

## Source-sink relationships in radish plant

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### Abstract

The problem of source-sink relationships in di- and tetraploidal radish plants grown in hydroponic cultures was investigated in two stages of their development: with intensively growing swollen hypocotyl and in the period of actively accumulating nutrients in the storage organ.

It was found, that the proportion between the mass of organs, their RGR and NAR was very similar in di- and tetraploidal populations, probably owing to a similar rate of photosynthesis and pattern of assimilates distribution.

The high variability of swollen hypocotyls size is slightly correlated with the size of the whole aerial part and is not correlated with the rate of photosynthesis in leaves. Partial defoliation of radish plants did not affect the rate of photosynthesis of the remaining leaves. Only in the cotyledones the oldest donors of  $^{14}\text{C}$ -assimilates, a slight compensation of photosynthesis was reported. It may suggest, that the rate of photosynthesis in radish plants is not under the control of sink activity.

The size of the storage organ have determined in some extent its attractive force and influenced the amount of  $^{14}\text{C}$ -assimilates exported from their donors. Translocation of photosynthates from the young, still growing leaves was conditioned mainly by their retention power. Therefore, in young radish plants cotyledons were the main donor of  $^{14}\text{C}$ -assimilates.

### INTRODUCTION

In order to stimulate crop growth and yield development, the principles governing the distribution of assimilates and their storage should be better understood. One of the most characteristic features of many cultivated plants has been the increase of the storage capacity of the harvested organs (Evans, 1975a). The relationship between accumulation of nutrient in storage organs and rate of photosynthesis is the subject of many controversial discussions (Humphries, French,

1969; Finn, 1974; Moorby, 1970, 1974; Neals et al., 1968; Spence, Humphries, 1972).

A high variability in the size of the storage organ in particular radish plants grown under the same conditions seems to be a good object for studying of relationships between storage capacity and photosynthetic rate (or activity). Some plants were able to store in swollen hypocotyl about 50 per cent of their dry matter (Starck, 1973a, b). In other plants the contribution of that organ to total plant dry matter was much lower. Therefore the question arises whether the rate of growth and accumulation of sugars in storage organs depends mainly on the rate of photosynthesis, on the level of assimilates supply as consequence of activity of photosynthesis of the whole plant and on the pattern of nutrients distribution. The problem of source-sink relationships in di- and tetraploidal populations, was investigated. The supply of assimilates was modified by partial defoliation.

#### MATERIAL AND METHODS\*

Radish cv. *Szkarłatna z białym końcem* diploidal population and the cv. *Tetra Hłowiecka* tetraploidal\* one were grown out of doors in hydroponic cultures (roots in diluted modified Hoagland solution and storage organ — in perlite), and only during night and rainfall — under greenhouse conditions.

Experiments were done in spring, in the period 1973—1975, with relatively young 23—26-days plants (with hypocotyl starting to swell) and with old plants (in most experiments — about 30 days of age) actively accumulating nutrients in the storage organ (Table I).

Plants at that stage of development completed probably cell growth in the storage organ; all  $^{14}\text{C}$ -assimilates were found in the supernatant as sugar fractions in contrast to younger plants which incorporated a great deal of  $^{14}\text{C}$ -substances into the ethanol-insoluble fraction.

In some experiments blades were removed to check the effect of partial defoliation on the rate of  $^{14}\text{CO}_2$  assimilation and on export of assimilates from the remaining donors. Exposure to  $^{14}\text{CO}_2$  was done in a plexiglass chamber during 20—30 min. in particular experiments. The translocation period continued in most experiments up to 2 hrs or 6 hrs (from the beginning of  $^{14}\text{CO}_2$  liberation). The figures in the tables and on the drawings are averages of 3 or 4 replications, one plant in each.

All labelled plants were harvested, immediately frozen in dry ice, cut into particular plant organs and stored at  $-15^\circ\text{C}$ . Total radioactivity as well as that of the fraction soluble in 80 per cent ethanol (supernatant)

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was estimated with a G-M thin end-window counter or gas flow counter. Sugars, separated from the ethanol-soluble fraction by the use of an ion exchanger were estimated by the phenol method.

Simultaneously with exposure to  $^{14}\text{CO}_2$ , samples of dry matter of the particular plant organs were collected in 3 replications, including two or three plants in each and the surface of blades and cotyledons was measured. In expts. I and II some parameters of growth analysis were calculated (NAR and RGR)\*. Relationships between the investigated characters were calculated assuming a linear model of regression:

$$y = Bx + \varepsilon$$

where:  $y$  is the vector of dependent random variable

$x$  „ „ „ of independent random variable

$\varepsilon$  „ „ „ of differences from regression function

$B$  „ coefficient of regression

In the case of nonhomogenic data derived from particular treatments, the parameters of the function of regression were estimated from the values of random variables obtained from differences from mean of treatments according to the model of linear classification as belowe:

$$y_j = Y_{ij} - \bar{y}_i$$

$$x_j = X_{ij} - \bar{x}_i$$

Where  $y_{ij}$  and  $x_{ij}$  are data of experiments and  $\bar{y}_i$  and  $\bar{x}_i$  are means of particular treatments of the correlated characters. Coefficients of Pearson correlation were calculated and verified for their significance at the probability level  $\alpha = 0.05$  or  $0.01$ . Coefficients of determination  $r^2 \cdot 100\%$  were also calculated indicating what percentage of variability of the dependent variable is determined by the influence of the independent variable.

## RESULTS

For a general characteristic of relationships between the rate of growth of particular plant organs some biometric analyses, based on their fresh matter, were performed on populations consisting of 149 *Tetra Hlowiecka* old plants, grown on nutrient solution under similar conditions as the plants of expt. IV, as well as on 39 younger and 57 older plants population (from expts. I, II, III) based on their dry matter (Table 2).

Generally speaking the variations of size of storage organ and roots highly exceeded those of the aerial part. The correlation between root size and aerial part was significant in all the cases but with a relatively high coefficient of determination in young plants. Correlation between

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\* NAR — net assimilation rate, RGR — relative growth rate.

Table 1  
General characteristic of experiments

Expt. No.	Weather conditions		Age of plants (days)	<sup>14</sup> CO <sub>2</sub> -exposure				
	sunny days	No of night with temp. < 10°C		data	time (min.)	°C temperature		weather
						photo- synthesis	trans- location	
I	5	4	23	25.V.1973	30	20—29	18—24	cloudy
II	11	4	31	2.VI.1973	30	27—33	26—26	sunny
III	12 and 16	19 and 19	26 and 32	19.VI.1974	20	28—32	27—32	„
IV	13	4	25	31.V.1975	20	10—17	17—18	cloudy

the aerial part and the storage organ was significant in older plants, in contrast to young ones, with various coefficients of determination.

Tetraploidal radish plants differed distinctly from diploidal ones by their size, but the proportions between organs' dry matter and their RGR, was very similar in both populations (Table 3, expts. No. I, II in 1973 year), especially in younger plants. Storage organs contribution to the total plants dry matter was slightly higher in tetraploidal than in diploidal, older plants. Also NAR estimated for an 8-day period (between 23- and 31-days of their growth) was almost the same in both populations; for di- and tetraploidal plants NAR was 10.2 and 9.9 g · m<sup>-2</sup> · day<sup>-1</sup> respectively (data not presented in tables).

The relative growth rate of particular organs of young plants was calculated very roughly, for the whole period of their growth (data presented in Table 3 for expt. No. I) and also for the last few days (between 23-rd-day and 31-st of growth, expt. No. II, and 26-th-day and 32-nd, expt. No. III). In younger plants all organs grow at a similar rate. In the stage of active accumulation of nutrients in the swollen hypocotyl, RGR of that organ increased more then twice both in di- and tetraploidal radish plants (expt. II). In contrast the fibrous root growth rate decreased. The value of RGR examined in expt. III (done in 1974, during much worse weather conditions) indicated that in younger plants (in the period between 22-nd and 26-th day of their life) the storage organ accumulated more intensively dry matter than in the next period examined.

In the periods between the 23-rd and the 31-st (expts. I and II), and 26-rd and 32-nd day (expt. III) accumulation of sugars in the storage organ was observed. In older plants almost all <sup>14</sup>C transported to that organ was found in the supernatant (Table 3), as sugars. It may suggest, that physiological growth of the storage organ (division and elongation of cells), is already accomplished and the second phase — accumulation of sugars starts.

Table 2  
Biometric characteristic of tetraploid radish plants growth

Estimation	On dry matter basis (expts 1973—1974)				On fresh matter basis expt. 1975 (149 plants)			
	young plants (39 plants)				old plants (57 plants)			
	$\bar{x}$ (mg)	s	V%	$\bar{x}$ (mg)	s	V%	$\bar{x}$ (g)	V%
aerial part	111.6	30.9	27.7	256.0	57.9	22.6	4.90	20.4
storage organ	22.0	9.4	42.9	183.9	83.9	45.6	4.01	36.4
roots	34.8	15.8	45.4	52.2	17.8	34.1	1.37	37.9
correlations and regressions								
	b yx	r	$r^2 \cdot 100\%$	b yx	r	$r^2 \cdot 100\%$	b yx	$r^2 \cdot 100\%$
aerial part (x) and storage organ (y)	0.08	0.27	7.3	0.71	0.48*	23.0	0.29	3.8
aerial part (x) and roots (y)	0.26	0.52*	27.0	0.11	0.34*	11.5	0.23	19.6

coefficients:

b yx = regression

r = correlation

$r^2 \cdot 100\%$  = determination

s = standard deviation

$\bar{x}$  = mean of mass (dry or fresh)

V% = coefficient of variation  $\left( V = \frac{s}{\bar{x}} \cdot 100 \right)$

\* = significant correlation at  $p = 0.05$ .

\*\* = " " " "  $p = 0.01$

Table 3

Characteristic of growth, dry matter distribution and

Age of plants and No of experiments	Populations	Blades with apical part			Petioles		Cotyledons	
		d.m. (mg)	contribution to total d.m. (%)	RGR g/g·day	d.m. (mg)	contribution to total d.m. (%)	d.m. (mg)	contribution to total d.m. (%)
23-days No I	Di	41	35.3	0.16	5	4.1	33	28.5
	T	70	38.0	0.18	9	5.0	46	25.3
26-days No III	T	105	55.0	0.23	15	7.6	—	—
31-days No-II	Di	165	38.3	0.17	25	5.8	32	7.4
	T	231	34.5	0.15	47	7.0	45	6.7
32-days No III	T	257	48.3	0.14	33	6.1	—	—

Di — diploidal plants

T — tetraploidal plants

The relative amount of  $^{14}\text{CO}_2$ -assimilation by the whole plants of the tetraploidal population exceeded distinctly that of diploidal ones (Table 4), especially in the early stage of their development, mainly owing to the bigger size of the leaves. The differences in the rate of  $^{14}\text{CO}_2$  assimilation, calculated per dry matter or area of blades, in 23-day plants of comparable populations were rather small or almost none- in older plants.

In plants deprived of one of the oldest leaves (7 days before  $^{14}\text{CO}_2$ -exposure), compensation of photosynthesis in diploidal, and tetraploidal plants was insignificant. Only in cotyledons the rate of  $^{14}\text{CO}_2$  assimilation exceeded that of the control one by up to 50% in both populations. On the basis of the comparison of the relation between the rate of  $^{14}\text{CO}_2$  assimilation by the blades and cotyledons in both experiment, the supposition can be drawn that with the lapse of time between expt. I and II (8 days) the cotyledons aged markedly; their photosynthetic rate (on dry matter basis) constitutes, in expt. I, about 70% of that in blades, but decreased to slightly more than 40%, of control plants — in expt. II; in series partially defoliated — this proportion decreased much less. It suggest, that in plants with reduced area of leaves, ageing of cotyledons was retarded (Table 4). The same conclusion may be advanced on the basis of the higher proportion of  $^{14}\text{C}$ -substances incorporated into the fraction of aminoacids and organic acid in cotyledons of partially defoliated plants (data not presented).

In expts. I and II distribution of labelled assimilates was estimated 30 min., 2- and 6-hrs from the beginning of  $^{14}\text{CO}_2$  exposure (Table 4 and Fig 1.). After 2 hrs translocation export of  $^{14}\text{C}$ -assimilates, produced in 30 min was almost completed, as in Hofstra and Nelson's investi-

sugar content in radish plants (Experiments No. I, II, III)

Storage organ					Roots		
d.m. (mg)	contribution to total d.m. (%)	RGR g/g·day	% of <sup>1</sup> $^{14}\text{C}$ - supernatant	sugar content mg/g d.m.	d.m. (mg)	contribution to total d.m. (%)	RGR g/g·day
14	12.1	0.12	84	162	23	20.0	0.14
24	12.9	0.14	86	136	34	18.8	0.15
27	14.0	0.25	63	69	44	23.4	0.21
165	38.3	0.31	100	214	44	10.2	0.08
290	43.3	0.31	91	223	57	8.5	0.06
178	33.4	0.16	85	222	65	12.2	0.11

1) % of  $^{14}\text{C}$ -supernatant — as 100 percent assumed total radioactivity of storage organs after 2 hr translocation

gations (1969); after 6 hrs total radioactivity of the whole plant decreased, probably owing to the loss of  $^{14}\text{CO}_2$  in respiration (Table 4).

The distribution pattern of  $^{14}\text{C}$ -assimilates is presented on Fig. 1. In 23-day plants cotyledons constitute the main donor of current assimilates, as already reported Voronkova et al. (1973). Specific radioacti-

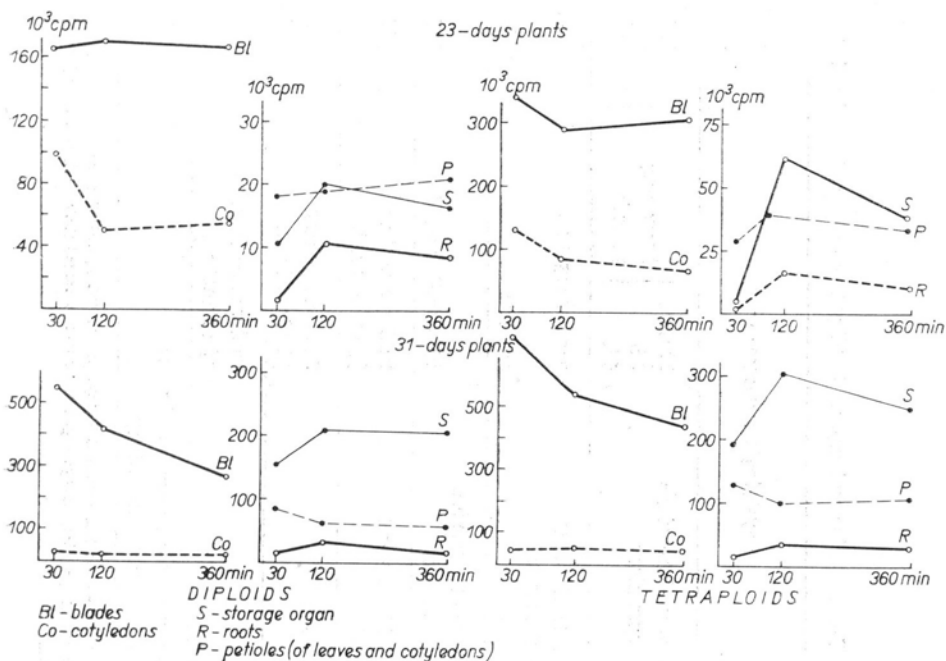


Fig. 1. Distribution of  $^{14}\text{C}$ -assimilates in 23-rd and 31-st day radish plants (expts No. I, II)

Table 4

$^{14}\text{C}$ -assimilation and export of  $^{14}\text{C}$ -photosynthates from the blades and cotyledons of di- and tetraploidal radish plants (expt's. No I, II)

Physiological parameters		Expt. I 23-days plants			Expt. II 31-days plants			
		Diploidal		T	Diploidal		Tetraploidal	
		Di	T		C	Def	C	Def
Radioactivity of the whole plant $10^3$ cpm/plant	30 min. 2 h 6 h } harvesting periods	296 272 268	511 485 457		845 747 587	819 593 599	1100 1034 855	1042 1065 820
Relative rate of blades $^{14}\text{CO}_2$ -assimilation (in $10^3$ cpm)	per 100 mg d.m.	464	505		341	396	343	300
	per $\text{dm}^2$	1976	2438		1020	1189	1033	900
Relative rate of cotyledons $^{14}\text{CO}_2$ -assimilation	$10^3$ cpm/100 mg d.m.	357	332		144	217	147	207
Petioles (of blades and cotyledons)	fresh matter (mg) % of total rad.	157 6.5	391 8.1		541 7.6	292 6.5	909 10.1	1014 8.1
Storage organ	fresh matter (mg) % of total rad.	145 7.4	508 12.7		2213 29.4	1715 25.5	6349 29.3	5413 31.8
Roots	fresh matter (mg) % of total rad.	352 4.0	477 3.2		583 3.7	495 5.4	591 3.5	992 3.9
Total export to storage organ and roots (percentage of total radioactivity)		11.4	15.9		33.1	30.9	32.8	35.6

C — control; Def — one leaf removed 7 days before  $^{14}\text{CO}_2$ -assimilation;

Figures concerning: petioles, storage organ and roots presented their fresh matter and their contribution to total radioactivity of the whole plant (in percentage); plants harvested after 2hr translocation.



vity of cotyledons decreased in an 80 min. period almost twice (data calculated from Fig. 1). Blades and apical part exhibit in that period of development very high retention of assimilates (Fig. 1) they exported in 6 hrs only a low percentage of labelled compounds in di- and slightly more in tetraploidal plants. In older plants, blades were the main source of photosynthetic products (they exported about 20—30% of  $^{14}\text{C}$ -assimilates), but cotyledons contributed in very low proportion to the total  $^{14}\text{C}$ -photosynthetic activity (Fig. 1).

Radioactivity of petioles was relatively stable during the whole experimental period; in both experiments they did not import (or only a very low amount)  $^{14}\text{C}$ -substances from blades, even after 6 hrs (Fig. 1). Older plants with much bigger acceptor's, exported to the storage organ and roots more than twice as much labelled assimilates as younger ones (Table 4). In older plants (expt. II) the swollen hypocotyl accumulated about 30% of all labelled  $^{14}\text{C}$ -photosynthetic products similarly in all series. Such an increment of translocation to the storage organs in older plants may depend on a reduction of assimilates retention, in donors or on an increase of sink activity or generally on changes in physiological stage of the whole plants; in older plants the contribution of mature leaves, with higher exporting possibilities increased as compared to that of all the other leaves.

To check the effect of storage organs size (or in relative values, of its contribution to the fresh matter of the whole plant), on their share in  $^{14}\text{C}$ -assimilates exported from  $^{14}\text{C}$ -donors, some statistical calculations were performed (coefficient of correlation, regression and determination) on the basis of data obtained in particular experiments, with intact plants (Nos I to IV), done with di- and tetraploidal populations (Table 5). A very high (and statistically significant) correlation was found, with high

Table 5  
Relationships between the size of storage organs and their share  
in  $^{14}\text{C}$ -assimilates exported from  $^{14}\text{C}$ -donors

Populations	Parameters compared	n	$b_{yx}$	$r_{yx}$	$r^2 \cdot 100\%$
Diploidal	x — fresh weight (g) y — % of total rad.	27	3.83	0.61**	36.8
	x — % of fresh weight y — % of total rad.	27	0.51	0.60**	35.5
Tetraploidal	x — fresh weight (g) y — % of total rad.	32	2.67	0.69**	47.8
	x — % of fresh weight y — % of total rad.	32	0.40	0.78**	60.5

Figures with \*\* — significant at  $p = 0.01$ .

Other symbols — like in table 2.

n = number of replications.

coefficient of determination, between both parameters. It suggests that the "sink power" of the storage organ is related, among the other things with their size.

To check the second possibilities the next two experiments (No. III and IV), were performed (on tetraploidal population only), with young and old plants exposed to  $^{14}\text{CO}_2$  simultaneously in the same chamber. In both experimental groups, with small and bigger size of storage organ three series were examined:

- I — intact plants — as control (c),
- II — with only one leaf (young but almost fully expanded) — labelled with  $^{14}\text{CO}_2$ : all the others were removed in the afternoon one day before exposure, (y),
- III — as in series II, but the only one, rather old leaf was  $^{14}\text{CO}_2$  labelled, (o).

In all series of ext. III cotyledons were also removed at the same time with other leaves, but not — in expt. IV.

The 26-day plants used in expt. III were physiologically younger than 23-day plants used in expt. I as was already mentioned probably owing to worse weather conditions during their growth (Table 1). In their storage organ cell growth not completed yet; they incorporated about 40 per cent of  $^{14}\text{C}$ -substances into the ethanol-insoluble fraction (data presented in Table 3).

Total assimilation of  $^{14}\text{CO}_2$  of the whole experimentally manipulated plants of each series was incomparable because of differences in the size of blades  $^{14}\text{C}$ -donors, in control and defoliated plants (Table 6).

The rate of  $^{14}\text{CO}_2$  assimilation of younger leaves, was higher than in older leaves (calculated per dry matter, expt. III) both in younger and older plants. To check if these differences were connected only with the age of blades or also with the limited supply of assimilates in partially defoliated plants, in expt. IV (done also on tetraploidal population, at the stage of active accumulation of substances in the storage organ), radioactivity of each leaf of the control plants were analysed separately (Fig. 3). The rate of  $^{14}\text{CO}_2$  assimilation (calculated on fresh mass basis), independently of defoliation treatment, was much higher (and statistically significant) in younger leaves than in older ones. In the blades no compensation effect was observed. On the contrary, the rate of  $^{14}\text{CO}_2$  assimilation of cotyledons increased in defoliated plants (differences statistically insignificant).

The changes in radioactivity of the apical part did not indicated their share in  $^{14}\text{C}$ -substances exported from the labelled blades and cotyledons (Table 6) probably owing to  $^{14}\text{CO}_2$  assimilation "in situ". Their specific radioactivity (in expts. III and IV) did not change significantly in the space of time between two harvesting periods (100 min.). A small amount

Table 6  
Effect of age of labelled leaf on  $^{14}\text{C}$ -assimilates distribution

Parameters examined	Harvesting period	Experiment No III						Expt. No IV			
		young plants			old plants			old plants			
		c	y	o	c	y	o	c	y	o	o
Radioactivity of the whole plant ( $10^3$ cpm)	in A	103	38	48	141	75	55	3733	1099	932	
Fresh matter (mg) of $^{14}\text{C}$ -labelled blades (and cotyledons)	in A	1325	354	522	2385	722	994	4588	1671	1525	
		a	b	a	c	ab	c				
Specific rad. of blades $10^3$ cpm/g fr.m.	in A	62.8	88.5	73.0	41.5	79.1	37.3	—	—	—	
Apical part	in A	7.3	6.6	10.0	6.0	7.0	7.8	78.1	48.9	31.6	
	in B	8.9	7.0	7.0	8.7	6.8	5.1	56.4	38.1	38.5	
	in B	24.4	15.9	15.9	11.1	13.8	31.7	7.6	20.5	22.6	
Petioles	in A	1.6	0.9	1.3	1.2	0.9	0.9	11.1	9.7	14.5	
	in B	2.3	1.2	1.7	1.3	1.2	0.7	14.0	7.9	12.5	
	in B	7.3	4.0	7.5	6.3	4.8	4.7	5.9	1.5	5.5	
Roots	in B	373	351	389	892	997	923	2463	2460	2259	
	in B	6.4	5.7	7.3	5.3	5.1	6.7	4.7	6.8	4.6	

c— control series (intact plants), y- and o- plants with one leaf labelled:

young (y) or old (o), all the other leaves removed

Harvesting periods:

A — 20 min from the beginning of  $^{14}\text{CO}_2$  exposure

B — 2 hrs

Percent of total radioactivity — radioactivity of the whole plant assumed as 100 %.

Specific radioactivity designated by the same letter — do not

differ significantly at  $p = 0.05$ .

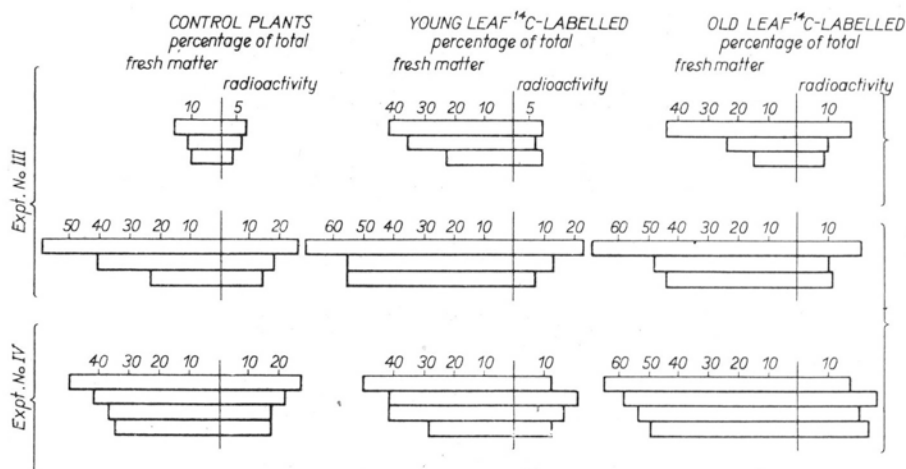


Fig. 2. Comparison of the contribution of storage organs fresh matter to that of the whole plant and their share in  $^{14}\text{C}$ -assimilates exported from the different sources of labelled photosynthates, (old or young leaves, in partial defoliated plants). Expts No. III, IV. Diagrams presents particular replications: upper diagrams — young plants, middle and lower — old plants

of radioactive substances were also transported from  $^{14}\text{C}$ -donors to the petioles.

The proportion of  $^{14}\text{C}$ -assimilates migrating to the roots did not depend very much on the age of plants in spite of bigger roots, neither did it depend on the source of  $^{14}\text{C}$ -substances. It suggests that roots of older plants created a sink with relatively lower attractive force.

In contrast, transport to the storage organs in expts. III and IV depends on their contribution to dry matter of the whole plant both in older and younger plants of the control series (as described before; data illustrated in Table 5), as well as in young plants with  $^{14}\text{C}$ -labelled old leaf (Fig. 2 and Table 7); coefficients of correlation and determination were relatively high but insignificant owing to the very low number of replications. In the series with a young leaf  $^{14}\text{C}$ -labelled, possessing a high retention power, the various size of the storage organ did not affected export of  $^{14}\text{C}$ -assimilates to that organ, especially in young plants. On the basis of the changes in blades specific radioactivity of the particular leaves (data calculated as averages of replications) in the space of time between both harvesting periods (100 min.), export of  $^{14}\text{C}$ -assimilates was calculated. In old leaves 60 percent of labelled substances were transported from the blades (Fig. 3), but 30—40 percent from young leaves. Cotyledons exported 37 percent of  $^{14}\text{C}$ -photosynthates in control plants, 41 and 58 percent in series with old and young leaf  $^{14}\text{C}$ -labelled, respectively. These data indicate again, that export of assimilates from young, still growing leaves is determined mainly by their

Table 7

Relationships between size of storage organ (assumed as  $x$ , in mg fresh matter), and their share in  $^{14}\text{C}$ -assimilates exported from various  $^{14}\text{C}$ -donors assumed as  $y$ , in percentage of radioactivity transported to storage organ)

$^{14}\text{C}$ -labelled leaves	young plants				old plants			
	n	$b_{yx}$	$r$	$r^2 \cdot 100\%$	n	$b_{yx}$	$r$	$r^2 \cdot 100\%$
All — control	3	0.53	0.86	74.4	7	0.39	0.92**	84.7
Young	3	-0.03	-0.25	6.2	7	0.36	0.50	25.3
Old	3	0.35	0.98	95.5	7	0.26	0.52	26.6

Symbols — like in table 2 and 5.

retention power and that only cotyledons — the oldest  $^{14}\text{C}$ -donors, in series with most seriously restricted supply of acceptors, exported a higher proportion of their  $^{14}\text{C}$ -assimilates.

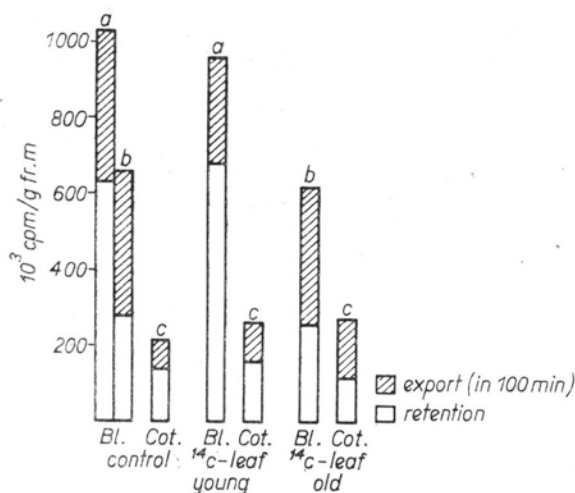


Fig. 3. The rate of  $^{14}\text{CO}_2$  assimilation and export of labelled products from leaves of different age and cotyledons in intact and partial defoliated plants (expt. IV).

## DISCUSSION

Accumulation of nutrients in storage organs undoubtedly depends not only on the global supply of assimilates to all acceptors, but also on the competitive ability of storage organ (Evans 1975 a, b; Heslop-Harrison, 1969). According to the opinion of many authors (Flinn, 1974; Humphries, French, 1969; Lenz, 1974; Neals et al., 1968; Spence, Humphries, 1972, and others), the attractive forces located in acceptors of assimilates may have some controlling influence on the rate of photosynthesis in the source leaves and the pattern of assimilates distribution. If transport of assimilates is restricted by some conditions,

the rate of photosynthesis is often depressed and vice versa, if new acceptors appears. In the case of experimentally modified plants, involving manipulation of sources (e.g. partial defoliation), photosynthesis of remaining leaves increased, as indicated by some authors (King et al., 1967; Wareing et al., 1968, and many others). Loach (1970) showed that sugar beet varieties with large root/shoot ratio maintained a high net assimilation rate during the later stage of their growth, owing to high accumulation of sugars in roots. Also Habeshaw (1973) suggested, that the rate of photosynthesis can be linked directly to the sink activity, controlling the rate of translocation from the leaves.

Relationships between source — sink were investigated also in other plants, storing nutrients in vegetative organs. According to Moorby (1970) the dominant factor controlling the rate of photosynthesis in potatoes was the rate of tuber growth. In sugar beet NAR depends on the root size (Humphries, 1964).

On the basis of measurement of intact plants from particular experiments described above, statistical calculations of relationships between the highly variable size of the storage organ and the rate of  $^{14}\text{CO}_2$ -assimilation (of di- and tetraploidal populations) was performed. Fresh mass of the storage organ ( $x$ ) did not correlate with the rate of  $^{14}\text{CO}_2$  assimilation calculated per fresh mass of blades and cotyledons — all donors of assimilates (denoted as  $y$ ).

Replications $n$	Coefficients of:		
	regression $b_{yx}$	correlation $r_{yx}$	determination $r^2 \cdot 100\%$
54	6.74	0.11	1.0

It may suggest, that in radish plants the relationship between sink activity of the storage organ and the rate of photosynthesis is more complicated than in other plants, described above.

Neither was there any compensation effect in the reported experiments also in blades of plants deprived of one leaf, 7 days before  $^{14}\text{C}$ -exposure, nor in severely defoliated plants but one day before assimilation measurement. A small compensation was observed only in old organs — cotyledons, as response to a diminished source of assimilates with unchanged demand of acceptors. The conclusion on the lack of relationship between the rate of photosynthesis and the size of the storage organ should be drawn with caution, especially, since the reported experiments with defoliation describe short term effects. Internal control of photosynthesis in leaves may be a long-term effect, as Bull postulated on the basis of his experiments with defoliation or shading of sugar cane (after Evans, 1975 a).

Mokronosov and Ivanova (1971) observed, that defoliation of potatoes stimulated photosynthesis of the remaining leaves only when 30—50 per cent of leaves were removed, but inhibited — in more severely defoliated plants. In other species, in some experiments, e.g. in barley, defoliation also did not cause compensation of photosynthesis (Ryle et al., 1975), and only in some cases caused it in sunflower and bean plants (Starck, Ubysz, 1974).

On the basis of the results described and discussed in other papers very often no conclusive evidence was found of a simple feedback control of photosynthesis by acceptors; (in sugar cane — Glasziau, Bull, 1971, as well as in red beet — Austin, 1972). According to Mokronosov's opinion (1973), in the case of fluctuation of the growth rate, the fluctuation in the rate of photosynthesis can be due to temporary deposition of assimilates in blades, probably in their free spaces.

Independently of the lack of correlation between the rate of photosynthesis and size of the storage organ, the question is still open concerning the cause of a high variability of mass of the radish swollen hypocotyl. Some correlation (but not very high, with rather variable and low determination coefficient) between size of the aerial part and that of the storage organ, indicated indirectly the possibility of correlation between growth of the storage organ and photosynthetic activity of the whole plant.

The second possibility are the differences in efficiency of export of assimilates from their donors.

The effect of acceptors on the amount of assimilates transported from the blades was observed in many plants, eg. potatoes (Moорby, 1968), sugar beet (Habeshow, 1969), peas (Harvey, 1973). The same is reported in the experiments described in present paper as well as in previous ones, done also with radish plants (Starck, 1973 a, b). Therefore, acceptors with high mobilizing power stimulated export of assimilates from their donors.

Another possibility is connected with differences in assimilates distribution among particular acceptors. Competition between the storage organ and roots is little probable; translocation of  $^{14}\text{C}$ -assimilates to roots was much less variable than that to the swollen hypocotyl; the coefficient of correlation and determination between  $^{14}\text{C}$ -translocation to roots (x), and to the storage organ (y) (expressed as percentage of radioactivity of total plants) was very low:

$$n=30; \text{byx}=0.0301; r=0.071; r^2 \cdot 100\% = 0.5\%$$

All the above mentioned facts suggest that roots have priority over the storage organs as a growing acceptor, as was already observed by other authors (see review of Evans, 1975 b). This supposition, concerning the hierarchy of priority among acceptors in radish plants was sug-

gested before in the case of limited supply of assimilates under shading conditions, where growth of the storage organ was reduced more drastically than that of all the other organs (Starck, 1973 a, b). Therefore the amount of storage substances in the swollen hypocotyl depends on some limitation of the mobilizing power or storage capacity. According to Glasziou's and Gayler's idea (1972), the total pull of the storage organ is a function of its metabolic activity. Complex relations determine the final effect: growth and accumulation, but one of the most important factor is the activity of enzymes involved in the accumulation process (Ricardo, 1974 a, b). This problem will be the subject in the next investigations.

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*Współzależność pomiędzy donorami i akceptorami asymilatów  
w rzodkiewce*

*Streszczenie*

Celem pracy było zbadanie współzależności pomiędzy akceptorami i donorami asymilatów u di- i tetraploidalnych populacji rzodkiewki, rosnącej w kulturach hydroponicznych. Badania prowadzono w początkowej fazie intensywnego wzrostu zgrubienia oraz w okresie akumulacji substancji pokarmowych w tym organie.

W badanych okresach wykazano zbliżone proporcje masy poszczególnych organów u di- i tetraploidalnych populacji, wynikające między innymi ze zbliżonego wzoru dystrybucji  $^{14}\text{C}$ -asymilatów. Również takie parametry analizy wzrostowej jak NAR oraz RGR u obu populacji miały podobne wartości liczbowe.

Próbowano wyjaśnić fizjologiczne przyczyny bardzo dużych różnic w wielkości zgrubienia hypokotylu. Nie są one skorelowane z intensywnością fotosyntezy w ilościach a tylko nieznacznie z wielkością całej części nadziemnej, a stąd i z aktywnością fotosyntetyczną całej rośliny.

Udział organu zapasowego w wykorzystaniu  $^{14}\text{C}$ -asymilatów transportowanych z liści i liścieni jest silnie skorelowany z jego masą, szczególnie w fazie akumulacji pokarmów w tym organie. U młodszych roślin eksport asymilatów jest determinowany głównie siłami retencji w blaszkach liściowych, szczególnie w młodych, rosnących liściach. W tym okresie głównymi donorami asymilatów są liścienie.

Częściowa defoliacja roślin nie powodowała wzrostu intensywności fotosyntezy w pozostałych na roślinie liściach, natomiast w liścieniach obserwowano zwiększone natężenie fotosyntezy i stymulację eksportu asymilatów.