ON THE CONTENT OF CELL-WALL CONSTITUENTS IN VARIOUS PLANT MATERIALS

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The cell-walls of plants are composed principally of carbohydrates and lignin. The cell-wall carbohydrates are polysaccharides made up of neutral and acidic sugar components. The most common of these polysaccharides is cellulose, while the others are classified under the general term of hemicelluloses.

Very few of the studies on cell-wall carbohydrates have included quantitative determinations of various sugar anhydrides. Such numerical data have been presented by GAILLARD (3, 4), WAITE and GORROD (12) and JARRIGE (5) chiefly on certain grasses and legumes. STERNKOPF (11) determined some hemicellulose constituents in green maize, while ANDREWS et al. (1) studied, mainly quantitatively, the polysaccharide composition of various plant leaves.

The purpose of the present investigation was to determine the quantitative composition of the cell-walls in different plants and in some cases in different parts of the same plant. The results obtained by the procedures used were compared with the amounts of membrane substances determined by the method of PALOHEIMO and PALOHEIMO (7) and with crude fibre.

Material and methods

The plant materials investigated included both feeding stuffs as well as plant material not intended for animal consumption. The analysis procedures have been described by the author in another paper (10). It can be mentioned, however, that fructosan in the grasses was extracted with cold water, and that also in this investigation all of the uronic anhydrides were included in the hemicellulose, since they were not separated into different fractions.

Table 1. Analytical data on the content of cell-wall constituents in various plant materials.

	% of dry weight: Hemicellulose: Neutral sugar anhydrides	Hemicellulose: Uronic anhydrides	Cellulose	Crude lignin	Total cell-wall substances	% of total cell-wall substances: Hemicellulose: Neutral sugar anhydrides	Hemicellulose: Uronic anhydrides	Cellulose	Crude lignin	% of total neutral sugar anhydrides of hemicellulose: Galactose anhydride	Glucose anhydride	Arabinose anhydride	Xylose anhydride	Mannose anhydride	Rhamnose anhydride	Crude protein, % of dry weight	Ash, % of dry weight
Timothy, leaf stage	12.4	4.7	16.1	3.5	36.7	33.8	12.8	43.9	9.5	10	15	25	50			20.0	6.9
Cocksfoot, pasture stage	16.2	4.8	22.2	4.4	45.6	35.5	10.5	44.3	9.6	10	20	20	50			17.2	11.3
Meadow fescue, »	15.1	5.1	21.1	4.9	46.2	32.7	11.0	45.7	10.6	10	20	20	50			18.8	13.0
Meadow grass, »	18.4	4.2	24.6	5.4	52.6	35.0	8.0	46.8	10.2	10	10	20	60			14.2	7.9
Cocksfoot, early heading stage	20.1	4.8	22.7	7.0	54.6	36.8	8.8	41.6	12.8	5	10	10	75			12.6	7.0
Meadow fescue, early heading stage	19.9	4.7	26.1	7.7	58.4	34.1	8.0	44.7	13.2	5	10	10	75			12.1	6.0
Timothy, blooming	20.1	4.2	28.6	9.3	62.2	32.3	6.8	46.0	14.9	5	10	10	75			8.6	5.6
» straw	23.0	4.0	29.0	12.2	68.2	33.7	5.9	42.5	17.9	5	10	10	75			4.4	4.9
Rye, straw	23.6	3.6	34.0	14.2	75.4	31.3	4.8	45.1	18.8	+++	5	10	85			2.8	6.0
Common reed (*Phragmites communis*) June 21	19.4	4.0	27.4	9.3	60.1	32.3	6.6	45.6	15.5	+++	5	10	85			16.3	9.4
Rush (*Scirpus lacuster*), Aug. 22	15.8	6.0	26.5	8.6	56.9	27.8	10.5	46.6	15.1	10	++	15	75			10.3	7.8
Sedge (*Carex gracilis*), June 22	18.0	5.8	23.9	10.6	58.3	30.9	10.0	41.0	18.1	5		20	75			17.5	6.1
Oat hulls	32.9	4.6	30.2	13.8	81.5	40.4	5.6	37.1	16.9	+++	5	10	85			1.4	6.3
Wheat bran	24.6	3.0	7.5	6.6	41.7	59.0	7.2	18.0	15.8	+++	5	40	55			15.7	6.7
Red clover, leaf stage ..	11.0	10.0	9.2	4.8	35.0	31.4	28.6	26.3	13.7	25	30	30	15	+	+	28.0	10.6
» blooming ..	12.6	10.2	16.9	10.4	50.1	25.1	20.4	33.7	20.8	20	15	25	40	+	+	15.2	7.2
» heads	10.8	11.0	12.8	11.4	46.0	23.5	23.9	27.8	24.8	30	20	30	20	+	+	20.0	6.4
» leaves	10.6	10.9	9.5	5.2	36.2	29.3	30.1	26.2	14.4	20	40	25	15	+	+	28.7	8.5
» blooming, upper halves of stalks	12.6	11.1	22.5	8.2	54.4	23.1	20.4	41.4	15.1	20	10	20	50	+	+	8.9	5.9
Red clover, blooming, lower halves of stalks	15.0	9.3	26.0	10.1	60.4	24.8	15.4	43.0	16.8	15	20	10	55	+	+	7.8	5.3
Lucerne, later leaf stage ..	11.4	10.4	12.8	5.9	40.5	28.1	25.7	31.6	14.6	25	25	25	25	+	+	27.4	11.5

Marrow-stem kale, leaves	10.2	12.9	7.8	3.6	34.5	29.6	37.4	22.6	10.4	30	30	30	10	+	++	20.2	15.2
Marrow-stem kale, stalk rind	11.4	16.9	14.0	1.8	44.1	25.9	38.3	31.7	4.1	30	10	40	20	+	++	7.5	11.1
Marrow-stem kale, vascular bundles	16.2	6.9	29.3	15.5	67.9	23.9	10.2	43.1	22.8	10	5	5	80	+		4.1	3.9
Swede, tops	10.5	12.6	8.2	3.8	35.1	29.9	35.9	23.4	10.8	30	30	30	10	++	++	25.4	10.5
» peeled	10.7	9.9	7.5	0.8	28.9	37.0	34.3	25.9	2.8	20	40	30	10	++		10.7	5.8
» rind	11.0	15.2	10.3	2.7	39.2	28.0	38.8	26.3	6.9	30	15	35	20	++	++	17.3	7.5
Sugar beet tops	7.7	8.3	6.6	3.6	26.2	29.4	31.7	25.2	13.7	30	+	60	10		++	16.0	14.2
» pulp	20.2	16.2	23.1	6.9	66.4	30.4	24.4	34.8	10.4	20	10	65	5		++	14.2	5.1
Chickweed (*Stellaria media*)	8.9	9.1	11.1	1.9	31.0	28.7	29.4	35.8	6.1	30	20	30	10	10	++	28.4	21.7
Birch leaves (*Betula verrucosa*)	11.3	9.0	7.2	14.4	41.9	27.0	21.5	17.2	34.3	25	25	25	25	+	++	19.8	3.9
Alder leaves (*Alnus incana*)	10.4	8.5	5.9	8.5	33.3	31.2	25.5	17.8	25.5	25	30	30	15	+	+	26.2	4.3
Aspen leaves (*Populus tremulus*)	10.7	8.8	9.3	10.1	38.9	27.5	22.6	23.9	26.0	20	20	30	30	+	+	18.7	4.3
Equisetum pratense, June 30	13.4	15.0	17.0	4.1	49.5	27.1	30.3	34.3	8.3	30	30	10	+++	30	+	20.7	15.4
Equisetum limosum, July 16	14.2	15.9	20.5	4.8	55.4	25.6	28.7	37.0	8.7	30	30	10	+	30	+	11.0	15.8
Dryopteris linnaeana, leaves, July 1	9.6	8.7	10.6	19.2	48.1	20.0	18.1	22.0	39.9	35	45	10	10	+	+	20.1	7.6
Sphagnum recurvum	22.4	13.8	19.8	3.4	59.4	37.7	23.2	33.4	5.7	40	25	5	25	5	++	6.5	3.9
Polytrichum commune	29.3	6.1	18.5	21.8	75.7	38.7	8.1	24.4	28.8	30	30	5	5	30	+	6.2	2.7
Cladonia rangiferina	64.5	2.8	10.1	3.0	80.4	80.2	3.5	12.6	3.7	35	25			40		3.9	2.6
Spruce wood (*Picea excelsa*)	17.6	3.3	46.0	24.1	91.0	19.4	3.6	50.4	26.5	10	10	10	30	40		0.3	0.2
Pine wood (*Pinus silvestris*)	14.7	3.4	39.6	25.1	83.0	17.7	4.3	47.7	30.3	10	10	10	30	40		0.6	0.2
Birch wood (*Betula verrucosa*)	21.5	4.2	40.0	15.7	81.4	26.4	5.2	49.1	19.3	++	++	+	100	+		0.2	0.2
Alder wood (*Alnus incana*)	18.3	4.8	35.7	19.0	77.8	23.5	6.2	45.9	24.4	5	10	+++	85	+		1.6	0.3

Results and discussion

Table 1 presents the contents of cell-wall carbohydrates and crude lignin as determined by the author's analysis scheme. In order to characterize the nature of the samples, the crude protein and ash contents are also shown.

The first plant group consists of various grasses as well as two sedge plants. Also oat hulls and wheat bran are listed there. A characteristic feature of the grasses is the high content of cellulose and hemicellulose, which, with the exception of uronic anhydrides, increases with age. The composition of the hemicellulose in the different grass species of the same growth stage is rather similar. Xylose anhydride is the dominating component already at the early leaf stage, and its proportion increases in older plants. Anhydrides of galactose, glucose and arabinose occur to some extent in plants of all ages. The cell-wall carbohydrate composition of rush and sedge resembles very closely that of the grasses. The quantitative nature of their hemicellulose is also similar, except that they contain slightly more uronic anhydrides. The composition of oats hulls is comparable to that of straw, whereas wheat bran differs appreciably from the other plant materials included in this group.

The composition of leguminous cell-walls diverges widely from that of the grasses. The former contain less cellulose and also less neutral sugar anhydrides of hemicellulose, while their content of uronic anhydrides is more than double that of the grasses. The cellulose content of clovers increases as the plant ages, but the increase in hemicellulose is quite small and the uronic anhydride content is independent of the growth stage, just as is the case with the grasses. The composition of clover leaves at the flowering stage of the plant is approximately the same as that of young clover plants in the spring at the leafy stage; the flowers and buds contain more cell-wall substances than the leaves, and the stalks are especially rich in cellulose and lignin. All the analysis results from lucerne agree with what would be expected from clover at the same growth stage. The composition of hemicellulose in legumes differs greatly from that in grasses and segde plants. The principal neutral sugar anhydrides are the same as in grasses and in angiosperms as a whole, but the xylose content of clover is relatively low. The legume samples also showed traces of mannose and rhamnose, which are lacking in the grasses.

A distinguishing feature of root crops and their tops is the high sugar content and the low cell-wall content. Of the latter group of substances, uronic anhydrides are abundant and xylose anhydrides scanty. The hemicellulose composition in tops of the same genus is quite similar, a feature noted also in other related plants. This appears to be a suitable characteristic for the chemical taxonomy of plants. The cell-wall composition of the leaves and stem cortex of marrow-stem kale is similar, while that of the vascular bundles of the stem resembles wood and straw. The rind of swedes is richer in cell-wall substances, especially xylose, than the leaves of the plant, while the pulp is very low in such substances, as was to be excepted. The content of uronic anhydrides in this group of plant materials is high, particularly in the rind; this is also evident from the composition of sugar beet pulp. The compound involved is evidently galacturonic anhydride, characteristic of pectic substances. *Stellaria media*, a common weed in fields of root crops, resembles in its cell-wall composition the tops of root crops. The hemicellulose composition of this plant is unusual, since it is the only one of the angiosperms studied by the author in which there were more than traces of mannose anhydride.

The leaves of trees are found to contain surprisingly small amounts of cell-wall polysaccharides. Their total amount, together with crude lignin, make up only about 40 % of the dry matter. It is also notable that such leaves contain 9.5—12 % sugars and even 9.5—12 % crude fat (according to PALOHEIMO et al., 8), so that only 15 % is undetermined substances, and these include organic acids other than uronic acids.

Although the analysis procedure is intended for animal feeding stuffs, it is apparently suitable also for cryptogams and woody materials, even though some cases give erroneous values for crude lignin. For instance, the unusually high lignin content of the hair-cap moss (*Polytrichum*) is due to the fact that the core of its stem does not dissolve in the polysaccharide hydrolysis used. On the other hand, the low percentage of lignin in hard woods as compared with soft woods arises from the fact that certain materials in hard wood, which some investigators regard as lignin, dissolve in diluted acid, in this case in the hemicellulose hydrolysing solution (cf. 9).

The different families of cryptogamous plants investigated in the present studies differ greatly from one another in their cell-wall composition. Common to all of them are their abundance of mannose anhydride and their deficiency of pentose anhydrides. Large amounts of uronic anhydrides are found in *Equisetum* and *Sphagnum*. Lichen (*Gladonia*) is exceptional, since no pentose anhydrides are to be found in it.

The hemicellulose polysaccharides in wood are readily hydrolysable in the conventional acidic solution, since the combined amounts of mannose and xylose in the cellulose hydrolysate make up only 10—15 % of the total sugars. There is more mannose than xylose. Distinct differences are observed in the hemicellulose composition between hard and soft wood. In the former, hemicellulose is composed principally of xylose anhydride, while in the latter mannose anhydride is the primary component.

In Table 2 the sum of the cell-wall constituents is compared with Paloheimo's membrane substances and crude fibre. In column c it can be seen that the membrane substances amount to 35—115 % of the above-mentioned sum. In grasses there are only small amounts of cell-wall materials which are soluble in dilute acid. The leaves and flowers of red clover are more readily soluble than grasses, while the stems are less easily dissolved. Root crops and their tops, as well as the leaves of trees, are also readily soluble. In wood, clover stalks and certain other plant materials the membrane substance percentage was found to be higher than the sum of the cell-wall fractions. This may be due to several reasons: to analytical errors, to the presence in the cell-walls of organic components other than carbohydrates and lignin, or to the fact that lignin dissolves more readily in the concentrated acid used in the polysaccharide hydrolysis than in the dilute acid used for determining the membrane substances. This latter dilute solution consisted of 0.05 N hydrochloric acid. It is somewhat

Table 2. Cell-wall contents of the materials in Table 1 compared to the membrane substances (Paloheimo's method) and crude fibre.

	a	b	c	d	e	f
	Total cell-wall substances from Table 1.	Membrane substances (Paloheimo's method) % of dry wt.	% of item a	Crude fibre % of dry wt.	% of item a	Ratio cellulose: crude fibre
Timothy, leaf stage	36.7	30.9	84.2	18.3	49.9	1: 1.14
Cocksfoot, pasture stage	45.6	34.8	76.3	24.6	53.9	1: 1.11
Meadow fescue, pasture stage	46.2	34.6	74.9	23.6	51.1	1: 1.12
Meadow grass, pasture stage	52.6	45.0	85.6	28.2	53.6	1: 1.15
Cocksfoot, early heading stage	54.6	47.8	87.5	28.4	52.0	1: 1.25
Meadow fescue, early heading stage	58.4	52.0	89.0	32.0	54.8	1: 1.23
Timothy, blooming	62.2	56.2	90.4	35.2	56.6	1: 1.23
» straw	68.2	61.3	89.9	37.4	54.8	1: 1.29
Rye, straw	75.4	79.1	104.9	47.5	63.0	1: 1.40
Common reed (*Phragmites communis*)	60.1	57.8	96.2	34.0	56.6	1: 1.24
Rush (*Scirpus lacuster*)	56.9	53.6	94.2	31.3	55.0	1: 1.18
Sedge (*Carex gracilis*)	58.3	52.4	89.9	29.1	49.9	1: 1.22
Oat hulls	81.5	79.1	97.1	40.1	49.2	1: 1.33
Wheat bran	41.7	20.0	48.0	10.5	25.2	1: 1.40
Red clover, leaf stage	35.0	18.0	51.4	11.3	32.3	1: 1.23
» blooming	50.1	38.9	77.6	27.8	55.5	1: 1.64
» » heads	46.0	29.5	64.1	21.6	47.0	1: 1.69
» » leaves	36.2	16.6	45.9	11.2	30.9	1: 1.18
» » upper halves of stalks	54.4	59.8	110.0	42.2	77.6	1: 1.88
» » lower » »	60.4	64.5	106.8	47.8	79.1	1: 1.84
Lucerne, later leaf stage	40.5	26.7	65.9	18.9	46.7	1: 1.48
Marrow-stem kale, leaves	34.5	21.4	62.0	11.3	32.8	1: 1.45
» » stalk rind	44.1	25.9	58.7	17.0	38.5	1: 1.22
» » vascular bundles	67.9	74.2	109.3	53.8	79.2	1: 1.84
Swede, tops	35.1	18.2	51.9	10.6	30.2	1: 1.29
» peeled	28.9	10.2	35.3	7.6	26.3	1: 1.01
» rind	39.2	19.0	48.5	13.3	33.9	1: 1.29
Sugar beet tops	26.2	15.5	59.2	9.4	35.9	1: 1.42
» pulp	66.4	37.8	56.9	24.4	36.7	1: 1.06
Chickweed (*Stellaria media*)	31.0	21.0	67.7	12.6	40.6	1: 1.14
Birch leaves (*Betula verrucosa*)	41.9	23.5	56.1	15.6	37.2	1: 2.17
Alder » (*Alnus incana*)	33.3	15.9	47.7	12.8	38.4	1: 2.17
Aspen » (*Populus tremula*)	38.9	24.6	63.2	18.3	47.0	1: 1.97
Equisetum pratense	49.5	32.2	65.1	20.0	40.4	1: 1.18
» *limosum*	55.4	40.9	73.8	24.7	44.6	1: 1.20
Dryopteris linnaeana, leaves	48.1	28.2	58.6	15.6	32.4	1: 1.47
Sphagnum recurvum	59.4	67.3	113.3	45.9	77.3	1: 2.32
Polytrichum commune	75.7	69.0	91.1	33.8	44.6	1: 1.83
Cladonia rangiferina	80.4	69.1	85.9	30.7	38.2	1: 3.04
Spruce wood (*Picea excelsa*)	91.0	92.2	101.3	75.0	82.4	1: 1.63
Pine » (*Pinus silvestris*)	83.0	88.2	106.3	70.4	84.8	1: 1.78
Birch » (*Betula verrucosa*)	81.4	91.6	112.5	63.2	77.6	1: 1.58
Alder » (*Alnus incana*)	77.8	89.7	115.3	63.6	81.7	1: 1.78

surprising to observe that even with such mild hydrolysis, more than one-half of the total cell-wall substances in certain plant materials dissolved.

According to the data in the last column in Table 2, crude fibre makes up 25—85 % of the sum of the cell-wall constituents. Crude fibre is regarded as containing only a part of the cell-wall substances, and the composition of this part has been found by many investigators to vary in different plants materials (e.g. 2, 6). In the present experiments a definite correlation is to be seen between the solubilities in the membrane and crude fibre determination processes. Another observation which can be made is that in all the materials in which the crude fibre exceeded 60 % of the sum of the cell-wall components, the membrane percentage was higher than this sum.

Since crude fibre is considered as roughly corresponding to the amount of cellulose, comparisons are made in the last column between the cellulose and fibre contents. In general, the amount of crude fibre is 1—2 times that of cellulose. In a couple of the cryptogams and in the leaves of trees the figure is above 2. In this respect there are differences between different plant species. At an early growth stage the difference between the cellulose and crude fibre percentages is smaller than at later stages, and in some delicate plant tissues there is practically no difference between the amounts of cellulose and crude fibre.

Summary

In this investigation, analyses were made of the contents of hemicellulose, cellulose, crude lignin, crude protein and ash in 43 different plant materials. In addition, the proportions of various sugar anhydrides in the hemicellulose fraction were determined. The carbohydrate analyses were made by hydrolysing to monosaccharides, except for the uronic anhydrides, which were determined by the decarboxylation method. The sum of the cell-wall constituents thus determined was subsequently compared with Paloheimo's membrane substances and crude fibre.

Large variations in the cell-wall composition were found between different plant materials. Furthermore, there were large differences in the solubility of the cell-wall substances of different plant materials in the hydrolysing procedures used in determinations of membrane substances and crude fibre.

The hemicellulose composition of different species in the same genus and even in the same family was found to be similar in definite plant parts and at definite growth stages. This appears to be a generic characteristic in the chemical taxonomy of plants.

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SELOSTUS:

SOLUSEINÄMIEN KOOSTUMUKSESTA ERILAISISSA KASVIAINEISSA

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Yliopiston kotieläintieteen laitos, Helsinki.

Kasvien soluseinämät ovat koostuneet pääasiassa hiilihydraateista ja ligniinistä. Soluseinämähiilihydraatit ovat neutraaleista ja happamista sokeriyksiköistä rakentuneita polysakkarideja. Näistä on selluloosa yleisin. Muista käytetään tavallisesti yhteisnimitystä hemiselluloosa.

Tutkimuksessa esitetään 43 eri kasvimateriaalin hemiselluloosa-, selluloosa-, raakaligniini-, raakaproteiini- ja tuhkapitoisuus sekä hemiselluloosafraktiosta lisäksi eri sokerianhydridien osuudet. Edelleen siinä verrataan soluseinämäaineiden summaa Paloheimon menetelmällä määritettyyn kettoaineeseen sekä raakakuituun.

Tutkimuksessa todettiin suuria eroja eri kasviaineiden soluseinämäainekoostumuksessa ja samoin soluseinämäaineiden liukoisuudessa kettoaine- ja raakakuitukeitoissa.

Saman kasvisuvun ja kasviheimonkin eri lajien hemiselluloosan koostumus todettiin hyvin samanlaiseksi tietyssä kasvuvaiheessa ja tietyssä kasvinosassa. Se näyttää olevan eräs kasvien kemialliseen taksonomiaan sopiva lajituntomerkki.