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Characterisation of the extractable pectins and hemicelluloses of the cell wall of glasswort, *Salicornia ramosissima*

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Cell walls of glasswort (*Salicornia ramosissima* Woods), a halophytic Chenopodiaceae, prepared as alcohol-insoluble solids, were found to be rich in arabinose, galacturonic acid, glucose and proteins, and contained 0·7% ferulic acid and 3·8% acetic acid. Pectic and hemicellulosic polysaccharides were extracted by cyclohexanediaminotetraacetic acid, hot dilute acid, cold dilute alkali and concentrated alkali (twice), with yields of 2·9, 19·1, 4·7, 7·4 and 1·9% of the alcohol-insoluble solids, respectively. Protein-rich material precipitated upon dialysis. The dialysed fractions were fractionated by ion-exchange chromatography, and the main fractions were analysed by gel-filtration and glycosyl linkage analysis. The hot acid extract contained 46·2% arabinose and 28·9% galacturonic acid, with high degrees of methylation and acetylation (65 and 45, respectively). It could be fractionated into a low-molecular-weight arabinan rich in ferulic acid, and a pectic fraction still relatively rich in neutral sugars. The concentrated alkali extracts were rich in xylose (33·4 and 23·6%, respectively). They were separated by ion-exchange chromatography into a fucogalactoxyloglucan and a glucuronoarabinoxylan.

INTRODUCTION

Salicornia (glassworts) is a genus of halophytic plants that belong to the Chenopodiaceae, members of which (spinach, beet) have the peculiarity for dicotyledons of possessing ferulic acid substituents in their cell walls. *Salicornia* grow on coastal salty silts (Lahondère, 1985). They are annuals, and present a singular appearance, with segmented fleshy stems, leaves reduced to scales and hardly visible flowers. Dark green in summer, they flower in August and September, and often turn reddish in autumn. They were used as a source of alkali for soap and glass manufacture and defatting of cloth from the Middle Ages to the end of the eighteenth century. They grow notably in abandoned salt marshes of the French Atlantic coast, where they are harvested for local consumption as pickles.

Previous work, focussed on the cell walls of sugar-beet and spinach, have shown that their constitutive pectins are feruloylated, and that the ferulic acid moieties are carried by the neutral side chains (Fry, 1983; Rombouts & Thibault, 1986; Guillon & Thibault, 1989). The feruloyl substituents might play an important rôle in the control of growth in these plants, as in cereals (Fry, 1983). It has been generally assumed since that all Chenopodiaceae shared the same pecularities, which might give rise to a cell wall structure markedly different from that of other dicotyledons, devoid of ferulic acid. However, the only Chenopodiacea which has a cell wall that has been studied in detail is the sugar-beet.

The authors studied the cell walls of *Salicornia ramosissima* Woods to check whether they share the characteristics which have been assigned to the Chenopodiaceae.

MATERIALS AND METHODS

Plant material

Glassworts (*Salicornia ramosissima* Woods) were picked in July 1991 in a salt marsh in Talmont-Saint Hilaire (France). The top 10 cm of the fleshy stems were manu-

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ally separated and stabilised by boiling for 20 min in EtOH (1·5 litres of 96% EtOH for 712 g of fleshy stems).

Preparation of alcohol-insoluble solids (AIS)

After grinding in a Waring blender, the glassworts were extracted with 70% EtOH until the filtrate was sugar-free (phenol/sulphuric acid test) and the alcohol-insoluble solids were dried by solvent-exchange (96% EtOH and acetone).

Extraction of the AIS

Ten grams of AIS were treated sequentially three times each with 400 ml of 0·05 M CDTA (cyclohexanediaminotetraacetic acid) (pH 5·3) at room temperature, 0·05 M HCl at 85°C and 0·05 M NaOH (containing 0·5 g/litre of $NaBH_4$) at 4°C, and twice with 1 litre of 4 M NaOH (containing 0·5 g/litre of $NaBH_4$) at room temperature. The CDTA, hot dilute acid and cold dilute alkali extracts gave the CDTA-soluble pectins (CSP), acid-soluble pectins (HSP) and alkali-soluble pectins (OHSP) fractions, respectively, and the concentrated alkali extracts resulted in the two concentrated alkali-soluble fractions COHS1 and COHS2. The extracts were brought to pH 4·5 with 1 M NaOH for HSP and pure acetic acid for OHSP, COHS1 and COHS2. They were extensively dialysed against distilled water, centrifuged to eliminate the dialysis precipitate, and freeze-dried. The term 'extract' later refers only to those fractions which did not precipitate upon dialysis.

Chromatography

Ion-exchange chromatography

For analytical purposes, aqueous solutions of the freeze-dried extracts (~12 mg) were injected on a column (20 cm × 1·6 cm) of DEAE Sepharose CL-6B (Pharmacia). They were eluted with 0·05 M succinate buffer (pH 4·8, 50 ml), followed by a linear gradient from 0·05 M to 1 M (pH 4·8, 80 ml) and 50 ml of 1 M succinate buffer (pH 4·8). The flow rate was 24–30 ml/h. Fractions of approximately 5 ml were collected and assayed for uronic acids and neutral sugars. Semi-preparative ion-exchange chromatography was performed on a 20 cm × 2·6 cm column of DEAE Sepharose CL-6B. Approximately 50 mg was injected, the volumes of buffer were doubled, and 10 ml fractions were collected.

Gel-filtration chromatography

The main fractions from ion-exchange chromatography were injected on a Sephacryl S500 column (82 cm × 2·6 cm) and eluted ascendingly with 0·1 M succinate buffer at pH 4·5 at 30 ml/h. Approximate 4 ml fractions were collected and assayed for uronic acids, neutral sugars, proteins (absorbance at 280 nm) and ferulic acid (absorbance at 375 nm after having been brought to pH 10 (Rombouts & Thibault, 1986)). The void (V_0; amylopectin) and total (V_t; glucose) volumes of the column were 172 and 355 ml, respectively. HSPn was injected on a column of 40 cm × 1·6 cm (15 ml/h, 1 ml fractions, V_0 15 ml and V_t 31 ml). Results are expressed as a function of $K_{av} = (V_e - V_0)/(V_t - V_0)$, with V_e the elution volume of the fraction.

Analytical methods

All values were calculated on a moisture-free basis. Uronic acids and neutral sugars were determined by the automated metahydroxydiphenyl (Thibault, 1979) and orcinol (Tollier & Robin, 1979) assays, respectively, the latter being corrected for interfering uronic acids. Neutral sugars were analysed by GLC as alditol acetate derivatives (Englyst & Cummings, 1984) after 2 h hydrolysis by 1 M H_2SO_4 at 100°C, preceded by 1 h prehydrolysis by 13 M H_2SO_4 for insoluble products. Galacturonic and glucuronic acids were differentiated by HPLC on an Aminex HPX-87H column (300 mm × 7·8 mm, Bio-Rad) eluted with 0·5 mM H_2SO_4 at 60°C, after 2 h hydrolysis by 2 M trifluoroacetic acid at 120°C.

Phenolic acids were measured as described by Rombouts and Thibault (1986). Briefly, the phenolic acids are exterified by 2 N NaOH at 35°C under argon, then extracted by ether (four times) after bringing the solution to pH 2 with HCl. The pooled ether extracts are evaporated to dryness and the phenolic acids are redissolved in methanol for injection on a Rsil C18 column eluted by water:methanol:acetic acid (73:26:1 in volume) at room temperature. They are detected by their absorbance at 280 nm. Free organic acids were solubilised in water at room temperature for 1/2 h with stirring and analysed by HPLC on an Aminex HPX-87H column (300 mm × 7·8 mm, Bio-Rad) eluted with 5 mM H_2SO_4 at 45 C. Methyl and acetyl esters were determined according to the method of Voragen *et al.* (1986). The degrees of methylation (DM) and acetylation (DA) were calculated as molar ratios of methanol and acetic acid, respectively, to galacturonic acid.

Nitrogen was analysed by an automated Kjeldahl method. Proteins were calculated as $N \times 6{\cdot}25$.

Methylation analysis was carried out according to Hakomori (1964), using lithium methylsulfinyl anion with a contact time of 1 h. Acidic fractions were converted into their H^+ form by percolating the solutions through an Amberlite IR-120 resin to ensure dissolution in dimethyl-sulphoxide. Methylated polysaccharides were extracted with $CHCl_3$-CH_3OH (2:1, v:v), washed three times with distilled water, air-dried at 40°C and then hydrolysed with 90% formic acid (1 h, 100°C) and 2 M trifluoroacetic acid (90 min, 120°C). The hydrolysed partially methylated sugars were converted

into their alditol acetates using perchloric acid as a catalyst (Harris *et al.*, 1984) and analysed by GLC on a fused-silica capillary column (30 m × 0·32 mm) bonded with OV-225. The oven temperature was 175°C for 15 min and then increased 5°C/min to 220°C. Other conditions were: injector temperature 210°C; detector temperature 240°C; split 60–80 ml/min; hydrogen as carrier gas at 0·7 bars. Peak identification was based on retention times using inositol as internal standard and on e.i. fragmentation patterns using the OV-225 column coupled to a Delsi-Nermag R10-10C mass spectrometer with a source temperature of 250°C. The partially methylated alditol acetates were quantified using the FID signal and the effective carbon responses determined by Sweet *et al.* (1975).

Intrinsic viscosity ($[\eta]$, ml/g) was calculated by measuring the flow times of solutions of pectins in 0·155 M NaCl at 25·0 ± 0·1 C in an automatic Ubbelhode viscosimeter (Amtec, Nice, France) and by using the double extrapolation to zero concentration based on Huggins and Kramer equations (Axelos & Thibault, 1991).

RESULTS

Composition of the cell walls and extracts

The AIS represented 3·1% of the fresh weight of the starting material. It was rich in carbohydrates (Table 1), notably arabinose, galacturonic acid, and glucose; the pectins were highly methylated and acetylated, and contained ferulic acid (identified by HPLC against an authentic standard). The AIS contained a relatively high proportion of proteins. Isolation of cell wall material as AIS has the drawback of inducing co-precipitation of a number of cytoplasmic components, such as starch, tannins, cytoplasmic proteins and some organic acids. Indeed, the AIS of glasswort was contaminated by organic acids, mainly oxalic acid (4·9%), and citric acid (0·2%), and probably cytoplasmic proteins. About 95% of the glucose was of cellulosic origin.

Most of the AIS was solubilised during the successive extractions (86·2%). There were however substantial losses, which were due partly to loss of particulate material on and in the sintered glass filters during liquid/solid separations, and could also be due to hydrolysis, notably of the arabinose-containing polymers, during the hot acid extraction, and β-elimination of the pectins in alkaline conditions. The extraction yield calculated in terms of polysaccharides, their substituents and proteins was of 66%. In all extracts, dialysis induced precipitation of a material relatively rich in proteins. The material that precipitated during dialysis had a carbohydrate composition close to those of the soluble material, with an enrichment in glucose for the precipitates from the 4 M NaOH extracts. The dialysis precipitates were not investigated further. The CDTA only extracted 2·9% of the cell walls, corresponding to approximately 4% of the galacturonic acid. The main extract was HSP: the hot dilute acid solubilised material rich in arabinose and galacturonic acid, with a high ferulic acid content. Approximately 57 and 39% of the arabinose and of the galacturonic acid, respectively, were solubilised at this step. The proportion of galactose in this pectic fraction was low (4·3%,

Table 1. Yields and composition of the AIS and extracts from glasswort. The yields are given in per cent weight of the total AIS, and the compositions in per cent weight of the individual fractions

	Yield[a]	Rha	Fuc	Ara	Xyl	Man	Gal	Glc	GalA	GlcA	Proteins	Methanol	Acetic acid	Ferulic acid	Organic acids	Ash
AIS		1·7	0·3	14·5	3·8	0·8	2·9	13·0	13·5	2·8	17·1	1·7 (71)[b]	3·8 (84)[c]	0·7	5·1	7·3
0·05 M CDTA, 20 C:																
Soluble	1·7	0·9	0·6	15·2	6·2	4·5	9·2	6·9	22·8	2·1	7·5			0·3		
Dialysis precipitate	1·2			2·1	0·1	0·1	1·8	0·5	2·2		51·6					
0·05 M HCl, 80 C																
Soluble	18·0	2·2	0·3	46·2	0·3	0·3	4·3	0·2	28·9	4·5	17·4	3·4 (65)	4·5 (45)	1·7		
Dialysis precipitate	1·5	0·6	—	12·9	—	0·2	2·0	0·6	9·7		36·9					
0·05 M NaOH, 4 C																
Soluble	3·6	2·9	1·0	21·8	2·4	0·4	9·0	0·5	18·4	6·2	17·4	tr	tr	0·8		
Dialysis precipitate	1·1	2·4	0·2	0·6	0·7	3·0	2·0	5·5	2·1		67·6					
4 M NaOH, 20 C:																
Soluble	5·4	0·8	0·8	4·1	33·4	4·6	4·9	14·0	3·4	5·7	11·9	tr	tr	0·0		
Dialysis precipitate	2·0	0·5	0·5	1·8	16·7	0·8	1·3	15·0	5·1		37·8					
4 M NaOH, 20 C																
Soluble	1·4	0·8	0·6	5·3	23·6	2·0	5·2	8·5	4·6	4·7	11·1	tr	tr	0·0		
Dialysis precipitate	0·5	0·5	0·1	1·2	9·5	0·4	0·9	15·0	2·8		35·0					
Residue	13·8	0·3	0·1	2·0	1·1	—	1·1	92·0	1·7	0·7	2·0	tr	tr	0·0		

[a]Per cent of the AIS.
[b]DM.
[c]DA.
tr, Trace.

i.e. an Ara/Gal ratio above 10). The degree of acetylation calculated for this fraction was high (45), but lower than in the AIS, probably because galacturonic acid was not the sole carrier of acetyl substituents. Treatment with cold dilute alkali only extracted a minor proportion of pectic material, which still contained a significant amount of ferulic acid. The concentrated alkali extracts (hemicelluloses) were rich in xylose and glucose. The 4 M NaOH extracted a total of 9·3% of the original AIS. Both extracts were rich in xylose and glucose, and contained a notable proportion of galactose, mannose, glucuronic acid and fucose, in addition to residual arabinose and galacturonic acid. The final residue contained 92% glucose, presumably of cellulosic origin.

Characterisation of the pectic fractions

The three pectin extracts CSP, HSP and OHSP, were fractionnated by ion-exchange chromatography on DEAE Sepharose CL-6B. CSP gave one main retained fraction (CSPr) composed mostly of galacturonic acid (Table 2). The non-retained material represented 25% of CSP. It was composed almost exclusively of neutral sugars, notably glucose and xylose. HSP was separated into a non-retained fraction, HSPn, representing 45% of the carbohydrates of HSP and very rich in arabinose, and a retained fraction, HSPr, composed mostly of galacturonic acid. Most of the ferulic acid (~2/3) was in HSPn, though its ferulic acid/arabinose ratio was lower than that in HSPr. HSPr had a high proportion of arabinose (34 mol%) and approximately 1 rhamnose for 10 galacturonic acid residues. The elution pattern of OHSP showed two minor non-retained fractions, one composed mostly of neutral sugars (OHSPn) and the other of uronic acid (OHSPn'), probably as low-molecular-weight moieties, as they were not retained on the column. The main fraction (85% of the sugars) was retained. OHSPr was rich in neutral sugars, with approximately 1 rhamnose for 4 galacturonic acid residues, and a higher proportion of galactose than HSPr.

Table 2. Sugar composition (mol%) of the pectin fractions obtained by ion-exchange chromatography

	CSP		HSP		OHSP	
	CSPn	CSPr	HSPn	HSPr	OHSPn	OHSPr
Rha	0·2	1·1	0·3	3·5	4·4	9·1
Fuc	2·2	0·1	—	0·2	0·8	0·4
Ara	11·4	13·2	90·3	21·7	28·7	37·1
Xyl	15·6	1·3	0·2	1·6	7·9	2·5
Man	22·9	—	0·7	—	12·1	—
Gal	8·3	7·1	0·7	6·3	9·5	12·8
Glc	35·1	0·9	0·8	1·5	12·2	—
GalA	4·3	76·3	7·6	65·2	14·3	38·1
Fer/Ara	nd	1/119	1/48	1/23	nd	1/45

nd, Not determined

The main fractions from ion-exchange chromatography (CSPr, HSPn, HSPr and OHSPr) were chromatographed on Sephacryl S500 (Fig. 1). The pectic fractions CSPr and HSPr were highly polydisperse, and their neutral sugar distributions did not follow exactly those of the uronic acids. They showed one main galacturonic acid peak with close apparent molecular weights (K_{av} values of ~0·6), with higher molecular weight material in HSPr, and a heterogeneous distribution of the neutral sugars. The intrinsic viscosity of HSPr was 138 ml/g, giving a viscosity-average molecular weight of 29 700 Da (using the relation of Owens *et al.* (1946)). The arabinan fraction HSPn appeared to be highly homogeneous and of relatively low molecular weight (K_{av} ~ 0·7–0·8). OHSPr was eluted between K_{av} 0·6 and 0·9, and elution patterns of the neutral and acidic sugars were again different. Ferulic acid co-eluted with neutral sugars in HSPr, HSPn and OHSPr.

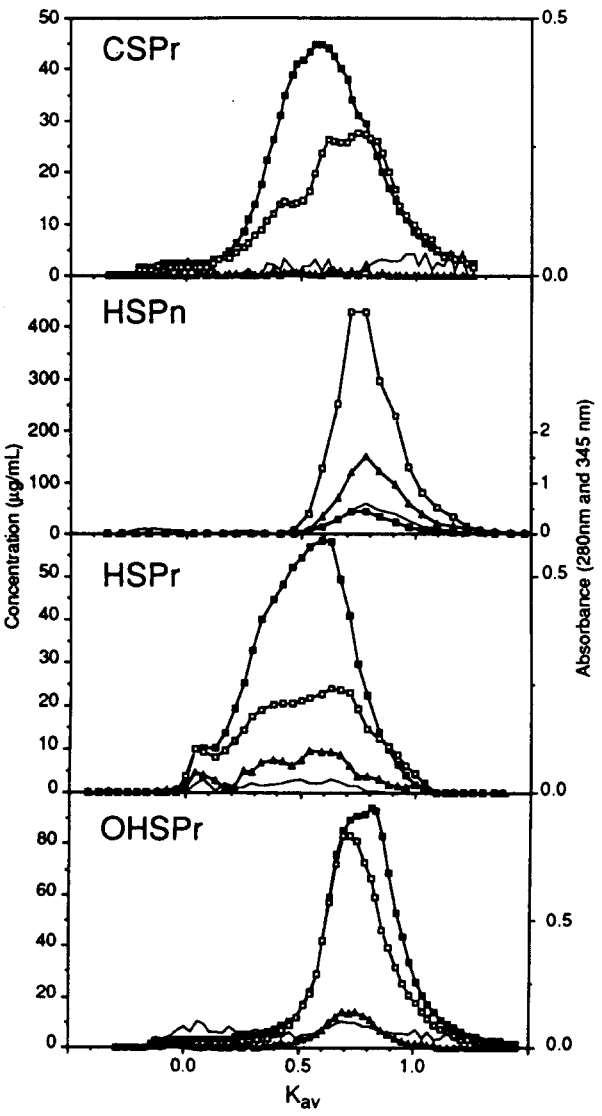

Fig. 1. Gel-filtration chromatography of the main pectic fraction on Sephacryl S500 (elution buffer: sodium succinate 0·1 M, pH 4·5). For coding of the fractions, see Table 3. (■) Uronic acids; (□) neutral sugars; (△) absorbance at 375 nm (ferulic acid); (—) absorbance at 280 nm (proteins).

Glycosidic linkage analysis of the pectic fractions HSPn, HSPr and OHSPr (Table 3) indicated that the pectin side chains were composed mostly of a 1,5-linked arabinan with substitution on O-3. HSPn was almost pure arabinan. In HSPr and OHSPr, the galactose appeared to be present mostly as type II galactan (1,6- and 1,3-linked galactose). Only about one-third of the rhamnose residues carried side chains (on O-4). OHSPr was very rich in rhamnose and the arabinose side chains of this fraction were less substituted than in HSP.

Characterisation of the hemicellulose fractions

The two hemicellulose extracts COHS1 and COHS2 were separated by ion-exchange chromatography into two main fractions with similar compositions (Table 4): COHS1n and COHS2n were rich in glucose and xylose, and contained some fucose and galactose, indicative of a fucogalactoxyloglucan. COHS1r and COHS2r were composed mostly of xylose (~70%), accompanied by uronic acid (identified by HPLC as glucuronic acid) and some arabinose, indicative of a glucuronoarabinoxylan. It also contained some galactose and rhamnose. The minor retained fractions COHS1r′ and COHS2r′ at higher buffer molarity were rich in rhamnose, arabinose and uronic acid, and appeared to be composed of residual pectic material.

The fractions COHS1n and COHS1r were further chromatographed on Sephacryl S500 (Fig. 2). COHS1n showed two peaks; the material eluting at the void volume was composed of xylose, glucose, mannose and galactose. The bulk of COHS1n eluted at $K_{av} \sim 0.7$. Its composition was characteristic of a fucogalactoxylo-

Table 3. Glycosidic linkage analysis of representative fractions from *Salicornia* cell walls

Methylethers	HSPn	HSPr	OHSPr	COHS1n	COHS1r
235 Ara	21·5	11·9	10·5	2·4	2·0
234 Ara	0·7		1·1	0·2	0·4
25 Ara	1·1	1·2	2·6	0·2	0·6
35 Ara	0·3		1·2	0·1	0·3
23 Ara	43·4	23·4	26·4	2·3	3·7
2 Ara	25·7	13·8	9·8	1·2	1·2
Ara	3·1	2·0	1·5		0·4
Total	95·8 (97·7)	53·4 (64·0)	53·1 (53·4)	6·4 (6·0)	8·6 (8·1)
2346 Gal		1·5	1·4	2·8	
246 Gal[a]		4·3	1·2		1·0
234 Gal		6·5	8·2		0·7
236 Gal	3·0	3·9	6·1		
346 Gal				5·2	
23 Gal		0·6	1·3		
24 Gal		1·6			
Total	3·0 (0·6)	18·5 (18·3)	18·3 (24·6)	8·0 (10·4)	1·7 (2·8)
34 Rha		15·7	16·3	0·4	0·5
3 Rha		8·1	7·7	0·5	0·5
Total	0 (0·3)	23·7 (10·2)	24·0 (16·7)	0·9 (1·4)	1·1 (1·9)
234 Xyl	0	1·1	0·7	10·3	1·7
23 Xyl.34 Xyl	0·6	0·9	0·5	11·6	70·5
3 Xyl.2 Xyl	0·5		2·8	0·6	14·5
Total	1·1 (0·2)	2·0 (2·4)	4·0 (4·8)	22·6 (26·3)	86·6 (84·5)
236 Glc		2·7	0·2	17·3	0·6
23 Glc				32·3	0·4
Total	(0·6)	2·7 (4·4)	0·2 (0)	49·6 (34·9)	1·0 (0·6)
234 Fuc		0·7	0·6	4·0	
Total	0 (0·0)	0·7 (0·7)	0·6 (0·5)	4·0 (3·9)	0 (0·1)
236 Man[a]				8·6	1·0
Total	0 (0·6)	0 (0)	0 (0)	8·6 (8·3)	1·0 (0·5)

Values in parenthesis: mol% found by the alditol acetates method.
[a]246 Gal and 236 Man were not separated.

Table 4. Sugar composition (mol%) of the fractions obtained from COHS1 and COHS2 by ion-exchange chromatography

	COHS1			COHS2		
	COHS1n	COHS1r	COHS1r′	COHS2n	COHS2r	COHS2r′
Rha	—	1·8	6·9	0·9	1·8	5·4
Fuc	3·6	—	—	3·9	—	—
Ara	6·9	5·5	14·3	7·8	6·6	26·2
Xyl	23·6	68·5	13·6	25·7	64·3	10·7
Man	8·3	—	7·1	6·2	1·8	—
Gal	10·0	2·7	6·6	8·6	3·2	13·1
Glc	37·2	—	—	40·5	—	3·5
Uronic acids	10·4	21·5	51·5	6·4	22·3	41·1

glucan. The identification of this fraction was confirmed by methylation analysis (Table 3). The glycosyl linkages evident were: terminal fucose, terminal and 2-substituted galactose, terminal and 2-substituted xylose, 4-substituted and 4,6-disubstituted glucose. The mannose was 4-linked, and probably present as a mannan. COHS1r eluted in one peak at $K_{av} \sim 0{\cdot}8$ with a shoulder at low K_{av} values, that had a slightly lower xylose content. COHS1r was composed mostly of 1,4-linked xylose. Approximately one-sixth of the xylose residues appeared to be substituted. The main substituent was glucuronic acid, explaining the low terminal/branched ratio found for this sample. Only one-quarter of the arabinose was terminal, indicating presence of short side chains rather than single residues, or residual contamination with an arabinan.

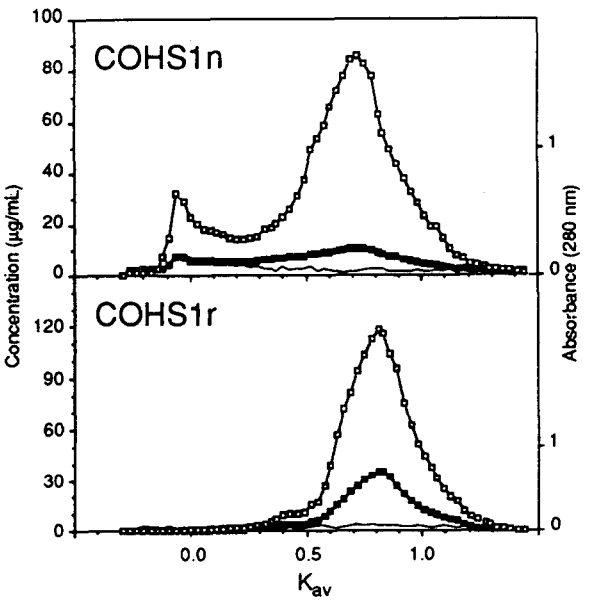

Fig. 2. Gel-filtration chromatography of the two ion-exchange fractions of COHS1 on Sephacryl S500 (elution buffer: sodium succinate 0·1 M, pH 4·5). (■) Uronic acids; (□) neutral sugars; (—) absorbance at 280 nm (proteins).

DISCUSSION

The cell walls of glasswort and notably their pectins showed a number of similarities with those of sugar-beet and spinach (Fry, 1983; Rombouts & Thibault, 1986; Guillon & Thibault, 1989). Their pectins are highly acetylated, as are those of sugar-beet (Pippen *et al.*, 1950), and they carry feruloyl substituents on their neutral side chains, as noted for spinach (Fry, 1983) and sugar-beet pulp (Rombouts & Thibault, 1986). As noted earlier (Rombouts & Thibault, 1986), the dilute alkali used for extraction of pectins (0·05 M NaOH) was not able to saponify the feruloyl esters. CDTA, a chelating agent often used for extraction of pectins (Selvendran & O'Neill, 1987), solubilises only a minor proportion of the glasswort pectins, which are mostly extracted with hot dilute acid. These pectins are very rich in neutral sugars, with unusually large proportions of arabinose and low amounts of xylose and glucose. The rhamnose to galacturonic acid ratios are high, indicating the presence of large neutral-side-chains-carrying ('hairy') regions (de Vries *et al.*, 1982). As with sugar-beet (Rombouts & Thibault, 1986), apple (Renard *et al.*, 1990) or carrot (Massiot *et al.*, 1988), these ratios increase from chelator-soluble to acid-soluble to alkali-soluble pectin. The hot acid extract contained a large proportion of almost neutral arabinan. This polysaccharide is probably generated by hydrolysis of 'hairy' regions of pectins molecules under the acidic extraction conditions, as it is not detected in the CDTA extract.

The hemicelluloses of the stem of glasswort appear different from those of sugar-beet pulp (Wen *et al.*, 1988). The concentrated alkali extracts were composed of almost equal amounts of fucogalactoxyloglucan and arabinoglucuronoxylan, together with minor amounts of residual pectic material. The simultaneous presence of those two types of hemicellulose was probably due to the presence of heterogeneous tissues, and notably secondary cell walls in vascular bundles (Massiot *et al.*, 1988). The arabinoglucuronoxylan was relatively linear, with only one substituted xylose out of six. The hemicelluloses had relatively low molecular masses. The K_{av}

value observed for the fucogalactoxyloglucan was similar to that obtained for apple fucogalactoxyloglucan. As in apple (Renard *et al.*, 1990), traces of fucogalactoxyloglucan were present in the first pectin extract (CSP), and could be detected in CSPn.

Compared to sugar-beet (Bertin *et al.*, 1988), and more generally to cell walls from other dicotyledons (Selvendran & O'Neill, 1987), the cell wall preparation was relatively poor in cellulose, and rich in proteins. However, that last value must be considered with care, as virtually all intracellular proteins coprecipitate with the AIS. Iraki *et al.* (1989) had found in carrot cells grown in hyperosmotic cultures a decrease of the cellulose content of the walls. The low cellulose content of the cell walls of *Salicornia* might be due to such a mechanism of diversion of carbon from synthesis of cell wall polysaccharides to osmotic adjustment (which occur in *Salicornia* by accumulation of organic compounds, e.g. betaïne, and salts).

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