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THE DISTRIBUTION OF CARBOHYDRATES IN ROOT AND STEM TISSUES OF THE TOMATO PLANT

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1. Introduction

During investigations on the nitrogen metabolism of tomato plants, knowledge of the qualitative and quantitative composition of the carbohydrates of various organs and tissues of these plants proved to be indispensable. As far as the author is aware no detailed data are available on the composition and distribution of the carbohydrates of the tomato plant. It is the purpose of this paper to report briefly some results which were obtained in a number of analyses of various parts and tissues of the stem-main root axis of the tomato plant.

2. Plants and methods

The experimental plant material consisted of tomato plants (Ailsa Craig) of 3 to 4 months old, grown in the greenhouse in sand culture.

From freshly excised plant parts the sugar fraction was extracted by repeated grinding in 80 to 90 per cent ethanol. The resulting homogenates were centrifuged and aliquots of the supernatants were taken for further purification by means of ion-exchange resins (Zeo-Karb 215 and Amberlite IRA 400, carbonate form). Where concentration of a solution was desirable, it was evaporated at room temperature under vacuum. For identification of the sugars, descending chromatograms were run at 23° C on sheets of Whatman no. 3 MM filter paper. The solvent used was n-propanol-benzyl alcohol-formic acid-water (50: 72: 17: 20).

Sucrose, glucose and fructose appeared to be the only sugars of quantitative importance, and therefore, they could be determined directly in the deionized extract. Total free and combined aldose was determined by the method of Timell, Glaudemans and Currie (1956). The total amounts of free and combined glucose and fructose were determined according to Nelson (1944), by measuring before and after acid hydrolysis. Free and combined fructose were determined according to Roe (1934) and the method used by Rorem, Walker and McCready (1960). The amounts of sucrose, glucose and fructose present in the extracts could easily be calculated from the figures obtained by these methods.

The sugar-content figures obtained by direct chemical analyses of the extracts and those obtained by densitometric scanning of paper chromatograms (VAN DIE, 1960) were generally in good agreement with each other. The chemical analyses, however, proved to be more rapid and more accurate. Chromatographic scanning, therefore, was used for confirmative purposes only.

Starch contents were estimated by comparing the iodine colour intensities of perchloric acid extracts of stem sections (CARTER and NEUBERT, 1954) with the colour made from a standard starch obtained from tomato leaves by the procedure of PORTER and MARTIN (1952).

3. RESULTS

a. Paper chromatography of the carbohydrates. The presence of a considerable number of carbohydrates in the 80 per cent ethanol extracts of various tomato plant parts could be demonstrated. Besides the major constituents glucose, fructose and sucrose, at least 6 other sugars were present in small or trace amounts. Their Rg values (glucose = 1.00) were 0.05, 0.13, 0.38, 0.88, 1.60 and 2.08. These values correspond with the positions of stachyose, raffinose, maltose, an unknown, xylose and ribose. The unknown sugar gave a blue-green colour with the orcinol reagent of KLEVSTRAND and NORDAL (1950), and is probably a heptulose.

Glucose, fructose and sucrose represent about 90–95 per cent of the ethanol soluble sugar fractions from root and stem tissues; the remainder is mainly the maltose — like sugar. The other sugars mentioned could only be detected if large amounts of carbohydrates were applied to the chromatograms.

b. The characteristic differences between the sugar composition of the root system and the stem are demonstrated in Fig. 1. Glucose is the main component of the sugar fraction from the stem, whereas in the roots fructose is a major constituent. An analysis of a series of sections of the stem — main root axis of one plant (Table 1) — shows a more or less regular decrease of the glucose component in the alcohol

TABLE 1

Amounts of sucrose, glucose and fructose (in μ Moles per gram fresh weight) in a series of sections of a stem — main root axis of a tomato plant.

	Sucrose	Glucose	Fructose
stem top	5	83	1
,,	14	70	29
,,	28	41	20
,,	31	43	7
,,	28	45	1
,,	31	38	7
stem base	23	15	29
root top	23	11	12
,,	27	6	17
root end	19	7	14

soluble sugar fraction with increasing distance from the top of the stem. The sucrose content of the sugar fractions simultaneously increases in a downward direction. As demonstrated in Fig. 2, such an increase is also observed in the starch content of the stem sections. Thus it appears that a shift in carbohydrates from glucose to sucrose and starch occurs in the stem cells with increasing distance of these cells from the apical meristem of the stem.

The relatively low glucose content of the roots probably depends on the absence of pith parenchyma in this plant part.

c. The distribution pattern of the sugars in the different tissues of a stem internodium was established by punching a number of short cylinders of about 1 mm diameter and 15 mm length from the regions of the pith, the intravascular phloem bundles, the secondary xylem, the phloem-cortex parenchyma, and from the epidermis-cortex chlorenchyma region. Fig. 3 shows the concentrations of free and combined monoses in the sugar fractions of these tissues. The figures demonstrate the dominant position of sucrose in both the secondary xylem and the internal phloem strands. The glucose present in the latter tissue region may be derived from pith cells in which the phloem strands are embedded and which could not be removed. In the central pith cells glucose is the major constituent of the sugar fraction. The transition from central pith to secondary xylem is characterized by an increasing sucrose/glucose ratio, probably as a result of the increasing intravascular phloem/pith ratio.

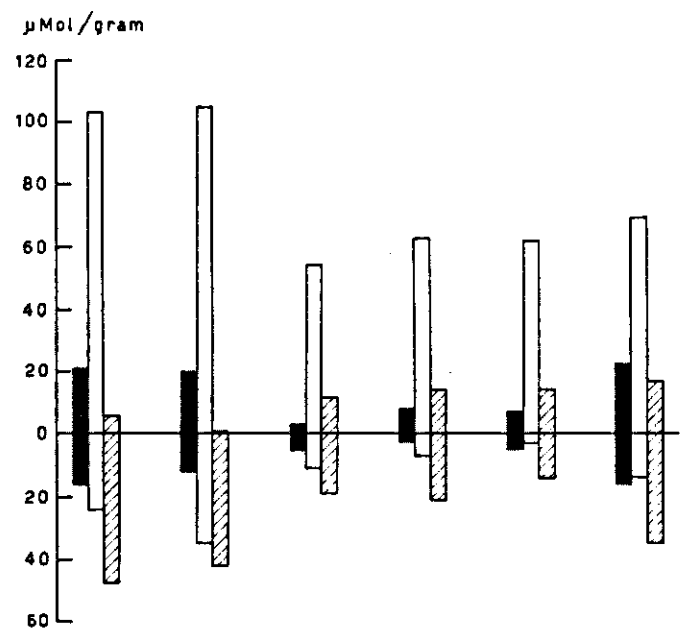

Fig. 1. Sugar composition of stem (above the abscissa) and root system (below the abscissa) of tomato plants. Black columns: sucrose; white columns: glucose; hatched columns: fructose.

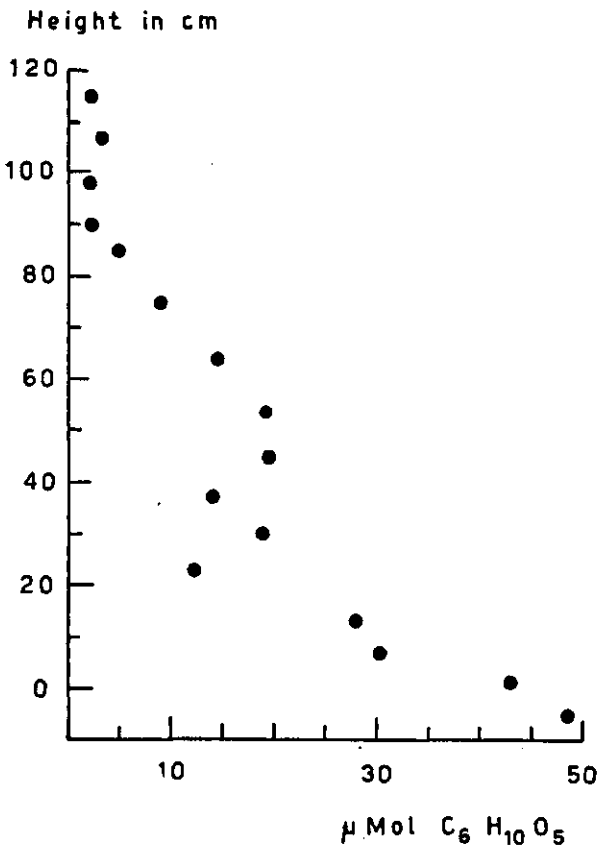

Fig. 2. The relation between the starch content along of the stem axis and the height at which the sections were taken.

d. The composition of the pith cells appears to vary according to the age of the stem part in which they occur. The same is probably true of the composition of the secondary xylem of the stem-main root axis. Tables II and III show the results of a number of analyses of secondary xylem and central pith, each derived at a different height along the stem-main root axis of the same plant. There is clearly a

TABLE II

Amounts of sucrose, glucose and fructose in μ Moles per gram fresh weight of xylem.

Date	Plant part	Sucrose	Glucose	Fructose
15-5-60	stem	39	7	3
30-5-60	stem	32	6	2
31-5-60	stem	31	2	2
1-6-60	stem [1]	28	2	0
1-6-60	stem-root transition [1]	40	1	3
1-6-60	main root [1]	43	6	0

[1] Derived from the same plant.

TABLE III

Amounts of sucrose, glucose and fructose (in μ Moles per gram fresh weight) of central pith tissue, derived from a series of stem sections taken from the top to the base of a tomato plant.

Plant part	Sucrose	Glucose	Fructose
stem top	4	139	10
	4	117	8
	10	91	12
	30	68	10
	24	62	0
stem base	25	58	12

correlation in the pith of the tomato stem between sugar composition and distance from the stem apex. With increasing distance, or, in other words, with increasing age, the sucrose/glucose ratio increases. Fig. 4 shows that the storage of starch also takes place especially in the older parts of the ptih.

4. DISCUSSION

Under greenhouse conditions a continuous lignified xylem cylinder is formed in the lower parts of the tomato stem. The elements of this secondary xylem apparently remain alive: their cytoplasm is retained, and they have prominent nuclei. They divide radially despite the lignified cell walls (VENNING, 1949), and act in this respect similarly to wood rays, which do not occur. The secondary xylem of the tomato is consequently a tissue with a high content of living cells, and this will be one explanation for its high sugar content.

Remarkable is the finding that especially sucrose occurs in the xylem cells. Sucrose also forms the major part of the internal phloem region, but in the other parts of the tomato stem glucose is the main sugar. LEONARD (1936) also reported sucrose as main constituent in

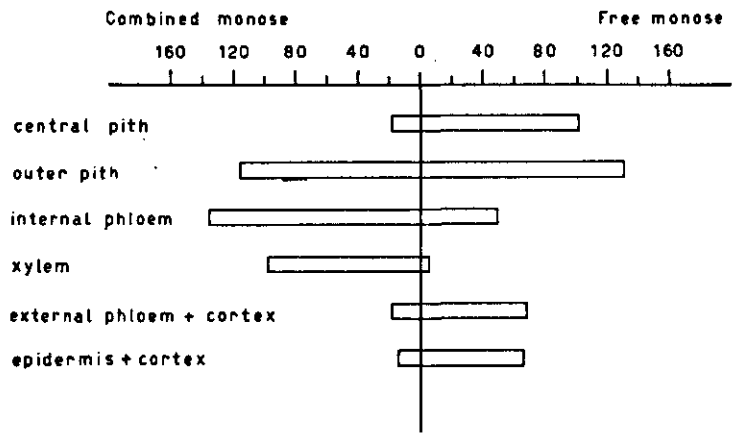

Fig. 3. The amounts of free and combined monose (sucrose) in several tissues of a stem section (Expressed as micromoles carbohydrate per gram fresh weight).

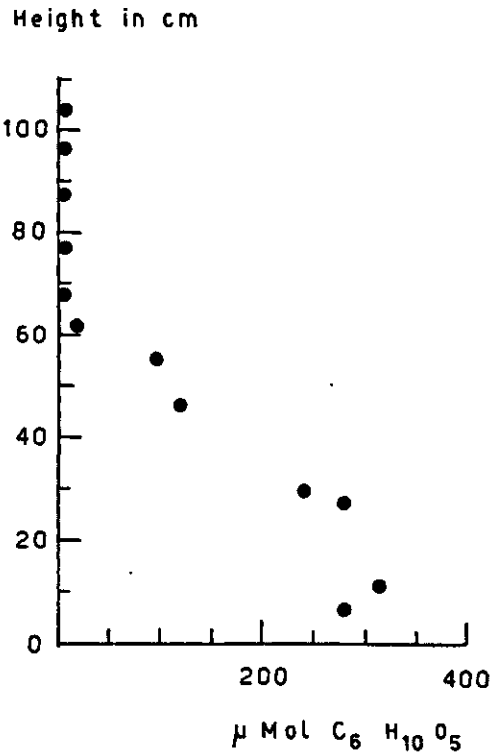

Fig. 4. The relation between the starch content of central pith parenchyma and the height at which the tissue was taken from the stem.

xylem and glucose as main constituent in the pith of *Helianthus* stems, while SIDERIS, KRAUSS and YOUNG (1937) reported similar data for aerial roots of *Pandanus*.

In the tomato axis, sugars are very probably translocated as sucrose, just as has been found for a number of other higher plants (ZIMMERMANN, 1960). The high sucrose content of the outer pith with its phloem strands may therefore point to a prominent role for the internal phloem in sugar translocation, a suggestion which also gets some support by anatomical data (EAMES and MACDANIELS, 1925).

A recent study of BACHOFEN and WANNER (1962) shows that the transport of photosynthetic assimilates to the fruits of *Phaseolus* occurs in the living xylem elements. It may be wondered whether also in the tomato plant a carbohydrate translocation in the living xylem cells takes place. Their high sucrose content could be an indication for such a role.

In longitudinal direction a correlation seems to exist between the extent of differentiation of the stem section as a whole (its distance from the apical meristem) and the sucrose/glucose ratio and the starch/glucose ratio in these stem sections. Probably the shift from

lower to higher molecular weight carbohydrates in the older parts of the stem is a consequence of the end of extension growth of their cells. A comparable phenomenon is known for apple trees, where starch starts to accumulate in the young tissues as soon as extension growth stops (PRIESTLEY, 1962).

SUMMARY

Characteristic differences in sugar composition were shown to exist between various tissues of stem and roots of the tomato plant. Secondary xylem and the region of the internal phloem strands proved to be rich in sucrose, while glucose was the dominant sugar in the pith parenchyma. Moreover a gradual increase in the sucrose/glucose and starch/glucose ratios with increasing distance from the top of the stem was demonstrated for whole stem and root sections as well as for their component tissues.

The relative amounts of xylem and pith in the stem on the one hand and the roots on the other partly explain the differences in sugar composition between these plant parts.

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