(H. V. Street, unpublished work). This is not in agreement with the work of McGeachin *et al.* (1957). These workers used the method of Van Loon *et al.* (1952), which is similar to the method of Street & Close (1956), the main difference being that starch is used as substrate instead of amylose as in the present method.

When the method of Van Loon *et al.* (1952) was applied with starch as substrate the results of McGeachin *et al.* (1957) could still not be confirmed, although citrate still inhibited amylase activity.

SUMMARY

1. The effect of citrate on the amylase activity of blood serum, urine and saliva has been investi-

gated and it has been shown that it inhibits the enzyme.

2. *iso*Citrate, malate, lactate, glycollate, α -aminoacetate, tartrate, *cis*-aconitate, glutarate, β -hydroxy- β -methylglutarate, tricarballoylate and oxalate have no effect on amylase activity.

3. Borate ions activate amylase activity.

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Oligosaccharides and Associated Glycosidases in Aspen Tissues

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The low-molecular-weight carbohydrates present in the saps of various trees have recently been reviewed by Stewart (1957). Relatively few reports on carbohydrases and transferase activities in tree tissues are to be found in the literature, however.

This paper describes studies with quaking (*Populus tremuloides*) and bigtooth (*P. grandidentata*) aspens, where, in addition to glucose and fructose (and a trace of xylose) the main sugar present in both xylem (1-year-old-xylem elements) and 'soft xylem' (newly differentiated tissue consisting of fibres, vessels and some cambial cells) is sucrose. Photomicrographs and a full description of these tissues have been given by Kremers (1957).

Small amounts of raffinose are also present, particularly in the xylem, and *O*- α -D-glucopyranosyl-(1 $\rightarrow$ 2)-*O*- β -D-fructofuranosyl-(1 $\rightarrow$ 2)- β -D-fructofuranoside (1^F- β -fructosylsucrose) has been identified as a component of the 'soft xylem'. Protein preparations from the cambial region of aspen show glycosidase and transferase activities.

MATERIALS AND METHODS

Healthy trees were selected in an experimental forest at the start of the growing season; they were in full leaf. Within 10–15 min. of felling, the tissues required for sugar analyses were collected and quickly placed in absolute

methanol. 'Soft-xylem' material was obtained by removing the bark from the bole and then slicing off the tissue with a knife blade held flat against the surface of the wood. Xylem was subsequently removed with a spokeshave.

All concentrations are expressed as g. of solute/100 ml. of solution unless otherwise stated.

Isolation and characterization of sugars. The collected tissues were filtered off from the methanol and re-extracted with hot methanol. The two methanolic solutions were then combined and concentrated to syrups by distillation under reduced pressure. These were examined on paper chromatograms (Whatman no. 1 paper) with ethyl acetate-acetic acid-water (A; 9:2:2, by vol.), butan-1-ol-pyridine-water (B; 6:4:3, by vol.) and propan-1-ol-ethyl acetate-water (C; 7:1:2, by vol.) solvents. *p*-Anisidine-HCl and resorcinol-HCl (Hough, Jones & Wadman, 1950) were used as spray reagents.

Small quantities of suspected sucrose and raffinose were isolated from xylem extracts (*P. grandidentata*) by partition chromatography on Whatman no. 3 MM paper with solvent A. Total hydrolysis of the raffinose was effected by heating at 95° with N-H₂SO₄ for 3 hr. The acid was then neutralized with BaCO₃ and the hydrolysate examined on paper chromatograms (solvent A). Yeast invertase (35°; 20 hr.) was used for a partial hydrolysis and the resulting products were again examined on paper chromatograms (solvents A and B).

1^F- β -Fructosylsucrose was obtained by passing an aqueous solution of the methanol extract of 'soft xylem' (*P. tremuloides*) through a small charcoal-Celite column (Andrews, Hough & Powell, 1956). The monosaccharides were eluted from the column with water and sucrose with aqueous 2.5% (v/v) ethanol. Elution with aqueous 50%

(v/v) ethanol removed the trisaccharide and on increasing the ethanol concentration in this fraction deliquescent crystals resulted. Recrystallization from ethanol containing a trace of water produced a stable white compound, m.p. 193°. Total acid and invertase hydrolyses were carried out as described for raffinose. With the invertase the glucose and fructose produced were determined quantitatively (Pridham, 1956). A partial acid hydrolysis of the trisaccharide was effected by heating with aqueous acetic acid (20%, v/v) for 6 hr. at 45° and the hydrolysate was examined on paper chromatograms (solvent A). The trisaccharide was also examined by high-voltage paper electrophoresis (0.1 M-borate buffer, pH 10.0; Gross, 1954).

Aspen-enzyme preparation. A series of different tissues were removed from the bole of a specimen of *P. grandidentata* and, after extraction with hot methanol, were analysed for N (micro-Kjeldahl method).

'Soft phloem' (180 g.; tissue consisting of young phloem and cambial elements) was removed with a knife from the inner bark of a young aspen (*P. grandidentata*) and immediately macerated with 0.1 M-phosphate buffer (pH 7.0; 800 ml.; 5°) containing sodium dithionite (0.1%), to prevent browning. The extract was filtered through glass wool, centrifuged at 3000 rev./min. and then dialysed against distilled water (5°) for 3-4 days in the presence of toluene. The resulting precipitate was removed by centrifuging. Ammonium sulphate was then added successively to the dialysed extract to 25 and 50% saturation. The precipitate resulting at the lower salt concentration was discarded but the bulk of the protein, which came down at the higher saturation, was filtered off, taken up in water and then dialysed under toluene against distilled water for 3-4 days (5°). The required amount of Na_2HPO_4 and NaH_2PO_4 to buffer the solution at pH 7.0 (0.1 M) was then added with continual stirring, the solution being kept at 5°.

The aspen-enzyme preparation (5 ml.) was incubated in the presence of toluene (37°) with phenyl- α -D-glucoside, maltose, phenyl- β -D-glucoside, cellobiose, arbutin, salicin, sucrose, raffinose, 4-O- β -D-xylopyranosyl-D-xylopyranose, potato starch and citrus pectin, each at a concentration of 5%. Incubations with 10% sucrose and 0.5% arbutin were also carried out, and all substrates were incubated with boiled-enzyme preparations to serve as controls. After

incubation for 48 hr. the solutions were examined on paper chromatograms for sugars, with the *p*-anisidine-HCl spray reagent (solvent A). Where arbutin was used as substrate the chromatograms [butan-1-ol-ethanol-water (D; 40:11:19, by vol.) and B solvents] were also examined for phenolic compounds by the use of diazotized *p*-nitroaniline- Na_2CO_3 spray reagent (Swain, 1953).

An unidentified phenolic compound (I) which was formed with arbutin (5%) as substrate was isolated as a brown syrup by partition on Whatman no. 3 MM paper (solvent D). Compound (I) was hydrolysed with $\text{N-H}_2\text{SO}_4$ (2 hr.; 95°) and the hydrolysate examined on paper chromatograms with solvents A and D.

The rates of formation of compound (I) and glucose were followed by incubating aspen protein (30 mg., freeze-dried from aqueous solution) with arbutin (1.0%) in 0.1 M-phosphate buffer (10 ml.; pH 6.1) at 37°. Samples (1 ml.) were withdrawn at various intervals of time, deproteinized by the method of Sevag, Lackman & Smollens (1938) and the free glucose and (I) were determined by quantitative paper-chromatographic methods (Pridham, 1956, 1957; Fig. 1).

The effect of D-glucose (1.0%) and D-glucono-1:4-lactone (0.19%) on the formation of compound (I) was studied by incubating these compounds with arbutin (5.0%) and the aspen enzyme. Attempts were also made to synthesize *p*-hydroxyphenyl glucosides by incubating the enzyme with a mixture of quinal (1.0%) and (i) D-glucose (3.0%) and (ii) gentiobiose (3.0%).

RESULTS

Paper-chromatographic studies with methanol extracts of the xylem and 'soft xylem' of *P. tremuloides* and *P. grandidentata* showed clearly that glucose, fructose and sucrose (and generally a trace of xylose) were present in all cases. Sucrose was characterized by crystallization from aqueous ethanol [m.p. 179°; $[\alpha]_D^{25} + 64.7^\circ$ in water (c, 10.0)] and by the preparation of the octa-acetate (m.p. 85-88°, mixed m.p. 86-88°).

A compound which cochromatographed with raffinose in two solvent systems was also detected; it was chiefly present in the xylem extracts. This sugar gave a yellow spot with *p*-anisidine-HCl and a pink colour with resorcinol-HCl, both of these reactions being indicative of a ketose-containing compound. Total acid hydrolysis yielded galactose, glucose and fructose and yeast invertase produced fructose and a disaccharide which cochromatographed with melibiose in acidic and basic solvent systems. Traces of high-molecular-weight sugars which may have belonged to the 'raffinose family' were also present.

In 'soft-xylem' extracts from both aspen species a sugar was detected which was chromatographically and electrophoretically indistinguishable from 1^F- β -fructosylsucrose. With these last-named techniques it was possible to distinguish between 1^F- β -fructosylsucrose and the isomeric trisaccharides 6^F- β -fructosylsucrose [*O*- α -D-glucopyranosyl-(1 $\rightarrow$ 2)-

Fig. 1. Incubation of aspen enzyme with arbutin (1.0%) at pH 6.1. O, *p*-Hydroxyphenyl- β -gentiobioside; Δ , free glucose.

O- β -D-fructofuranosyl-(6 $\rightarrow$ 2)- β -D-fructofuranoside] and 6^G- β -fructosylsucrose [*O*- β -D-fructofuranosyl-(2 $\rightarrow$ 6)- α -D-glucopyranosyl-(1 $\rightarrow$ 2)- β -D-fructofuranoside]. Complete acid hydrolysis yielded only glucose and fructose and treatment with dilute aqueous acetic acid produced mainly sucrose, together with some glucose and fructose. Yeast invertase completely degraded the sugar to glucose and fructose in a molar ratio of 1:2.

A determination of the alcohol-insoluble nitrogenous compounds in various tissues from aspen (Table 1) suggested that the highest protein concentration in the bole of the tree occurred in the cambial region (cf. Stewart, 1957).

On the basis of these results a protein solution was prepared from the 'soft-phloem' tissues and tested for carbohydrase and transferase activities. The results of this study are shown in Table 2. α -Glucosidase, β -glucosidase, α -galactosidase and sucrase all appear to be present in the preparation. With sucrose at 5% concentration only glucose and fructose were formed. However, with 10% of substrate there was definite evidence for the formation of 1^F- β -fructosylsucrose after incubation for 7 hr., and after 48 hr. there was a marked increase in the amount produced. Transferase activity was

also very apparent when arbutin was used as a substrate. In addition to the hydrolytic products, glucose and quinol, a slow-moving phenolic compound (I) was also detected on chromatograms [R_f values: solvent D, 0.25; solvent B, 0.38] at substrate concentrations of 0.5 and 5.0%. Compound (I) gave the same purple colour as arbutin with the diazonium reagent and was chromatographically identical to (*p*-hydroxyphenyl)- β -gentiobioside. Acid hydrolysis of compound (I) gave rise to quinol and glucose. The formation of (I) and the liberation of glucose was followed during the incubation of arbutin with aspen protein. As the concentration of compound (I) reached a maximum there was a rapid increase in the amount of free glucose in solution (Fig. 1). The inclusion of D-glucono-1:4-lactone or D-glucose in the reaction mixtures completely inhibited the formation of (I) and neither arbutin nor (I) was formed when D-glucose or gentiobiose and quinol were incubated with the aspen protein.

DISCUSSION

D-Glucose, D-fructose and sucrose commonly occur as free sugars in all plants. Raffinose, which has been detected chromatographically in sieve-tube exudates from a number of trees (Zimmermann, 1957) frequently accompanies sucrose in plant tissues (e.g. French, 1954; Bradfield & Flood, 1950; Cerbulis, 1955; Pridham, 1958) and D-xylose has also been detected in the free state in plants: for example, in fruits (Hay & Pridham, 1953; Ash & Reynolds, 1955) and in heartwood (Kritchevsky & Anderson, 1955).

The literature on the isomeric trisaccharides, 1^F- β -fructosylsucrose, 6^F- β -fructosylsucrose and 6^G- β -fructosylsucrose, is extensive. All these

Table 1. *Protein nitrogen in aspen tissues*

	N (%)
<i>P. grandidentata</i>	
Periderm	0.56
Secondary phloem	0.21
'Soft phloem'	1.34
<i>P. tremuloides</i> *	
'Soft xylem'	1.40
1-year-old xylem	0.28
2-year-old xylem	0.08

* Results obtained by Sultze (1956).

Table 2. *Carbohydrase and transferase activities of aspen-protein solution*

Substrate	Products detected by <i>p</i> -anisidine-HCl spray reagent	
Phenyl- α -D-glucoside	Glucose	—
Maltose	Glucose and trisaccharide (R_{glucose} 0.11; solvent A)	—
Phenyl- β -D-glucoside	Glucose	—
Cellobiose	Glucose and trisaccharide (R_{glucose} 0.11; solvent A)	—
Sucrose	Glucose, fructose and 1 ^F - β -fructosylsucrose	1 ^F - β -Fructosylsucrose formed only with substrate concentration of 10%
Potato starch	Glucose, disaccharide and trisaccharide	Hydrolysis products present only in traces
Citrus pectin	Galacturonic acid, galactose, arabinose	Present only in small amounts
Salicin	Glucose	—
Raffinose	Sucrose, galactose, glucose and fructose	Main products over 24 hr. incubation were galactose and sucrose
4- <i>O</i> - β -D-Xylopyranosyl-D-xylopyranose	Xylose	Only slight hydrolysis

compounds have been synthesized by the action of transfructosidases from various organisms on sucrose. 1^F - β -Fructosylsucrose and 6^G - β -fructosylsucrose were prepared by Allen & Bacon (1956) with enzymes from sugar-beet leaves and other plants and by Bacon (1954) and Gross, Blanchard & Bell (1954) with yeast invertase. 1^F - β -Fructosylsucrose has also been prepared by incubating sucrose with various fungal enzymes (Pazur, 1952; Barker & Carrington, 1953; Barker, Bourne & Carrington, 1954; Bacon & Bell, 1953) and with preparations from Jerusalem-artichoke tubers (Dedonder, 1952a) and *Aerobacter levanicum* (Feingold, Avigad & Hestrin, 1956). With *A. levanicum* 6^F - β -fructosylsucrose was also produced, as was the case with yeast invertase and sucrose (Albon, Bell, Blanchard, Gross & Rundell, 1953; Bacon, 1954).

With regard to the natural occurrence of these compounds in plant tissues, 1^F - β -fructosylsucrose and higher homologues have been found in artichoke tubers (Bacon & Edelman, 1951; Dedonder, 1952b), and this trisaccharide, together with 6^G - β -fructosylsucrose, has recently been reported to be present in onion, leek, Italian ryegrass and tall oatgrass. 6^F - β -Fructosylsucrose may also occur in these grasses (Bacon, 1959) and its presence in perennial ryegrass has definitely been established by Schlubach, Lübbers & Borowski (1955). 6^G - β -Fructosylsucrose has tentatively been identified in extracts from ripe bananas by Henderson, Morton & Rawlinson (1959), and these workers have shown that banana preparations exhibiting invertase activity can synthesize fructosylsucrose derivatives from sucrose. Fructose-containing oligosaccharides have also been tentatively identified by paper-chromatographic methods in a number of other plant species. These have been listed by Bacon (1959).

In general it would appear that the fructosylsucrose derivatives are peculiar to plant tissues which have relatively high sucrose concentrations. This is particularly well illustrated with the onion, where the only scales having the oligosaccharides are those towards the centre of the bulb, which have high sucrose concentrations (Bacon, 1959). Also in the banana the formation of 6^G - β -fructosylsucrose occurs as the fruit ripens and the glucose, fructose and sucrose content increases. In aspen the 1^F - β -fructosylsucrose would appear to accumulate in the cambial region, which again has a high sucrose concentration (Kremers, 1957). Under such conditions the formation of 1^F - β -fructosylsucrose by a transfructosidase would be favoured. No trisaccharide was detected in the xylem, where the sucrose concentration is much lower; however, this could also be due to the absence of the necessary transferase in this tissue. High sucrose concentrations (10–20%) have also commonly been used

to prepare fructosylsucrose derivatives (*in vitro*) with the various transfructosylases that have been mentioned, and with the aspen enzyme a substrate concentration of 10% was apparently necessary in order to produce detectable amounts of 1^F - β -fructosylsucrose within a reasonable period of incubation. No detailed search for other fructosylsucrose derivatives was undertaken and the possibility that such compounds were also present in 'soft xylem' or the aspen-protein incubation mixtures or in both should not be ignored.

A further general point is that, in the majority of cases, naturally occurring fructosylsucrose derivatives have been isolated only from plant-storage tissues. With aspen, however, the trisaccharide is present in a meristematic tissue with a high metabolic activity.

The examination of the enzymic activity of the 'soft-phloem' proteins showed that many of the commonly occurring plant glycosidases (Sumner & Myrbäck, 1950) are present in these aspen tissues. The results are supported by the observations of Sosa (1940) and Bois & Chubb (1942), who have detected invertase, maltase, emulsin and amylase in species of birch, and by Kuprevich (1949) and Meeuse (1949, 1952), who report amylase activities in other deciduous trees. Zimmermann (1958) believes that there is an α -galactosidase in sieve-tube cytoplasm. The importance and exact functions of these enzymes in trees, as in other plants, remain obscure.

Transglucosylation and transfructosylation reactions were also evident where sucrose and arbutin were used as substrates. In the latter case the mechanism would appear to be a β -glucosidase-catalysed transfer of glucose from arbutin to a second arbutin-acceptor molecule, similar reactions having been demonstrated with enzyme preparations from broad-bean and almond seeds (J. D. Anderson, L. Hough & J. B. Pridham, unpublished results). Evidence to support this mechanism is given by the fact that β -glucosides were readily hydrolysed by the protein preparation and this activity and the synthesis of (*p*-hydroxyphenyl)- β -gentiobioside were completely suppressed by D-glucono-1:4-lactone (Conchie & Levvy, 1955) and D-glucose (Jermyn, 1955), both of which can inhibit β -glucosidase. Attempts to use quinol as a direct acceptor of glucose failed; the purification procedure used for the enzyme preparation makes it unlikely that uridine diphosphate glucose is participating in the reaction.

SUMMARY

1. Sucrose is the main oligosaccharide present in both the cambial region and young-xylem elements of aspen.

2. Raffinose and 1^F - β -fructosylsucrose are also present, the former being mainly associated with the xylem and the latter with the 'soft xylem'.

3. A protein preparation from the 'soft phloem', when incubated with sucrose, produced glucose, fructose and 1^F - β -fructosylsucrose. The preparation also exhibited marked α - and β -glucosidase and α -galactosidase activities.

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Condensed Tannins

4. THE DISTRIBUTION AND DEPOSITION OF TANNINS IN THE HEARTWOODS OF *ACACIA MOLLISSIMA* AND *SCHINOPSIS* SPP.*

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The pattern of the distribution of monomeric and polymeric leucofisetinidins, of tannins and non-tannins, and of the number-average molecular weight of the tannins in a cross-section of the heartwood of *Schinopsis quebracho-colorado* (syn. *S.*

lorentzii) was examined by Roux (1958b) and by Roux & Evelyn (1958b). A possible mechanism for the formation of tannins in quebracho woods (*Schinopsis* spp.) has been discussed by White (1958). This work has now been extended to include the vertical distribution of heartwood components, and in the present study comparisons are also made

* Part 3: Roux & Maihs (1960).