

## The effect of daughter plant removal on the migration of $^{14}\text{C}$ -assimilates in strawberry

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The problem of interaction between acceptors and donors of assimilates, especially the character and localization of power causing the translocation of organic substances are still little known. Many authors suggest that the distribution of assimilates in plants is determined by "balance of supply" (Joy 1963), as well as the capacity of organs as a sink of assimilates, (Mason, Maskell 1928; Thorne 1964; Thrower 1964; Wardlow 1965, and others).

The aim of the present study was to investigate the role of strawberry daughter plant — an acceptor of assimilates in the translocation from the mother plant to the runner. Strawberry seemed to be a good object for experimental work; mother plants produce — more than one runner, therefore it is possible to investigate, on the same plant, the relation between the size of daughter plant and the rate of migration of photosynthates.

In all previous experiments, (Starck 1963, 1964a, b), the chief concern was the effect of roots on the longitudinal transport. Nevertheless it was suggested, that one of the reason of decreasing translocation in the stem of plants deprived of roots, could have been the change of the rate of lateral movement from the phloem into the surrounding tissue. The strawberry runner may be easily divided into an outer and inner part, exactly on the layer of pericycle fibres. Therefore in the experiments reported the effect of daughter plant removal on the longitudinal as well as on the radial movement was investigated.

### MATERIAL AND METHODS

Three experiments were carried out with strawberry var. "Regina", cultivated in the field, or in pots, (expt. 1). In experiments 2 and 3, plants were transferred into water culture (five fold diluted modified Hoagland solution — Johnson 1957), few days before exposure to  $^{14}\text{CO}_2$ .

The first two were pilot experiments, done in one replication and the third — was based on the results of the former ones. Expt. 3 was done in three replications, one plant in each. All the mother plants had two runners: younger one with small daughter plant (about 0.3 g of fresh weight) and an older one, with bigger daughter plant, (about 1.4 g of fresh weight).

In most cases only the blades of the mother plants were exposed to  $^{14}\text{CO}_2$ , all the other organs were shaded and the runners were placed in polyvinyl bags

(expt. 1, 2). In expt. 3, in four treatments all the organs, except the blades of mother plants were shaded with light proof paper, but in the last treatment the whole aerial part of plants were exposed to  $^{14}\text{CO}_2$  and light to check the photosynthetic rate of all green organs. In all experiments the plants were exposed to  $^{14}\text{CO}_2$  in plexiglass chamber, as described before (Starck 1964 a), all the conditions of this exposition are presented in detail, in table 1.

Table 1  
Condition of exposition (atmosphere with  $^{14}\text{CO}_2$ )

Experiment No	Date	Condition of photosynthesis				Condition of translocation		Condition for runners during $^{14}\text{CO}_2$ — photosynthesis
		hrs of exposition	t°C	radioactivity per plant	conc. of $^{14}\text{CO}_2$ % v/v	time hrs	t°C	
1	26.X.1963	11 <sup>40</sup> —12 <sup>40</sup>	13—14	5 $\mu\text{C}$	0,04 r. sp. = 4,25	1.5 3.0	15—20	light
2	12.V.1964	11 <sup>10</sup> —11 <sup>30</sup>	22—26	—*)	0.05	4.0	21—28	light
3	4.VII.1964	9 <sup>05</sup> — 9 <sup>25</sup>	22—23	26 $\mu\text{C}$	0.06 r. sp. = 1,67	0.5 2.0 4.0	18—23	light or darknes

\*) Exposition were done with the other experiment

r. sp. = specific radioactivity of  $^{14}\text{CO}_2$   $\mu\text{C}/\text{mg}$

After exposure, the plants were divided into: blades, apical part\*, crown, roots, daughter plants and runners, cut into 5—6 cm segments, (experiments 2 and 3). In expt. 2 also flowers with stalk were separated. In some treatments of expt. 3,

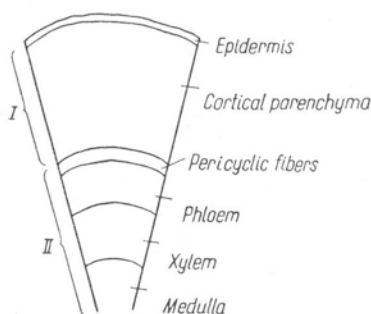


Fig. 1. Transverse section of runner.

I—outer part; II—inner part.

the runners were separated into the outer and inner tissue (Fig. 1). The samples were immediately frozen and than progressively analysed for total radioactivity. The analytical procedure was mostly the same as before (Starck 1963, 1964). The

\* Apical part include stem apex with the youngest leaves.

significance of the effect of daughter plants removal on the translocation of photosynthates was statistically calculated. Analysis of variance was applied (Snedecor's F test), and deviation between the averages was calculated by Student's t test, and so was the interaction of the factors examined. Most of these calculations were done on the relative values (percentage of total  $^{14}\text{C}$  in the whole plant after transformation according to the Bliss table).

## RESULTS

Pilot experiments: No 1, 2.

The results of expt. 1, done in autumn and expt. 2 — done in spring are presented in table 2. Expt. 1 comprised measurements of  $^{14}\text{C}$ -translocation after 1,5 and 3 hrs translocation, feeding time included. The differences between total radioactivity are mainly due to the different weight of blades, assimilating  $^{14}\text{CO}_2$ . Total radioactivity in expt. 1, calculated per 1 g of blade fresh weight of intact plants

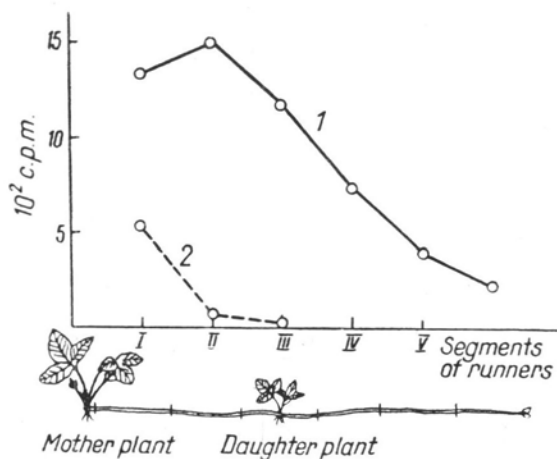


Fig. 2. Distribution of  $^{14}\text{C}$ -assimilates in the strawberry runners (Expt. 2).

1 — with daughter plant; 2 — without daughter plant

was  $2170 \times 10^2$  cpm and for plants without daughter —  $2080 \times 10^2$  cpm. In expt. 2 it was respectively:  $811 \times 10^2$  and  $854 \times 10^2$  cpm. The rate of translocation, especially in expt. 1, seems to be very low. Most  $^{14}\text{C}$ -assimilates were found in petioles and apical part. The radioactivity of the later part was considered as the result of  $^{14}\text{C}$ -translocation, but also included  $^{14}\text{C}$ -photosynthesis "in situ". In expt. 1 the radioactivity of runners was located mainly near the scale leaf, which was situated outside the polyvinyl bag and assimilated  $^{14}\text{CO}_2$ , (data not presented). Therefore it is difficult to compare translocation into the runner with and without daughter plants, especially after 1.5 hrs. The runner of a plant without daughter was more radioactive probably owing to  $^{14}\text{C}$ -photosynthesis carried out by the bigger scale leaf, (its weight was more than twice of an intact runner).

After 3 hr translocation, in expt. 1 and after 4 hrs — in expt. 2, migration of

Table 2

Influence of daughter plant on the translocation of  $^{14}\text{C}$ -assimilates in strawberry (Pilot experiments, in one replication)

Part of plant	Experiment 1 (1962) Autumn										Experiment 2 (1963) Spring					
	1.5 hrs					3 hrs					4 hrs					
	with daughter plants		without daughter plants			with daughter plants		without daughter plants			with daughter plants		without daughter plants			
	total radioactivity $10^2$ cpm	fresh weight %	total radioactivity $10^2$ cpm	fresh weight	%	total radioactivity $10^2$ cpm	fresh weight	total radioactivity $10^2$ cpm	fresh weight	%	total radioactivity $10^2$ cpm	fresh weight	total radioactivity $10^2$ cpm	fresh weight	total radioactivity $10^2$ cpm	fresh weight
Blades	5858.6	97.6	4611.2	95.6	2.55	6608.1	89.7	3.22	4947.0	92.6	2717.6	83.3	3756.7	3.35	88.8	4.40
Petioles	40.5	0.7	13.1	0.3	0.60	113.9	1.5	0.72	109.5	2.0	99.0	3.0	173.9	1.30	4.1	2.45
Apical part	47.7	0.8	123.5	2.6	0.30	466.0	6.3	0.37	249.6	4.7	estimated with blades					
Crown	21.7	0.3	11.2	0.2	1.22	108.6	1.5	1.24	19.6	0.4	96.3	2.9	83.2	1.59	2.0	2.23
Runners	5.8	0.1	14.2	0.3	0.56	29.1	0.4	0.50	8.1	0.1	54.2	1.7	0.7	0.68	0.1	0.71
Scale leaf	1.1	<0.1	51.5	1.0	0.22	2.8	<0.1	0.12	9.5	0.2	—	—	—	—	—	—
Daughter plant	24.6	0.4	0.93	—	—	37.5	0.5	0.79	—	—	108.3	3.3	—	0.91	—	—
Roots	—	—	—	—	—	—	—	—	—	—	126.9	3.9	100.8	7.55	2.4	7.90
Peduncle and fruits	—	—	—	—	—	—	—	—	—	—	61.7	1.9	116.3	0.57	2.6	0.85
Total plant	6000.0	100.0	4824.7	100.0	5.45	7366.0	100.0	6.96	5343.3	100.0	3264.0	100.0	4231.6	15.95	100.0	18.54
Total plant except $^{14}\text{C}$ -assimilating organs	140.3	2.3	162.0	3.4	2.90	755.1	10.2	3.74	386.8	7.4	546.4	16.7	474.9	12.60	11.2	14.14

\* radioactivity of the whole plant assumed as 100%.

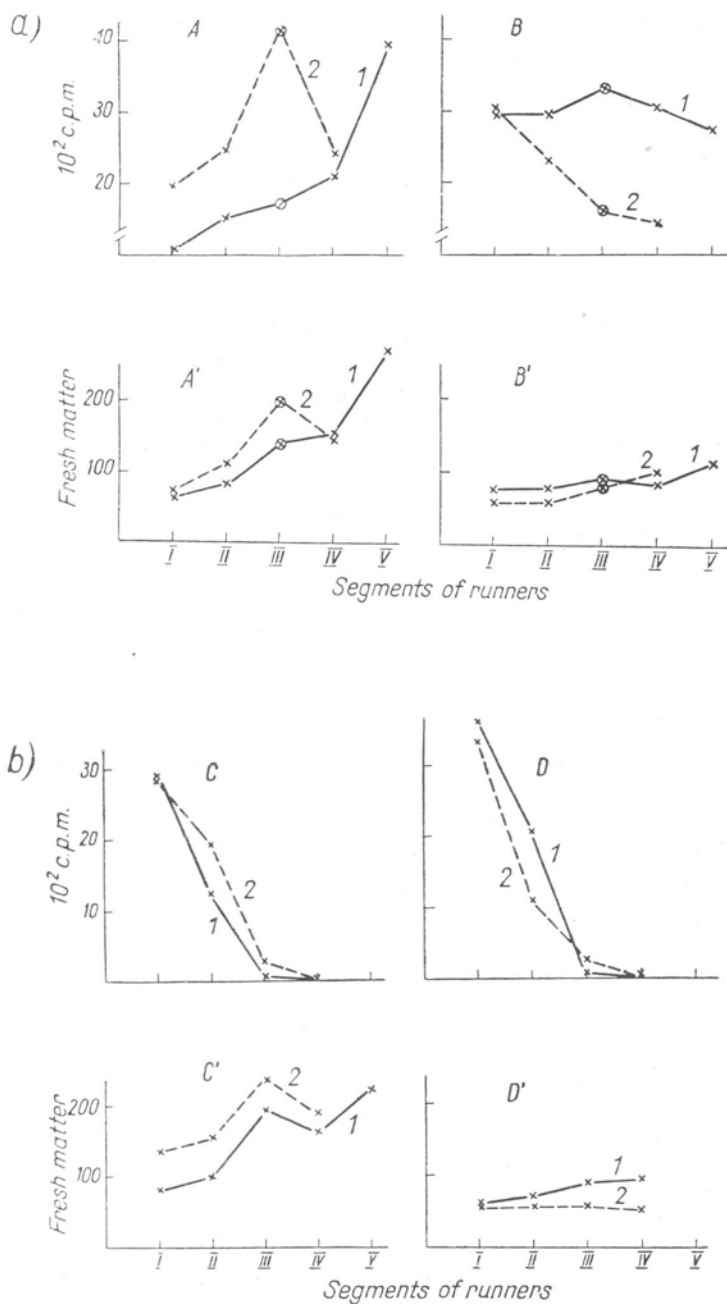


Fig. 3. Distribution of  $^{14}\text{C}$ -assimilates in the strawberry runners (Expt. 3).

*a* — intact plant; *b* — plants after excision of daughter plants; *AA'* — outer part: *A* — radioactivity, *A'* — fresh weight; *BB'* — inner part: *B* — radioactivity, *B'* — fresh weight; *CC'* — outer part: *C* — radioactivity, *C'* — fresh weight; *DD'* — inner part: *D* — radioactivity, *D'* — fresh weight.

1 — older runner; 2 — younger runner

Table 3

Influence of daughter plants on the  
(average of three  
Experi

Part of plant		30 min				2 hrs			
		Control				with daughter plant			
		total radioactivity		soluble in ethanol 10 <sup>2</sup> cpm	f.w. g	total radioactivity		Soluble in ethanol 10 <sup>2</sup> cpm	f.w. g
		10 <sup>2</sup> cpm	% 1)			10 <sup>2</sup> cpm	%		
Blades		20156.6	91.3	17537.1	13.70	18102.3	97.0	14549.0	12.23
Apical part		55.4	0.3	—	0.48	131.6	0.7	—	1.04
Petioles		123.5	0.6	—	4.47	367.3	2.0	240.4	4.10
Crown		0	0	0	1.47	30.6	0.2	—	0.77
Older runner	daughter plant	1369.7	6.2	619.0	1.47	0	0	0	1.49
	runner	31.1	0.1	—	1.23	7.7	<0.1	—	1.37
Younger runner	daughter plant	332.7	1.5	183.5	0.41	0	0	0	0.26
	runner	10.2	<0.1	—	0.82	1.53	<0.1	—	0.88
Roots		0	0	0	16.27	trace	trace	trace	7.55
Total plant		22079.2	100.0	—	40.32	18654.8	100.0	—	29.69
Sum of petioles, crown, runner, roots		—	—	—	26.14	420.9	2.3	—	16.42

1 Radioactivity of the whole plant assumed as 100%

\* Significant differences  $p = 0.05$

\*\* Significant differences  $p = 0.01$

assimilates in plants without daughters was a little lower than in the controls. In both experiments, translocation into the crown, as well as into the runner and roots (in expt. 2), was reduced after removal of daughter plant. The total amount of <sup>14</sup>C-assimilates transferred to the foot stalk and fruits was a little larger after excision of daughter plant. The distribution of labelled assimilates in the runners of expt. 2, is presented in fig. 2. In intact runner, decreasing gradient of radioactivity up to its end was found. In the runner without daughter plant — radioactivity was detected only in the first segment.

translocation of  $^{14}\text{C}$ -assimilates in strawberry  
replications)  
ment 1964

				4 hrs							
without daughter plant				with daughter plant				without daughter plant			
total radioactivity		soluble in ethanol	f.w. g	total radioactivity		soluble in ethanol	f.w. g	total radioactivity		soluble in ethanol	f.w. g
$10^2$ cpm	%	$10^2$ cpm		$10^2$ cpm	%	$10^2$ cpm		$10^2$ cpm	%	$10^2$ cpm	
22457.3	97.0	18489.0	13.23	15172.7	88.9	11304.0	13.28	23745.3	89.9	18497.0	13.13
220.7	1.1	—	0.80	439.9	2.6	258.2	0.99	973.1	3.7	627.1	1.53
398.3	1.7	235.2	4.13	561.6	3.3	340.9	3.90	764.5*	2.9	497.7	3.70
53.2	0.2	—	1.18	186.2	1.1	85.5	0.73	271.9	1.0	157.0	0.89
—	—	—	—	110.5	0.6	53.0	1.38	—	—	—	—
trace	trace	trace	1.20	250.5	1.4	173.0	1.10	100.2**)	0.4*	89.4	0.99
—	—	—	—	54.8	0.4	43.4	0.30	—	—	—	—
0	0	0	0.98	184.9	1.1	138.0	0.76	100.0**)	0.4*	75.1	0.82
0	0	0	7.50	103.4	0.6	—	5.30	469.9	1.7*	—	7.0
23147.5	100.0	—	29.02	17064.5	100	—	27.74	26427.9	100.0	—	28.06
451.5	1.9	—	14.99	1451.9	8.5	—	13.47	1706.5	6.4*	—	13.40

variations				interactions	
F	presence of daughter	age of runner	tissue	presence of daughter x age	tissue x age
F <sub>emp.</sub>	23.40	1.80	0.43	5.31	28.40
F <sub>t</sub>	p = 0.05 p = 0.01		4.49 8.53		

### Experiment 3.

This experiment was performed in three replications and included 5 treatments. As control for the whole experiment served plants collected after 30 min of translocation. All their parts were exposed to light during  $^{14}\text{CO}_2$  photosynthesis. The other treatments (intact plants deprived of daughter) were collected after 2 and 4 hrs of translocation (tab. 3).

Daughter plants assimilated a relatively high amount of  $^{14}\text{CO}_2$  in contrast to the outer tissue of runners. Radioactivity of this part of the runner was located mainly in the green tissue near the node with scale leaf, (data are not presented in the table). The inner part showed only traces of radioactivity.

After 2 hr translocation, radioactivity was still concentrated in the blades, in smaller degree — in petioles and in the apical part. In runners of intact plants, radioactivity was detected in the first two segments, but in runners without daughter plants — only traces were found. A more pronounced effect of cutting the daughter plant was observed after 4 hr translocation. The total migration of the assimilates in plants deprived of daughters, (expressed as percentage of total radioactivity in the whole plant), was lower, but the share of petioles (calculated in cpm) was higher in plants without daughter plant than in intact ones, (differences significant  $p = 0,05$ ). Removal of daughter plants caused an increase of  $^{14}\text{C}$ -translocation into the roots inversely as in expt. 2.

The marked differences in radioactivity of the apical part, between experimental treatments were not significant. In this organ the greatest variability between replications was observed probably as a consequence of differences in their fresh weight. The contribution of the apical part to the total fresh weight of the whole plant was 1,2 up to 5,5 percent in various plants. The radioactivity of this organ was the result of photosynthesis "in situ" and translocation, but was calculated in this experiment as  $^{14}\text{C}$ -assimilation.

The greatest differences in radioactivity between experimental treatments were found in the runner (Table 3). Translocation into the runner was depressed as a consequence of daughter plant removal. This depression was particularly marked in older runner, (interaction between age of the runner and presence of daughter plant was significant). The distribution of labelled compounds in radial direction depended on the age of the runner (Table 4), in younger runner, more radioactivity was located in the outer layer and in older ones, inversely — more  $^{14}\text{C}$ -assimilates were found in the inner tissues. (Interaction age  $\times$  tissue was significant). The ratio of radioactivity of the outer and inner tissue did not depend on the presence of daughter plants.

The distribution of radioactivity and fresh weight of inner and outer tissue of both groups of runners are illustrated in fig. 3A, B, C, D. In intact runners positive regression between radioactivity of outer tissue and their fresh weight was observed, Fig. 3A, (coefficient of regression  $b = 0,0128$  was significant at  $p = 0.01$ , coefficient of correlation  $r = 0.54$  at  $r_{\text{crit.}} = 0.487$  at  $p = 0.01$ ). The radioactivity of inner layer in older runner was distributed almost uniformly along



the runner, and in younger ones, a negative gradient of labelled compounds was observed (Fig. 3B).

In runners deprived daughter plants, radioactivity was detected only in the first two segments in both groups of runners and layers, (Fig. 3C, D). In the next segments — it was only the trace of radioactivity.

Table 4

Distribution of  $^{14}\text{C}$ -assimilates in runners after 4 hrs translocation (10<sup>2</sup> c. p. m.)

Experimental series	Younger runners			Older runners		
	outer part	inner part	O/I	outer part	inner part	O/I
With daughter plant	10.02	8.47	1.18	10.55	14.50	0.73
Without daughter plant	5.34	4.66	1.15	4.24	5.78	0.73
Effect of daughter plant removal	—4.68	—3.81	—	—6.31*)	—8.72**	—

\*) Significant  $p = 0.05$

\*\*) Significant  $p = 0.01$

O/I ratio of radioactivity of outer and inner part.

## DISCUSSION

In strawberry the relatively low amount of  $^{14}\text{C}$ -assimilates migrated from the blades as compared with other species (Starck 1964a, b). Even 4 hrs translocation established less than 20 percent of total radioactivity (in expt. 2) and half of that (in expt. 3). The share of runners and daughter plants in total radioactivity of the whole plant was rather small. From the other hand their radioactivity represented about 40 percent (in experiments 3), and about 30 percent (in expt. 2), of total  $^{14}\text{C}$ -translocated in 4 hrs., but only 10 percent, in autumn experiment.

In most experiments performed with strawberry, a marked decrease of  $^{14}\text{C}$ -translocation into the runner deprived of daughter plant was observed as compared with intact plants. This effect was more pronounced in runners after excision of bigger daughter plant than of a smaller one. Similar results were obtained in the previous experiments, (Starck 1964a), with lupin, where excision of some part of the roots affected  $^{14}\text{C}$ -distribution less, than the removal of the whole root system. This seems to suggest, that removal of some part of the acceptor-organ, or of an acceptor of different size, depressed differently the export of assimilates to that organ, as a consequence of "sink power" reduction.

The  $^{14}\text{C}$ -distribution in the inner tissue of runner may suggest, that "filling" of these tissue of intact, younger runner with the labelled compounds seems to be delayed as compared with that of older ones. Therefore the rate (and/or velocity)

of translocation, at least in the runner may depend on the capacity of the daughter plant as an acceptor of assimilates.

The reduced migration of  $^{14}\text{C}$ -assimilates was observed both in the inner and outer tissue (the ratio of the radioactivity of the outer and inner tissue did not change after removal of the daughter plant). This does not agree with Peel's experiment (1964), who claimed, that lateral transport of assimilates increased in willow cuttings with poorly developed roots, as compared with that in cuttings, with well developed roots.

In outer tissue, especially of young, intact runner, was found more than one half of  $^{14}\text{C}$ -assimilates, translocated to that organ. Therefore it is difficult to explain, why excision of the daughter plants produced a decrease of translocation to growing, outer tissue of runner. Similar results were obtained with bean plants, after excision of roots (Starck 1964a). In the stem of intact bean plants,  $^{14}\text{C}$ -assimilates accumulated in a relatively small amount in the roots which were not a dominant sink of assimilates and relatively high amount — in the lower part of the stem, probably as a result of lateral movement into the outer tissue surrounding the conductive bundles. Such an accumulation was not observed in plants deprived of roots. The accumulation of  $^{14}\text{C}$ -assimilates, in the lower part of the stem of intact plants, was not observed in the case, when roots were dominant acceptor — e.g. lupin (Starck 1964a). In that case roots removal caused basipetaly increasing gradient of labelled compounds in the stem.

All these facts seem to suggest, that removal of assimilate acceptor-organ, may interfere, in some cases with the migration of photosynthates into the other "sink", especially those, which are provided with assimilates by the same conducting bundles. This agrees with postulates of Nelson (1959), Czajlachian (1957), Thrower (1964), that the demand for assimilates is not sufficient condition for translocation into their acceptors.

Some other interaction between organs-donors and organs-acceptors seems possible. This influence may extend beyond organ-acceptor e.g. by the production of growth substances (Booth 1962; Hartt 1964; Hew-Chay-Sin 1965; Jakusz-kina 1956, 1962, Povolockaja 1962, Thrower 1964), which may directly or indirectly alter their "sink power". In experiments reported, the growth substances were not estimated, but removal of various organs produced the same changes in the pattern of  $^{14}\text{C}$ -distribution, (daughter plants and roots), and excision of the same organ, (e.g. roots in various plants) influenced migration of assimilates in a different way, or in a different degree, probably depending on their metabolic activity and the relationship between various acceptors of assimilates.

#### SUMMARY

The aim of present study was to compare the role of strawberry daughter plant in the translocation of assimilates, with that of roots in other species. Only in the autumn's experiment (No 1), where translocation was relatively low, daughter plants removal influenced a little migration of assimilates to the runner. In all the other cases a marked decrease of  $^{14}\text{C}$ -translocation to the

runner, deprived of daughter plant was observed, as compared with intact plant. This effect was more pronounced in older runners, after excision of bigger plants. The "filling" of the tissue, of intact, younger runners with  $^{14}\text{C}$ -assimilates, seems to be delayed as compared with that of older ones. The distribution of labelled compounds in radial direction, depended on the age of runner, but not on the presence of daughter plant. In younger runners, more labelled assimilates were located in the outer layer, inversely to the older ones.

All these facts seems to suggest, that the daughter plant — an acceptor of assimilates, influence the velocity (or/and rate) of translocation of assimilates in strawberry, in different degree depending on its "sink power". This effect was similar to that, exerted by roots removal, or some part of them, reported in previous paper, (Starck 1964a, b). The mechanisms of these effects are still little known.

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#### *Wpływ odcięcia rozmnóżki pączkowej na przemieszczanie asymilatów w truskawce*

##### Streszczenie

W celu scharakteryzowania roli różnych akceptorów w przemieszczaniu asymilatów, podjęto badania dotyczące wpływu rozmnóżki pączkowej na transport do rozłogów truskawki. Przeprowadzono trzy doświadczenia, w których śledzono rozmieszczenie radioaktywnego węgla w poszczególnych organach roślin kontrolnych i pozbawionych rozmnózek.

Rozmnóżka okazała się stosunkowo słabym akceptorem asymilatów, być może na skutek dość dużej aktywności fotosyntetycznej; jej udział w sumarycznej radioaktywności całej rośliny, był nieznaczny, pomimo, że w czasie ekspozycji w  $^{14}\text{CO}_2$ , umieszczano je w ciemności. Stwierdzono

jednak, że rozłogi wraz z rozmnóżką kumulowały ok. 30—40% znakowanych asymilatów, w stosunku do ilości  $^{14}\text{C}$  substancji, przemieszczonych z organów asymilujących  $^{14}\text{CO}_2$ . Tylko w jednym doświadczeniu, przeprowadzonym na jesieni, w którym transport asymilatów był nieznaczny, do rozłogów wraz z rozmnóżką przemieszczało się tylko około 10% znakowanych związków, transportowanych z organów asymilujących, co stanowiło zaledwie 1% sumarycznej radioaktywności całej rośliny. W tym przypadku, odcięcie rozmnóżki w bardzo nieznacznym stopniu wpłynęło na przemieszczanie asymilatów, w przeciwieństwie do dwóch pozostałych doświadczeń, gdzie stwierdzono znaczne zahamowanie migracji asymilatów w rozłogach, pozbawionych rozmnóżki. Stopień zahamowania zależał od wieku rozłogów i wielkości odciętego akceptora. Odcięcie większej rozmnóżki, starszego rozłogu, spowodowało wyraźniejsze zahamowanie transportu, być może na skutek jej większej aktywności jako organu-akceptora. W rozłogach młodszych, u roślin kontrolnych (tj. z rozmnóżką), stwierdzono malejący gradient radioaktywności, w tkankach wewnętrznych, podczas gdy w rozłogach starszych, znakowane związki były prawie równomiernie rozmieszczone na całej ich długości. Może to wskazywać, na wpływ wielkości akceptora na szybkość (a być może i intensywność) przemieszczania asymilatów.

Rozmieszczenie asymilatów w rozłogach, w kierunku radialnym, zależało również od ich wieku, natomiast nie zależało od obecności rozmnóżki. W rozłogach młodszych stwierdzono więcej  $^{14}\text{C}$ -asymilatów w tkankach zewnętrznych, głównie miękiszowych, natomiast w starszych — głównie w tkankach wewnętrznych, (m. innymi przewodzących).

Wszystkie powyższe fakty wydają się wskazywać, że odcięcie rozmnóżki pączkowej, podobnie jak odcięcie korzeni lub ich części (Starck, 1963, 1964a, b), wpływało na migrację asymilatów, w różnym stopniu zależnie od aktywności danego organu, jako akceptora.