The Influence of Fruit Yield on the Content and Distribution of Carbohydrates in Apple Trees

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The present report forms part of a series of studies on physiological factors concerned in the fruit production of apple trees. The studies were carried out at the State Research Station Blangstedgaard, Odense.

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The extent of fruiting in apple trees may considerably affect the growth and the distribution of growth (Hansen 1966, 1970c), as well as other processes such as production and translocation of the photosynthates of the leaves (Hansen 1967a, 1970b). The present experiments concerning the effects of fruiting on the contents and distribution of carbohydrates in the tree were undertaken in an attempt to elucidate other aspects of this complex of interacting problems. Large numbers of fruits, as opposed to no or only a few fruits on an apple tree, appear to cause a reduction of the accumulation of certain carbohydrates, for example in the woody parts of the spurs; at the same time, and in certain varieties in particular, fruiting appears to inhibit flower initiation (see e.g., Singh 1948). However, so far there has been no demonstration of any clear-cut causal relationship between these facts. It appears to be reasonable to assume that the leaves, as the main source of energy and building materials, play a decisive rôle in any possible interrelationship. Only a few previous investigations have included studies of the leaves; but since improved methods of analysis allow for better separation of certain compounds, we decided to include a number of experiments concerning this problem. Experiments using ^{14}C have shown that the majority of apple leaf photosynthates occur in the sugar alcohol sorbitol (Hansen 1967a, 1970a). Consequently, the present study focused on the substances in the soluble sugar fraction, ignoring for the present the high molecular carbohydrates, i.e., primarily starch, which has been a much favoured subject in many previous studies.

Material and Methods

The material on which the present carbohydrate analyses are based was taken from various field experiments and from one pot experiment, during the years 1963 to 1967:

A. One abundantly bearing and one non-bearing Graasten (Gravenstein) specimen, both planted 1949. On August 1st and December 2nd, 1963, 60 bark samples were taken from the trunk and main branches of each tree, by means of a cork borer.

B. Seven to nine pairs of biennially bearing Graasten trees, all planted in 1951, each pair consisting of two comparable trees, in the "on" and "off" year, respectively. Due to poor fruit fruit setting the difference in bearing between the trees at the 1965 and 1966 samplings was rather less pronounced than on previous occasions. Each sampling date (see Table 1) included 40 to 50 spurs with, and a corresponding number without, fruit taken from the most abundantly bearing and from the poorest bearing trees or branches, respectively. Within each set the leaves were divided into and analyzed in groups according to size for each additional 200-250 mg fresh weight per leaf.

C. Golden Delicious, planted 1958. Abundant flowering with a weak growth. In 1965 (see Table 1), 60 spurs with and without fruit, respectively, were taken at random from bearing trees on each date; in 1966 the samples were taken from, respectively, 12 trees fruiting abundantly, and 12 trees from which all fruit had been removed on June 25th, 1966. The samples were taken and analyzed parallel to those under B_2 and B_3, having been divided into similar groups according to size.

D. Golden Delicious, planted 1961, abundantly bearing trees compared to trees on which all flowers were removed each year. 50-100 leaves (from 12 trees) per sample.

The sampling dates for the spurs taken for experiments B-D may be seen in Table 1. Leaves and in some cases bark from these spurs were analyzed. In 1964, 80 bark samples were taken by means of a cork borer from a total of 8 trees from each of the sets of bearing and only slightly bearing trees in experiment B.

E. Pot experiment with Golden Delicious. Cultivation took place in sand culture with ample supplies of minerals by watering with nutrient solution. In 1966 14 trees were cultivated with a rich crop of fruit, whereas on 14 corresponding trees all fruits were removed on June 13th. In Octobre, 1966, 8 trees from each set were harvested and cut up. In 1967, half of the remaining 6 trees in each group were again cultivated without fruit (from May 31st), while the other half was allowed abundant fruiting. In both years, the trees without fruit showed vigorous growth.

In 1966 and 1967 leaf samples were taken from the bearing and non-bearing trees, respectively, at the dates given in Table 1. In 1966 one sample consisted of the leaves from 28 spurs (distributed on 14 trees), in 1967 of the leaves from 18 spurs (6 trees). In the case of fruit-bearing trees the leaves were taken from fruit-bearing spurs exclusively.

At the time of harvesting in the autumn of 1966, samples from each tree included a fresh sample (20 g.) from the roots as well as of the bark removed from the trunk, each batch having been first cut up and thoroughly mixed, and also a sample of sawdust sawn from the trunk. Bark samples were taken in a similar way at the time of harvesting in 1967.

Analysis

The fresh samples thus obtained, or representative parts of them (usually 10-20 g. fresh weight), were treated with boiling 80% aqueous methanol and left to stand at —15° C. For the analysis the samples were cut up in an ultra-turrax, extracted with 80% methanol in a Soxhlet apparatus, evaporated in vacuum at 40° C., and redissolved in water, following which sorbitol, glucose, and sucrose were separated by paper chromatography and the various fractions were analyzed (Hansen 1967a). The results are given in per cent. of the dry weight of the insoluble residue following the methanol extraction.

^{14}C experiments

On 14th-15th July and 9th-10th August, 1965, 8 μCi $^{14}CO_2$ was added per spur (4 replicates) of bearing and non-bearing spurs, respectively, of Graasten and Golden Delicious in materials B and C. The spurs were harvested after 28 hours. Experiments were made in a similar way on August 16th, 1966, but in this case harvesting took place 4, 25, and 94 hours after the onset of exposure.

In the case of the pot experiment with Golden Delicious (E), 5 μCi $^{14}CO_2$ was added to one of 5 different branch sections at 5 times during the period 11th Aug. to 13th Sept., 1966, on each of 3 bearing and 3 nonbearing specimens. Similarly, 4 branch sections of other trees received treatment 4 times during the period from 26th Sept. to 12th Oct. After harvesting, cutting and drying in the autumn of 1966, the content of ^{14}C was determined in the various parts.

Supplying and measuring ^{14}C took place as in previous studies (Hansen 1967a). The results are expressed in cpm (counts per minute), or calculated in per cent. of initially absorbed ^{14}C.

Results

Carbohydrate content in leaves

Table 1 shows the carbohydrate contents in leaves of fruit-bearing and non-bearing spurs. In previous studies on *Graasten* (Hansen 1967a), the contents of sorbitol and glucose were found to be higher in spurs without fruit. This appears

Table 1. Average contents of sorbitol, glucose and sucrose in per cent. of methanol (80%) insoluble residue, and corresponding relative contents (sorbitol = 100), in leaves from non-bearing (N) spurs and difference between these and corresponding values or fruit-bearing (F) spurs. Diffetent dates and experiments (see "Mat. & Meth.").

Exp.	Sample date	Sorbitol		Glucose		Sucrose		Relative values Glucose		Relative values Sucrose	
		N	F-N	N	F-N	N	F-N	N	F-N	N	F-N
		Graasten									
B_1	26/5 65	19.6	+1.8	5.67	—1.69	3.73	—0.71	28.9	—11.2	19.0	—4.9
	10/6 65	20.5	—3.5	4.78	—0.95	—	—	23.3	— 6.7	—	—
B_2	20/7 65	17.9	+0.1	4.91	—0.24	3.04	—0.93	27.4	— 1.5	17.0	—5.3
	17/8 65	14.1	+0.6	3.23	—0.65	1.98	+0.30	22.9	— 5.3	14.0	+1.5
	21/6 66	28.9	+0.2	5.07	—0.24	2.69	+0.33	17.5	— 0.9	9.3	+1.1
B_3	12/7 66	22.4	—0.4	3.83	+0.07	2.41	+0.41	17.1	+ 0.6	10.8	+2.0
	4/8 66	20.7	+0.4	3.18	—0.48	2.83	—0.67	15.4	— 2.6	13.7	—3.5
	31/8 66	18.6	+1.3	2.48	—0.44	2.93	—0.37	13.3	— 2.7	15.8	—2.5
Av. v. B_2 & B_3		20.4	+0.3	3.78	—0.33	2.65	—0.16	18.5	— 1.8	13.0	—1.0
		Golden Delicious									
D	28/9 64	18.8	—5.4	0.90	+0.39	5.36	+1.37	4.8	+4.8	28.5	+21.7
	15/9 65	18.5	—1.3	2.22	—0.12	5.30	+0.69	12.0	+0.2	34.1	+6.5
C_2	20/7 65	16.8	+0.5	2.96	+1.62	—	—	17.6	+8.9	—	—
	17/8 65	13.8	+1.8	2.69	+0.17	2.28	+0.42	19.5	—1.2	16.5	+0.8
	11/7 66	24.3	—3.9	2.60	—0.28	3.32	—0.58	10.7	+0.7	13.7	—0.3
C_3	3/8 66	24.0	—2.0	1.54	+0.22	5.58	+0.00	6.4	+1.6	23.3	+2.1
	30/8 66	23.9	—7.6	1.37	+0.29	4.52	+0.13	5.7	+4.5	18.9	+9.6
	22/9 66	21.6	—4.1	1.66	—0.08	6.44	+0.05	7.7	+1.3	29.8	+1.6
Av. v. C_2 & C_3		20.7	—2.5	1.97	+0.49	4.11	+0.12	9.5	+4.0	19.9	+3.3
	20/6 66	16.8	—3.3	2.77	—0.08	4.65	—0.91	16.5	+3.4	27.7	+0.0
	8/8 66	15.1	—2.5	1.29	+0.45	6.29	—1.77	8.5	+5.3	41.7	—5.9
E	6/9 66	16.9	—6.8	0.99	+0.07	4.52	—1.11	5.9	+4.6	26.7	+7.1
	16/10 66	16.7	—3.8	0.82	+0.27	4.04	—0.51	4.9	+3.5	24.2	+3.2
	17/8 67	23.3	—2.7	0.91	+0.76	5.19	+0.21	3.9	+4.2	22.3	+3.9
	6/10 67	20.3	—3.4	0.64	+0.69	4.44	+0.06	3.2	+4.7	21.9	+10.6
Av. v. E		18.2	—3.8	1.24	+0.36	4.86	—0.51	6.8	+4.3	26.7	+3.5

to be confirmed in the case of glucose in Table 1, but seems rather more doubtful for sorbitol. It should be emphasized however, that it proved impossible in 1965-66 to obtain material from trees with such extreme differences with regard to fruit-bearing (se Mat. & Meth.) as in the previous study. In the case of *Golden Delicious* the sorbitol content is highest in the leaves of spurs without fruit in nearly all cases (in experiment C_2 the differences in fruit-bearing were again less clear-cut). However, the glucose content in Golden Delicious as opposed to Graasten is often higher in leaves from bearing than from non-bearing spurs. If we eliminate possible differences in the basis for the calculations (insoluble residue) by considering the relative values, the difference between the varieties becomes rather more obvious, the glucose to sorbitol ratio for Graasten being highest without fruit, but for Golden Delicious with fruit, and the same applies here to the sucrose to sorbitol ratio. Apart from this the sucrose content shows no clear relation to bearing.

Table 2. Contents of sorbitol, glucose and sucrose in leaves of non-bearing and fruit-bearing spurs. Significant differences and interactions depending on leaf size in experiments B_2, C_2, B_3 and C_3 (cf. Table 1, average values for dates given there)

			mg. fresh weight per leaf			
Exp. C_2			<200	200-400	400-600	
Golden Delic.	Glucose	N	2.94	2.45	2.08	
		F	3.86*	3.95*	3.15*	
1965	Sucrose	N	2.67	2.48	2.41	
		F	3.33*	3.07	2.43	
Exp. B_3			<200	200-450	450-700	>700
Graasten	Sorbitol	N	26.4	22.9	21.7	22.8
		F	22.7*	23.6	22.6	21.9
1966	Glucose	N	4.38	4.44	3.70	3.42
		F	4.01	3.69*	3.08*	2.82

* significant difference between paired values

In order to determine whether the relation between bearing and leaf content might depend, *inter alia*, on leaf size (in the case of, e.g., biennial bearing Graasten the leaves of fruit-bearing spurs may be very much smaller than those of spurs without fruit, Hansen 1966), the samples in experiments B_2, C_2, B_3 and C_3 were divided after collection according to leaf size. In the Golden Delicious of 1965 the sucrose content of the small leaves in particular was highest in the fruit-bearing spurs and the glucose content decreased with leaf size in both spur types; for glucose the same applied in the case of Graasten 1965 (particularly for the fruit-bearing spurs), and here also the sorbitol content was higher in non-bearing than in bearing spurs for the smallest leaf size (Table 2). These facts are not in themselves sufficient to explain the connexion with fruiting as found by considering the average values, nor consequently the difference found between the two varieties. This applies also to changes in leaf content with season of growth (Table 1), where in several cases a reduction is found (sorbitol and glucose in 1965, sorbitol and glucose in Graasten and glucose in Golden Delicious in 1966).

Carbohydrate content in other parts

Bark from bearing an non-bearing spurs from 1964 samples, and a few from 1963 and 1965 (material B), was analyzed as leaves. At the beginning of the 1964 season (May-June) there was a tendency to higher contents of sorbitol, glucose and sucrose in the bark of non-bearing than in that of fruit-bearing spurs. However, the results are not presented here since there is a considerable margin of error on these results due to, e.g., variation in spur size and failure to separate the annual growth of the spur from the older parts; other studies suggest that among other

Table 3. Contents of sorbitol, glucose and sucrose in per cent. of methanol (80%) insoluble redisue in bark from trunk and main branches of biennial bearing Graasten, and in bark and wood from the trunk and in roots of abundantly bearing and defruited Golden Delicious. F = trees with fruit, N = trees without or with only few fruits

Material	Experiment	Sampling date	Sorbitol N	Sorbitol F	Glucose N	Glucose F	Sucrose N	Sucrose F
	A	1/8 1963	5.45	5.19	0.71	0.96	0.54	0.60
	Graasten	2/12 1963	5.25	5.64	1.18	1.61	2.64	2.39
	B	21/5 1964	4.63	4.42	1.05	1.05	0.71	0.86
Bark	Graasten	3/8 1964	4.97	4.93	1.11	1.26	0.14	0.17
		10/11 1964	4.29	4.79	2.35	2.10	2.10	1.75
	E	4-14/10 1967	5.04	5.57	0.04	0.16	0.80*	1.25
		21/10-7/11 1966	6.00*	5.00	0.57	0.67	3.95*	2.08
Wood	Golden	—	1.16	1.20	0.39	0.15	0.36	0.38
Root	Del.	—	3.74	4.08	0.30	0.37	3.06	2.98
Significant difference 1964			0.93		0.95		0.67	

factors growth, and hence the basis of calculations for the carbohydrate analyses, in these parts is affected in different ways by the fruiting condition (Hansen 1967a).

Bark samples from branches and trunk of biennial bearing Graasten were taken on a few occasions in 1963 and 1964, Table 3. The coefficients of variation are considerable (up to 35 per cent.), and there is no evidence of any decisive difference. In the case of the pot-grown Golden Delicious, significant differences were found only for the bark of the trunk; in the autumn of 1966 the sorbitol and sucrose contents were higher in non-bearing than in fruit-bearing trees, whereas in 1967 the case for sucrose was found to be reversed.

^{14}C experiments

In a previous study on the variety Graasten (Hansen 1967a), the rate of photosynthate transport out of the leaves, as measured by the reduction with time in the ^{14}C-content of the leaves following uptake of $^{14}CO_2$, was found to be higher from leaves on spurs with fruit than from those without. This applies also to the present experiments, Tables 4 and 5, both for Graasten and Golden Delicious; in addition, it may be seen that the rate of translocation away from the leaves is faster in the case of Golden Delicious than in that of Graasten, at least for fruit-bearing spurs.

Table 4. ^{14}C content in exposed leaves (in per cent. of total ^{14}C absorbed), 28 hours after the beginning of a 5-6 hours period of exposure. Materials B and C, 1965, average values for exposures July and August, 4 replicates

	Graasten	Golden Delicious	
Spurs with fruit.....	53.0	44.2	48.6
Spurs without fruit..	71.7	67.0	69.4*
	62.4 *	55.6	

* significant (95 %) difference

When $^{14}CO_2$ was supplied to fruit-bearing branch sections of pot-grown Golden Delicious in the late summer and autumn of 1966, approximately 70 per cent. of the photosynthates

Table 5. ^{14}C content in exposed leaves (per cent. of total ^{14}C absorbed) at different intervals after the onset of a 4 hour period of exposure. Materials B and C, 1966

hours	4	25	94
Graasten with fruit....	94.1	58.7	27.8
Graasten without fruit..	102.0	75.8	32.0
Golden Del. with fruit..	83.0	50.0	19.3
Golden Del. without fruit	101.3	71.2	43.1

Table 6. Exposure to ^{14}C of Golden Delicious with (F) and without (N) fruit. $^{14}CO_2$ (5 μCi) supplied to one of 5 branch sections per tree at different times between 11th Aug. and 13th Sept., or in other specimens, to 4 branch sections between 26th Sept. and 12th Oct., 1966. Experiment E, 3 replicates. a) concentration of ^{14}C (cpm - background) in the untreated parts; b) grammes dry weight of the various parts by autumn; c) and d) distribution of ^{14}C in per cent. of ^{14}C initially absorbed in treated and untreated parts. Values in a), b) and c), average of 6 trees, in d) average of 3 trees

			^{14}C-treated			other parts of tree			trunk			
			leaf	branch	fruit	shoot	spur	branch	bark	wood	root	total
a)	cpm	N				4	11	17	15	14	21	
		F				4	7	7	3	4	7	
b)	g.	N				116	66	617	60	298	558	
		F				53	37	399	49	208	228	
c)	^{14}C	N	15.0	7.5	—	0.7	0.4	15.5	4.4	6.2	17.3	67.0
	%	F	12.2	3.7	70.6	0.3	0.2	3.0	6.2	1.2	2.4	94.0
d)	1)	N	11.6	8.6	—							
		F	10.4	3.1	72.8							
	2)	N	18.5	6.3	—							
		F	14.1	4.4	68.3							

1) ^{14}C added at 5 dates, 11/8-13/9

2) ^{14}C added at 4 dates, 26/9-12/10

of the leaves were used for the growth of the fruit, leaving only a minor part for translocation to other parts of the tree (Table 6c). Consequently, the transport to branches, trunk and root in non-bearing trees does not only quantitatively greatly exceed that in fruit-bearing specimens, but the concentration of ^{14}C (cpm, Table 6a) is also greater. The results obtained with treated branch sections (Table 6d) indicate that fixation is highest in non-bearing shoots and branches in the first period, and possibly in the leaves in the second period, although these values should be treated with reservation due to variations in size of the branch sections, etc. In non-bearing trees more than 30 per cent. is lost through respiration, while in the fruit-bearing ones the loss is only about 6 per cent. (Table 6c, final column).

Discussion

A lower concentration of certain carbohydrates, starch in particular, in spurs etc. in fruit-bearing than in non-fruiting specimens has been demonstrated in several studies (Table 7), also in other tree species than apple trees (Priestley 1962, Kozlowski and Keller 1966), probably due to differential accumulation of carbohydrates. ^{14}C experiments (Table 6; Mochizuki 1962) show clearly the high consumption by the fruits of assimilates from the leaves, and that the intensity of growth or the accumulation must, as shown by the higher concentration of ^{14}C (cpm), be higher in the branches, thrunk and roots of trees without fruit. The analyses of, e.g., bark from the thrunk in Table 3 do not unequivocally show carbohydrates to be accumulated in higher concentrations in trees without than in trees with fruit. The apparent discrepancy may possibly be explained on the basis of a difference in growth intensity in the two years, as follows:

At the earlier date of sampling in 1967, growth may still haven been taking place in, e.g., trunk and roots in non-bearing trees, thus causing a consumption, while at the same time the basis

Table 7. Relation between extent of fruit-bearing in apple trees and the contents of certain carbohydrate fractions (per cent. of dry weight or fresh weight)

+ : conc. highest for poor fruit yields
—: » » » high » »
0 : no difference. Brackets signify slight or insignificant difference

Organ	Sugar Reduc.	Sugar Sucrose	Starch		
Spur			+		Gourley 1915
»	+		+		Hooker 1920
»	+	+	+		Harley 1925
»			+		Kraybill et al. 1925
»	(—)	—,0	0		Potter & Philips 1927
»	0		0	a)	— & — 1930
»	0	0	0, +	a)	Aldrich & Fletcher 1932
», buds	(—)		+		Harley et al. 1942
Shoot	—	(—)	+		— —
»	(0)		+		Finch 1935
»	(+)	(—)	+		Kato & Ito 1963
»			+		Schumacher 1962
Spur, bud	—	(+)			Feucht 1964
Parts above ground	0		0	a)	Mochizuki 1962
Roots	0		+		— —
»	—		+		Kazaryan & Arut. 1966

a) non-bearing spurs estabilished by removal of flowers or fruits.

for the calculation ("insoluble residue") of the carbohydrate analysis is increased; both these factors might contribute to, e.g., lower values for the sucrose concentration here than in fruit-bearing trees without growth in those parts. At the later sampling date in 1966, the growth in trunk and roots may be approaching its conclusion, causing an accumulation of, e.g., sucrose (Hansen 1967b, Christensen and Hansen 1969, cf. also dates Table 3, experiments A and B; also, in the above 1966 sampling period there was a general increase in the sucrose content, average values for trees sampled before Nov. 1st being 1.46 and 2.27 and after Nov. 1st 2.44 and 4.54 per cent., for bearing and non-bearing trees, respectively). This accumulation is likely to be lowest in the fruit-bearing trees, in which the fruit is still consuming assimilates. If this is the explanation, the accumulation of certain carbohydrates in certain organ must depend on the production and consumption in other organs as well as on the growth intensity in the organ in question. Similar considerations may contribute to the deviations between results from different investigations in Table 7.

Starch data, determined by a number of different methods, have been included in many investigations (Table 7). However, ^{14}C experiments suggest that in apple trees, sorbitol and sugar play a major part quantitatively both in the metabolism of the leaves and as reserves in other organs (Hansen 1967 a, b), and consequently the present study was focused on these compounds.

Relatively few authors have been concerned with the carbohydrate content of the leaves in relation to the extent of fruit-bearing of the tree. Kazaryan et al. (1965) find fewer, or smaller amounts, of sugars (i.e., maltose, sucrose, glucose and fructose) in leaves close to a fruit than in leaves on fruitless trees. In Citrus species the sugar and starch contents in the leaves are reduced during fruit development only to increase again following harvesting of the fruit (Mizuno & Hakamata 1967, Mizuno et al. 1968). The speedier transport out of the leaves when they are close to a fruit (Tables 4 and 5), may also be expected to cause a reduction of the accumulation in these leaves, as shown previously to be the case for sorbitol and glucose in Graasten (Hansen 1967a). Similar considerations appear to apply to certain substances included in the present study; but it is evident that not all compounds are affected in identical ways by the extent of fruiting, and that there is certainly a distinct difference between the two varieties used. In the case of Graasten the glucose concentration of the leaves, and the glucose/sorbitol ratio, are highest in the spurs without fruit, whereas for Golden Delicious the situation is reversed. This may be correlated to the apparently lower values in general for the glucose content in Golden Delicious, and the fact that the rate of translocation out of the leaves on spurs with fruit is higher in Golden Delicious (cf. also Hansen 1969). However, it is hardly possiblie on the basis of existing material to postulate why the leaf metabolism of the two varieties is to some extent affected differently by the close proximity of fruits; we can only establish that such appears to be the case.

Summary

When comparing leaves from spurs with and without fruit it was found that for Graasten the glucose content (per cent. of methanol insoluble residue) and the glucose/sorbitol ratio were highest in leaves from spurs without fruit, whereas for Golden Delicious the case was reversed. In the latter variety the sorbitol content was also highest in leaves from spurs without fruit. These differences could not be explained solely by differences in leaf size or changes with season.

Bark from trunks of Golden Delicious contained in the autumn of one year more sorbitol and sucrose in trees without fruit, but in another year the values were higher for the specimens with fruit. Analyses of other parts showed no conclusive differences, but the variations was condiderable.

By means of ^{14}C experiments the transport of assimilates out of the leaves was found to be faster on spurs with than without fruit, and also faster in the case of Golden Delicious than in that of Graasten.

When $^{14}CO_2$ was supplied in the late summer and autumn to branch sections of abundantly bearing Golden Delicious, the fruits used approximately 70 per cent. of the ^{14}C absorbed, while ^{14}C from the leaves of trees without was transported mainly to

branches, trunk and roots, so that both in absolute terms and in relation to existing material the content of ^{14}C was the highest here. The respiratory loss in the latter case was c. 30 per cent. as against 6 per cent. in fruit-bearing trees.

Oversigt

Frugtmængdens indflydelse på kulhydratindhold og -fordeling hos æbletræer

Ved sammenligning af blade fra sporer med og uden frugt var hos Graasten glucose-indholdet (pct. af methanol-uopløselig rest) og glucose/sorbitol-forholdet størst i blade fra sporer uden frugt, mens det hos Golden Delicious var omvendt. Hos denne sort var desuden sorbitolindholdet størst i blade fra sporer uden frugt. Disse forskelle kunne ikke forklares alene ved forskelle i bladstørrelse eller i tidsmæssige ændringer.

Bark fra stamme på Golden Delicious indeholdt om efteråret i et år mest sorbitol og sucrose hos træer uden frugt, men i et andet år mest i træer med frugt. Analyser af andre dele viste ikke tydelige forskelle, men variationen var betydelig.

Ved hjælp af ^{14}C blev assimilaternes transport ud af bladene fundet hurtigere på sporer med end på sporer uden frugt, og her igen hurtigere hos Golden Delicious end hos Graasten.

Ved $^{14}CO_2$-tilførsel sensommer-efterår til grenstykker på rigtbærende Golden Delicious forbrugte frugterne ca. 70% af den optagne ^{14}C, mens ^{14}C fra bladene hos træer uden frugt især blev transporteret til grene, stamme og rødder, så at ^{14}C-indholdet både absolut og i relation til det eksisterende materiale blev størst her. Respirationstabet var her ca. 30% med 6% i frugtbærende træer.

Litteratur

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