, indeed, of any dicot (21). Here, the extraction, purification, and partial characterization of another hemicellulose, a glucuronoarabinoxylan, from primary cell walls of suspension-cultured sycamore cells are described.

MATERIALS AND METHODS

Isolation of Cell Walls. The walls of suspension-cultured sycamore cells (*Acer pseudoplatanus*) were prepared as described (38).

Enzyme Purification. Endo-α-1,4-polygalacturonase from *Colletotrichum lindemuthianum* was purified (24) and checked for purity (29, 31), as described.

Enzymic Extraction of Pectic Polymers. The pectic polysaccharides were extracted from isolated sycamore cell walls by the action of the *C. lindemuthianum* endopolygalacturonase as described (19).

Base Extraction of Endopolygalacturonase-pretreated Walls. This was accomplished using a modification of the method of Bauer *et al.* (11). Endopolygalacturonase-pretreated walls (3.2 g) were suspended in 640 ml 0.5 M NaOH containing 1 mg/ml of sodium borohydride and stirred for 24 h at 2 C. Remaining insoluble material was removed by centrifugation at 8,000*g* for 15 min; the solubilized material was filtered through a GF/C glass fiber filter. The solution which passed through the filter was neutralized with 1 N acetic acid and exhaustively dialyzed against distilled H_2O for 24 h.

Gel Filtration Columns. A Bio-Gel P-100 column (1.5 × 90 cm) and an agarose A-1.5m column (1.5 × 32 cm) were equilibrated and eluted with 50 mM Na-acetate (pH 5.2). The void and included volumes of the columns were determined with blue dextran (Sigma) and NaCl, respectively.

Colorimetric Techniques. Neutral sugar concentrations were determined by the anthrone method of Dische (23) and uronic acid concentrations were determined by the *m*-hydroxydiphenyl method of Blumenkrantz and Asboe-Hanson (13). Pentose sugar concentrations were determined by the orcinol method of Dische (22).

Analysis of Glycosyl and Glycosyl-linkage Compositions. Glycosyl compositions were determined by the alditol acetate method of Albersheim *et al.* (1). Glycosyl linkage compositions were determined by combined GC-MS analysis of the partially methylated alditol acetate derivatives (12) and by comparison of GC retention times when standards were available. Methylation of polysaccharides was performed using a modification (35) of the procedure reported by Hakomori (27) using potassium dimethylsulfinyl anion instead of sodium dimethylsulfinyl anion (19). Trideuteromethyl iodide (Stohler Isotope Chemicals) was used as the methylating agent (in place of methyl iodide) to identify and determine the glycosyl linkages of methylated glycosyl residues in glucuronoarabinoxylan. The sequential addition of equal molar amounts of potassium dimethylsulfinyl anion and trideuteromethyl iodide was performed only once, before isolation of the methylated polysaccharide, in order to avoid base-catalyzed elimination of the methylated uronosyl residues.

The methylated polysaccharide was hydrolyzed by heating at 121 C for 1 h in 2 M trifluoroacetic acid. The resulting partially methylated aldoses were reduced with sodium borodeuteride to aid in mass spectral analysis of the alditol derivatives produced. The alditol derivatives then were acetylated.

Reduction of Uronosyl Residues. The glycosyl linkages of the uronosyl derivatives of glucuronoarabinoxylan were determined following reduction of the carboxyl groups of the hexuronosyl residues to yield the corresponding 6,6-dideutero hexosyl residues; reduction was accomplished by the method of Taylor and Conrad (39) using sodium borodeuteride and deuterium oxide. The unlabeled and dideutero-labeled hexosyl residues were distinguished by analysis of the fragment ions obtained during mass spectrometric analysis of the alditol acetate derivatives of these hexosyl residues. This also allowed quantitation of the uronosyl residues present in glucuronoarabinoxylan.

GC-MS. The alditol acetates were analyzed on column A,

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which contained 0.2% ethylene glycol succinate, 0.2% ethylene glycol adipate, and 0.4% XF-1150 on gas-chrom P (1). The partially methylated alditol acetates were analyzed on column A as well as on column B, a 25-m open tubular glass capillary column containing SE-30 (LKB, Broma, Sweden). All GC-MS analyses were carried out on a Hewlett-Packard model 5980A system coupled to a Hewlett-Packard model 5933A data system.

All of the GC flame-ionization responses to partially methylated alditol acetates were corrected to mole responses as described by Sweet *et al.* (37).

Base-catalyzed Degradation (β-Elimination) of Uronosyl Residues of Methylated Glucuronoarabinoxylan. The uronsyl residues of permethylated, non-carboxyl-reduced glucuronoarabinoxylan were degraded by treatment with $DMSO^{-}$ ion using the method of Lindberg *et al.* (32). In a typical experiment, 750 μg trideuteromethylated glucuronoarabinoxylan was dried overnight in a vacuum oven. DMSO (0.5 ml), freshly distilled from calcium hydride at 12 mm Hg and containing 0.02 ml of 2,2-dimethyl propane (as a water scavenger), was added to the sample which was placed in a sonicator for 1 h. The sonications were performed in a Heat-Systems-Ultrasonics, Inc. small cleaning sonicator. The sample then was made 0.9 M with respect to DMSO ion and was stirred for 24 h at room temperature. After 24 h, excess ethyl iodide was added to the sample which was stirred for an additional 24 h at room temperature and then fractionated on a LH-20 column (1 × 40 cm) which had been equilibrated in chloroform-methanol (50:50 v/v). Aliquots of the 0.4-ml column fractions were evaporated to dryness and assayed by the orcinol method for pentoses; the orcinol positive fractions were combined and their glycosyl-linkage compositions were determined.

Characterization of Glucuronoarabinoxylan Fragments. The glycosyl sequencing method of Valent *et al.* (41) was used to fractionate and characterize glucuronoarabinoxylan fragments. Trideuteromethylated glucuronoarabinoxylan (2 mg) was partially hydrolyzed with 2 M trifluoroacetic acid for 75 min at 70 C (determined by preliminary partial hydrolyses of the glucuronoarabinoxylan to give approximately 40% cleavage of 2-linked arabinosyl residues). The partially hydrolyzed glucuronoarabinoxylan was reduced, ethylated, and analyzed by high-performance liquid chromatography as described (41).

Determination of Whether Pentosyl Residues of Glucuronoarabinoxylan Possess Pyranosyl or Furanosyl Ring Form. The ring forms of the glycosyl residues of glucuronoarabinoxylan, whose ring form could not be determined by methylation analysis, were determined by the method of Darvill *et al.* (20).

Determination of Absolute Configuration of Glycosyl Constituents of Glucuronoarabinoxylan. The absolute configurations, D or L, of the glycosyl constituents of glucuronoarabinoxylan were assigned by the method of Gerwig *et al.* (25, 26) using SE-30 capillary column GC of trimethylsilylated (−)-2-butyl glycosides of the monosaccharides of the polysaccharide.

RESULTS

The base-solubilized material, obtained from endopolygalacturonase-treated cell walls, was applied to a DEAE-Sephadex A-50 ion-exchange column (1.5 × 8 cm) that had been equilibrated with 10 mM K-phosphate (pH 7.0). After sample loading, the column was washed with 2 column volumes of the phosphate buffer. Material that absorbed to the column was eluted using two 200-ml linear NaCl gradients (0.02 to 0.15 M and 0.15 to 1 M) in the phosphate buffer (Fig. 1). Column fractions 9 through 15 were pooled, dialyzed against distilled H_2O, and lyophilized.

The material obtained from the DEAE-Sephadex column was further fractionated by gel filtration on Bio-Gel P-100 yielding the

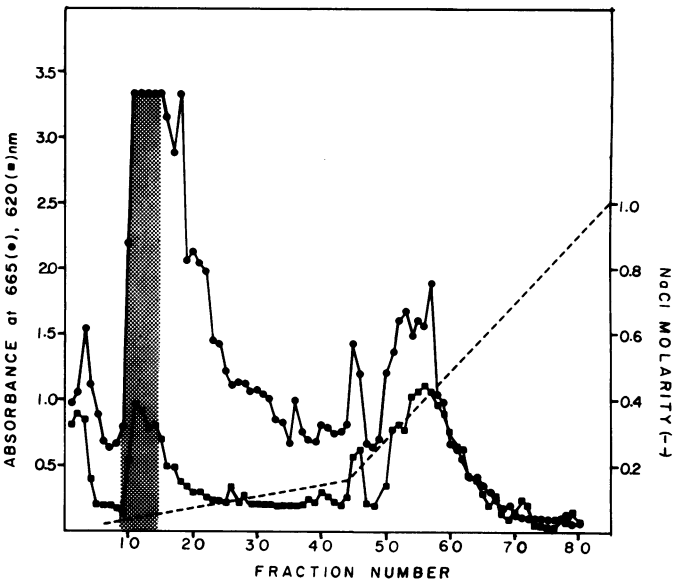

FIG. 1. Fractionation on a DEAE-Sephadex A-50 ion-exchange column of base-solubilized wall material obtained from endopolygalacturonase-treated cell walls. Collected fraction volume was 5 ml. Column fractions were assayed for neutral glycosyl residues by the anthrone method (23) (*A* at 620 nm) and for pentosyl residues by the orcinol method (22) (*A* at 665 nm).

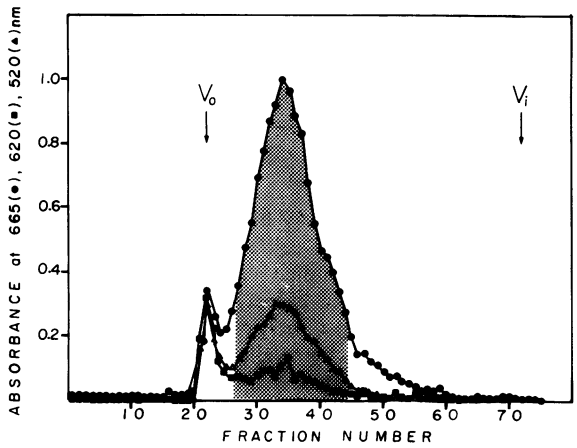

FIG. 2. Chromatography of material in fractions 9 through 15 of the DEAE-Sephadex column (Fig. 1), on a Bio-Gel P-100 column that had been equilibrated with 50 mM Na-acetate (pH 5.2). Collected fraction volume was 2 ml. Column fractions were assayed as described in the legend of Figure 1 with the addition of uronosyl residue detection by the *m*-hydroxydiphenyl method of Blumenkrantz and Asboe-Hanson (13) (*A* at 520 nm).

profile illustrated in Figure 2. Bio-Gel P-100 fractions 27 through 45 were combined, dialyzed against distilled H_2O, and lyophilized. The polysaccharide material from the Bio-Gel P-100 column then was chromatographed by gel filtration on agarose A-1.5m (Fig. 3).

Two carbohydrate-containing peaks eluted from the agarose A-1.5m column (V_e/V_0 = 1.73). Column fractions 36 through 38 contained greater than 90% glucosyl residues (Table I). Column fractions 22 through 29 were rich in xylosyl, arabinosyl and uronosyl residues (Table I; Fig. 3) and were pooled, dialyzed against distilled H_2O, and lyophilized. The polysaccharide in this peak represents approximately 5% by weight of the starting cell wall material and is referred to hereafter as the glucuronoarabinoxylan. Analysis of the residual wall after base extraction indi-

[3] Abbreviation: DMSO, dimethyl sulfoxide.

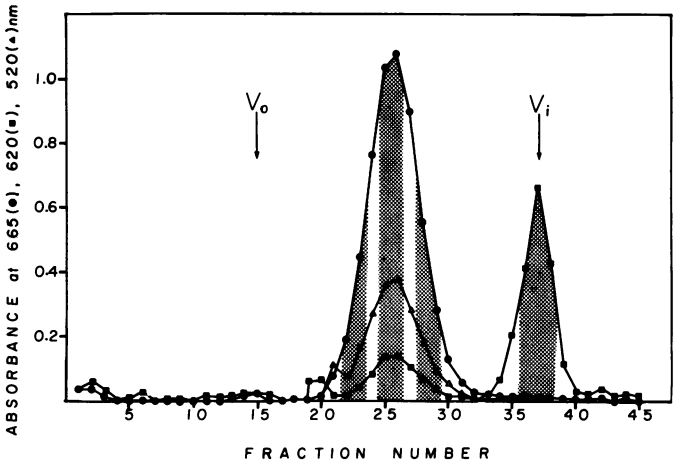

FIG. 3. Chromatography of material in fractions 27 through 45 from the Bio-Gel P-100 column (Fig. 2) on an agarose A-1.5m (1.5 × 32 cm) column that had been equilibrated with 50 mM Na-acetate (pH 5.2). Collected fraction volume was 1.5 ml. Column fractions were assayed as described in the legends of Figures 1 and 2. Column fractions 22 and 23, 25 and 26, 28 and 29, and 36 through 38 were combined separately and assayed by the alditol acetate method (1) for their neutral glycosyl residue compositions (Table I).

Table I. *Glycosyl Composition Analysis*

A comparison of the relative content of glycosyl residues (excluding uronosyl residues) in selected fractions of the agarose A-1.5m column depicted in Figure 3.

Glycosyl Residues	Column Fractions			
	22 and 23	25 and 26	28 and 29	36 through 38
	mol %			
Xylosyl	83.1	82.9	82.0	3.8
Arabinosyl	16.9	16.9	18.0	1.4
Galactosyl	0	0	0	1.3
Glucosyl	0	0	0	93.6

Table II. *Glycosyl and Glycosyl-linkage Compositions of Glucuronoarabinoxylan*

Glycosyl Residue	Glycosyl Composition	Glycosyl-linkage Composition		
		Determined Position of *O*-Trideuteromethyl Groups	Deduced Glycosidic Linkage	Amount
				mol %
Xylosyl	71.7	2, 3, 4	Terminal	10.6
		2, 3	4	47.1
		3	2, 4	24.9
Arabinosyl	16.9	2, 3, 5	Terminal	5.4
		3, 5	2	3.5
Glucuronosyl	6.6	2, 3, 4, 6	Terminal	4.7
4-*O*-Methyl glucuronosyl	4.9	2, 3, 6	Terminal	2.9

cated that there was <1% of the original 4-linked xylosyl residue content and, therefore, <1% of the glucuronoarabinoxylan remaining in the wall residue.

Glycosyl Composition of Glucuronoarabinoxylan. The alditol acetate-determined glycosyl composition of glucuronoarabinoxylan obtained by combining column fractions 22 through 29 of Figure 3 is given in Table II. The alditol acetates of the glycosyl residues were identified by comparing their GC retention times on Column A with the retention times of standards (1) and by their electron impact mass spectra (12). The glycosyl composition presented in Table II includes the alditol acetates of those hexosyl residues produced by reduction of carboxyl groups of hexuronosyl residues; these residues were identified during mass spectral analysis by the presence of 2 deuterium atoms on C_6.

Purity of Glucuronoarabinoxylan. The purity of the glucuronoarabinoxylan was assessed by determining the glycosyl residue composition of regions (Table I) of the polysaccharide peak as it eluted from the agarose A-1.5m column (Fig. 3). The relative content of the neutral glycosyl residues was very similar in each of three groups of column fractions examined between fractions 22 and 29. The polysaccharide eluting in column fractions 36 through 38 has a very different glycosyl composition (Table I).

Glycosyl-linkage Composition of Glucuronoarabinoxylan. The glycosyl-linkage composition of glucuronoarabinoxylan is given in Table II. The composition presented in Table II includes the dideutero-labeled hexosyl residues produced by reduction of carboxyl groups of hexuronosyl residues. Partially methylated alditol acetates were identified by comparison of retention times to those of standards obtained from araban (42), xyloglucan (11), and 1-*O*-methyl-β-L-arabinopyranoside (Sigma), as well as by electron impact mass spectra of the gas chromatographic effluent (12).

Methylation of glucuronoarabinoxylan with trideuteromethyl iodide established both the presence and the linkage of the 4-*O*-methyl glucuronosyl residue. The mass spectrum of the carboxyl-reduced, partially trideuteromethylated, acetylated hexitol obtained from the uronosyl residues of glucuronoarabinoxylan indicated the presence of both unmethylated and endogenously 4-*O*-methyl-substituted uronosyl residues; both types of uronosyl residues are terminally linked in the intact polysaccharide (Table II).

GC-MS analysis of the partially methylated alditol acetates obtained from carboxyl-reduced glucuronoarabinoxylan (Table II) determined that the terminal xylosyl and terminal glucuronosyl residues are in the pyranose ring form, and the terminal and 2-linked arabinosyl residues are in the furanose ring form. The 4- and 2,4-linked xylosyl residues were determined to be in the pyranose form by the method of Darvill *et al.* (20).

The xylosyl and glucuronosyl residues of glucuronoarabinoxylan were shown to be in the D-configuration, whereas the arabinosyl residues were found in the L-configuration (25, 26). Small amounts (less than 2%) of the other configuration cannot be ruled out by this method.

Mol Wt of Glucuronoarabinoxylan. The apparent mol wt (compared to globular proteins) of glucuronoarabinoxylan, as determined by gel filtration on Bio-Gel P-100 (Fig. 2) and agarose A-1.5m (Fig. 3), is approximately 1×10^5. A polysaccharide with a mol wt of 1×10^5 would have a degree of polymerization of approximately 600.

Attempts to Determine Glycosyl Residues of Glucuronoarabinoxylan to which Terminal Glucuronosyl and Terminal 4-*O*-Methyl Glucuronosyl Residues are Glycosidically Attached. The reactions used in this analysis are summarized in Figure 4. Glucuronoarabinoxylan was trideuteromethylated using only a single addition of potassium dimethylsulfinyl anion (Reaction 1 in Fig. 4). The single-step methylation resulted in the formation of methyl ethers of all the free hydroxyl groups and methyl esters of the carboxyl groups of the uronosyl residues. The trideuteromethylated glucuronoarabinoxylan was treated with potassium dimethylsulfinyl anion (0.9 M) in DMSO. This strong base caused β-elimination from C_4 of the uronosyl residues and resulted in the formation of Δ4:5 unsaturated uronosyl residues (Reaction 2a in

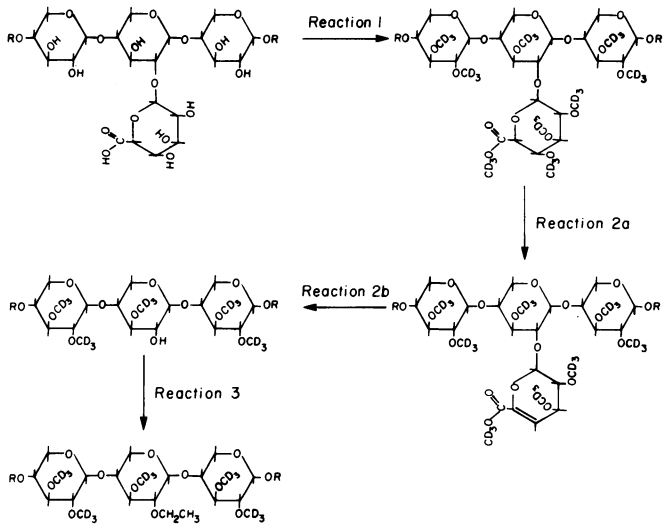

FIG. 4. The sequence of reactions thought to occur as a result of base-catalyzed β-elimination of a glucuronosyl residue in glucuronoarabinoxylan. The segment of the polysaccharide shown contains a sequence of three β-1,4-linked xylosyl residues with a glucuronosyl residue attached to C_2 of the central xylosyl residue. The reactions are described more fully under "Results." R, xylosyl residues continuing the backbone chain.

Fig. 4).

The unsaturated uronosyl residues undergo a second reaction in the presence of the strongly basic potassium dimethysulfinyl anion. This reaction (6) results in cleavage, by an undetermined mechanism, of the glycosidic bond between C_1 of the unsaturated uronosyl residue and the oxygen of the glycosyl residue to which the unsaturated uronosyl residue is attached (Reaction 2b in Fig. 4). This second reaction results in the formation of an unsubstituted (free) hydroxyl group on the glycosyl residues to which the unsaturated uronosyl residues had been attached. The free hydroxyl groups then were labeled by substitution with *O*-ethyl groups (Reaction 3 in Fig. 4) and thus, the points of attachment of the uronosyl residues were labeled.

The trideuteromethylated, potassium dimethylsulfinyl anion-treated, and ethylated polysaccharide was recovered by LH-20 chromatography, hydrolyzed, reduced, and acetylated. The resulting partially alkylated, partially acetylated alditols were identified by GC and GC-MS. It was observed that two positions in the polysaccharide were labeled with *O*-ethyl groups after β-elimination. These positions should be points of attachment of the terminal uronosyl residues in the glucuronoarabinoxylan. The averaged data of three experiments indicate that 20% of the glycosyl residues of glucuronoarabinoxylan were labeled with an *O*-ethyl group; 16% were 4-linked xylosyl residues with an *O*-ethyl group at C_2 and 4% were terminal xylosyl residues with an *O*-ethyl group at C_4.

A Neutral Disaccharide Originating from Glucuronoarabinoxylan. The disaccharide arabinofuranosyl$_f$-(1 → 2)-arabinofuranosyl$_f$1 → was isolated from glucuronoarabinoxylan and characterized by the method of Valent *et al.* (41). No other oligosaccharides of value in determining sidechain structure were obtained.

Treatment of Glucuronoarabinoxylan with Endo-β-1,4-xylanase. Glucuronoarabinoxylan was exhaustively digested by an endo-β-1,4-xylanase isolated from *Trichoderma pseudokoningii* (9). This resulted in hydrolysis of about 15% of the glycosyl linkages of glucuronoarabinoxylan and in the formation of oligosaccharides. Small xylosyl-containing oligosaccharides (up to 4 glycosyl residues in length) were fractionated on a Bio-Gel P-2 column equilibrated at 50 C; larger oligosaccharides containing arabinosyl, xylosyl, and glucuronosyl residues voided or nearly voided the same column.

DISCUSSION

Glucuronoarabinoxylan is a hemicellulosic polysaccharide not previously identified in the primary walls of dicots; this polysaccharide has now been shown to comprise approximately 5% of the primary walls of suspension-cultured sycamore cells. The glucuronoarabinoxylan was extracted by alkali from walls that had been pretreated with endopolygalacturonase. The polysaccharide then was purified to apparent homogeneity (Fig. 3; Table I) by ion-exchange chromatography on DEAE-Sephadex and gel filtration chromatography on both Bio-Gel P-100 and agarose A-1.5m columns.

The results of methylation analysis and the ability of an endo-β-1,4-xylanase to fragment the glucuronoarabinoxylan suggest that this glucuronoarabinoxylan possesses the β-4-linked xylopyranosyl backbone described for analogous polysaccharides in dicot secondary cell walls (43) and both the primary and secondary cell walls of monocots, of which only the Gramineae have been studied (4, 21, 28, 43, 44). Methylation analysis (Table II) shows that 4- and 2,4-linked xylosyl residues account for approximately 71% of the glucuronoarabinoxylan.

The uronosyl residues of glucuronoarabinoxylan were shown by methylation analysis to be nonreducing terminal residues (Table II). After β-elimination of the uronosyl residues of glucuronoarabinoxylan and labeling their point of attachment in the polysaccharide with *O*-ethyl groups, it was observed that C_2 of 2,4-linked xylosyl residues and C_4 of 4-linked xylosyl residues are possible points of attachment of the terminal uronosyl residues in glucuronoarabinoxylan. However, the results of that experiment were somewhat ambiguous as, for an unknown reason, possibly due to the removal of an unknown constituent, approximately twice as many xylosyl residues were labeled with *O*-ethyl groups (20%) as there are uronosyl residues in glucuronoarabinoxylan (Table II). This discrepancy makes it impossible to confirm the location of all of the terminal uronosyl residues in glucuronoarabinoxylan. However, at least a portion and perhaps all of the uronosyl residues are attached to C_2 of the 2,4-linked xylosyl residues as there are more than enough of these residues (16%) labeled with an *O*-ethyl group to account for attachment of all of the uronosyl residues (≃10%) in glucuronoarabinoxylan. However, the possibility that some of the uronosyl residues are attached to C_4 of 4-linked xylosyl residues cannot be ruled out.

There are reported examples of terminal glucuronosyl residues being attached to both C_4 and C_2 of xylosyl residues. Xylans present in the secondary cell walls of dicots have been shown to have terminal glucuronosyl residues attached to C_2 of backbone xylosyl residues (5, 36, 40), as have the xylans of the primary and secondary cell walls of monocots (2, 3, 8, 10, 14–17, 30, 33, 44–46); in addition, the monocot xylans of both oat stems (16) and bamboo leaves (44) have uronosyl residues attached to C_4 of 4-linked xylosyl residues, although the attachment of uronosyl residues to C_4 of xylosyl residues has not been reported in the secondary cell wall xylans of dicots. The presence of both terminal glucuronosyl and terminal 4-*O*-methyl glucuronosyl residues in the xylans of a single tissue is quite a common occurrence (8, 15, 16, 44–46).

Glucuronoarabinoxylan also possesses neutral arabinoxyl- and/or xylosyl-containing sidechains, a common structural feature of the primary and secondary walls of monocots (21) but not previously recognized to be present in the analogous polysaccharide in secondary cell walls of dicots. The presence of neutral sidechains, in addition to uronosyl-containing sidechains, in the glucuronoarabinoxylan of the primary dicot cell walls is evident from the results of glycosyl-linkage analysis (Table II) which shows that two-thirds of the terminal residues are either xylosyl or arabinosyl residues. Since, as expected, the number of terminal residues is equivalent to the number of branched residues (Table II), essentially each of the terminal residues terminates a sidechain. There are no acidic residues in the middle of a chain (all the uronosyl

residues are terminal); thus, all the terminal neutral glycosyl residues terminate neutral sidechains. Many or all of these neutral sidechains are attached to C_2 of 2,4-linked xylosyl residues. This was shown when 33% of the 2,4-linked xylosyl residues remained branched after β-elimination and subsequent ethylation; that is, the residues did not have *O*-ethyl groups at C_2.

The presence of arabinosyl-containing sidechains has been verified by the isolation, following partial hydrolysis of glucuronoarabinoxylan, of the disaccharide arabinosyl$_f$-(1 → 2)-arabinosyl$_f$ →. It was not possible to ascertain whether the 2-linked arabinosyl residue at the reducing terminus of this disaccharide is glycosidically attached in glucuronoarabinoxylan to the xylosyl residue in the backbone or to another neutral glycosyl residue in the sidechain. Arabinosyl-containing sidechains, namely *t*-arabinofuranosyl (2, 3, 7, 10, 14–18, 30, 33, 34, 44, 45) and xylosyl-(1 → 2) arabinosyl$_f$ → (3, 15, 16, 44) have been identified in analogous polysaccharides isolated from monocots but not from dicots. However, these arabinofuranosyl-containing sidechains of monocot xylans are usually found attached to C_3 of the xylosyl residues of the backbone apart from two instances where they are found on C_2 (34, 45, 46).

The arrangement of the various sidechains along the backbone chain has not been ascertained either here or in any previous study. The limited degree of cleavage (≃15%) by exhaustive endo-β-1,4-xylanase digestion of the glucuronoarabinoxylan suggests that sidechains, dispersed along the length of the backbone, may hinder cleavage by the enzyme.

It is now known that xyloglucan and glucuronoarabinoxylan, the two hemicelluloses of primary cell walls, are present in both dicots and monocots. In dicots, 19% of the primary cell wall is xyloglucan while 5% is glucuronoarabinoxylan; in monocots, the glucuronoarabinoxylans constitute a much higher percentage, about 25%, and the xyloglucan a much lower percentage, about 2% (21). Structurally, the glucuronoarabinoxylans from both sources appear similar; they both appear to possess a β-4-linked D-xylopyranosyl backbone, and both can have neutral and/or acidic sidechains attached to C_2 or C_3 of xylosyl residues (21). At the present time, polysaccharides, like glucuronoarabinoxylans, which can hydrogen-bond to cellulose (11), are considered to be structural polysaccharides (21); no other functions have been suggested.

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