The influence of roots on the translocation of photosynthates

Part I

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The problem of interaction between the translocation channel and surrounding tissues and especially the influence of acceptors on the translocation of assimilates have not been studied sufficiently. The acceptors of organic substances may affect translocation by a change of rate (or probably velocity) of outflow of assimilates from the leaves or by a change of the rate of translocation in the conducting tissue or by an influence on other processes. A certain role of roots in the translocation process has been suggested by a number of authors (Burr G. 1957; Humphries 1963; Kursanow 1957 a, b; Nelson C., Gorham P. 1957; Shiroya T. 1962; Starck Z. 1962, 1963). Other investigators did not observe any influence of roots on the migration of organic substances (Fujiwara Akio 1962; Gage R., Aronoff S. 1960).

In an earlier paper (Starck 1963), it was suggested that excision of the roots does not affect the total amount of ^{14}C -photosynthates translocated from the "feeding" leaves. Nevertheless the distribution pattern of ^{14}C -compounds in intact plants differed from that in derooted ones. The share of petioles in the total ^{14}C -photosynthates translocated from the source leaves was much higher in derooted than in intact plants. The causes of these discrepancies are so far not known enough. This seems only to support the presumption, that roots may have some effect on the translocation process, probably as an important acceptor of assimilates.

The work to be reported was undertaken to obtain further information concerning this effect especially, how long after derootment the pattern of ^{14}C -distribution changes. This was the reason, why the translocation of photosynthates in intact and derooted plants at different time after ^{14}C -feeding was studied.

Excision of roots is a drastic alteration of the plants and may influence, directly or indirectly, various physiological processes (e.g. photosynthesis, translocation, water balance), therefore in all the experiments reported here, $^{14}\text{CO}_2$ exposure was carried out on intact plants; subsequently the roots were cut off or specially treated.

MATERIAL AND METHODS

The plants were cultivated in a greenhouse either on a modified Hoagland solution (Johnson C. et al. 1957), with regard to lupine and sunflower, or on nutrient solution previously described (Turnowska-Starck 1960) for bean plant. Bean plants var. Saxa were used in the stage of primary leaves. The first trifoliate leaf just started to develop. During exposure to $^{14}\text{CO}_2$ in the morning or at noon; seedlings were kept outdoor in a glass or plexiglass chamber. Their roots were immersed in a diluted nutrient solution (usually 1/10 of 1/8 of normal strength) pH about 5.

In most experiments only leaves were allowed to carry on photosynthesis. In some of the experiments also cotyledons were the "feeding" organs. As a source of radioactivity BaCO_3 or Na_2CO_3 was used. After ^{14}C -photosynthesis, any residual radioactive CO_2 was absorbed by NaOH and then normal air passed through the chamber. The nutrient solution was exchanged after the feeding period and then the plants were divided into experimental series, which will be described separately for each experiment. The plants were allowed to translocate the labelled assimilates for 1 to 24 hours (feeding time included) under normal light and temperature conditions. Following this period plants were collected and separated into: leaves, apical part, stem cut into 2 or 3 cm segments, petioles and roots. Plant material was immediately frozen in dry ice and kept frozen all the time.

All the analytical procedure used for the determination of total radioactivity and radioactivity of 80% ethanol soluble and insoluble fraction have been previously described (Starck 1963).

The statistical analysis of all experiments was carried out by the use of variance analysis and Snedecor's test. The interaction between the examined factors was also calculated. For this purpose, mostly relative values of radioactivity were calculated for particular organs i.e. they were expressed in percentage of total ^{14}C in the whole plant or of total translocation. This percentage values were transformed into arc. sin. $\sqrt{\text{percentage}}$ according to the table of Bliss.

RESULTS

I. The influence of derooting on the translocation

Bean plant experiments. Two experiments were carried out with 20 days old seedlings of bean plant. Plants were allowed to carry on photosynthesis in an atmosphere containing $^{14}\text{CO}_2$, for 20 minutes with regard to experiment I and 30 minutes with regard to experiment II, in glass chambers (volume about 20 l). Radioactive carbon was liberated from $100\mu\text{C}$ of BaCO_3 . One hour after the beginning of

exposure to $^{14}\text{CO}_2$, four plants were collected as control (expt. I). The stem and petioles of two of them were kept in darkness during "feeding" time and only the blades were allowed to assimilate $^{14}\text{CO}_2$. All the green organs of the other two plants were exposed to light. Regardless of the differences in illumination of plants between both

Fig. 1. The effect of derootment on the distribution of ^{14}C -assimilates in the stem of bean plants (Radioactivity expressed as percentage of total radioactivity of the whole plants).

series, after 1 hour translocation, radioactivity was detected in the feeding leaves and only a trace in the petioles. No radioactivity was detected in the stem. This indicated that radioactivity found in petioles and stem, following a relatively longer period of translocations was due largely to the translocation and not to the photosynthesis *in situ*.

At the same time, when the control plants were collected (i. e. 1 hour from the beginning of exposure to $^{14}\text{CO}_2$); all the other plants were divided into two series: intact and derooted. They were collected at different times after tagging.

In experiment II, the plants were also divided into two experimental series: intact and derooted plants.

Table 1

The effect of roots removal on the distribution of radioactivity in bean plants, after 20 min, assimilation of $^{14}\text{CO}_2$

28-29 April, 1962. t photos. 15 to 18°C

Average of two plants

Trans- loca- tion period	Plant organs Treatment	Leaves		Petiole			Stem		Roots		Apical part		Total ra- dioactivity $\times$ 10^3 cpm	Total ¹⁾ transl. $\times$ 10^3 cpm	% of transloc.
		10^3 cpm	% of total ^{14}C	10^3 cpm	% of ^{14}C transl.	% of total ^{14}C	10^3 cpm	% of ^{14}C transl.	10^3 cpm	% of ^{14}C transl.	10^3 cpm	% of ^{14}C transl.			
2 hrs	intact	69.054	79.7	5.821	33.1	6.7	10.803	61.4	0.624	3.5	0.346	2.0	86.648	17.594	20.3
	derooted	81.080	89.7	5.386	57.8**	6.0	3.878	41.6**	—	—	0.053	0.6	90.397	9.317	10.3**
4 hrs	intact	70.877	68.9	9.437	29.5	9.2	18.288	57.2	3.166	9.9	1.078	3.4	102.835	31.958	31.1
	derooted	81.083	75.9	8.354	32.5	7.8	16.670	64.8	—	—	0.688	2.7	106.795	25.712	24.1**
8 hrs	intact	39.996	65.2	3.260	15.2	5.3	12.321	57.6	4.124	19.3	1.684	7.9	61.385	21.389	34.8
	derooted	49.515	79.2	3.138	24.2**	5.0	9.186	70.8	—	—	0.652	5.0	62.491	12.976	20.8**
12 hrs	intact	69.513	60.0	6.954	15.0	6.0	26.209	56.7	8.955	19.4	4.119	8.9	115.750	46.237	40.0
	derooted	76.068	64.5	10.467	24.9**	8.8	26.435	61.1	—	—	5.008	12.0	117.978	41.910	35.5*
24 hrs	intact	41.666	42.5	7.161	12.8	7.3	29.709	52.8	14.494	25.7	4.916	8.7	97.946	56.281	57.5
	derooted	60.621	60.2	9.057	22.6**	8.8	27.551	68.6*	—	—	3.521	8.8	100.750	40.129	39.8**

¹⁾ Total translocation = radioactivity of the plant without primary leaves.* Significant differences ($p = 0.05$).** Significant differences ($p = 0.01$).

The results of experiment I are presented in Fig. 1 and Table 1. All the data are average for two plants, analysed separately. The total radioactivity as well as translocation into separate organs of the investigated plants, varied a great deal within each treatment, but the general pattern of ^{14}C -distribution was very similar as regards the replications. Therefore the distribution of ^{14}C -compounds in the stem is presented as percentage of total radioactivity of the whole plant.

In all the cases examined, the total translocation in derooted plants was lower than in intact ones (Table 1). The effect of derootment is statistically significant, regardless of the period of translocation. No interaction was found between derootment and period of translocation. This may suggest, that both the factors examined influenced the translocation process independently.

In the first hours of translocation, the total radioactivity in petioles was almost the same, but with the lapse of time radioactivity of petioles of derooted plants was higher than that of control plants. These differences are more marked and statistically significant, when expressed in percentage of total radioactivity. Interaction between time and derootment was insignificant in the petiole.

In the stem of derooted plants, radioactivity was lower than in intact ones after 2 hours of translocation. These differences were decreasing as the translocation proceeded. Nevertheless, in most cases the relative level of stem radioactivity (expressed in percentage of total translocation) was higher in derooted than in intact plants.

The activity distance diagram of the stem of intact and derooted plants differed very much especially after 2 hour translocation period (Fig. 1). In the stem the effect of root excision on the translocation is statistically significant ($P=0,01$). In the whole experiment the interactions: time $\times$ derootment, time $\times$ segment's radioactivity $\times$ derootment are statistically significant ($P=0,01$). In derooted plants the "feeling" of the stem with labelled photosynthates seems to be delayed as compared to intact ones. After a longer translocation period these differences declined and then increased again especially after 24-hour translocation. The distribution gradient of ^{14}C -photosynthates in the stem, after 12- and 24-hour translocation period become positive (radioactivity increased in downward direction) especially in the stem of intact plants. This was due to accumulation of radioactive compounds in the lower part of stem. The share of upper segments of the stem in the total radioactivity changed only a little depending on the translocation period in both series.

The roots accumulated a lot of radioactivity already after four-hour translocation.

Translocation to the apical part of the plant (including the stem tip and very young trifoliate leaf) was very small in all the plants. The differences after 2 hour translocation between radioactivity of apical part

Table 2

The effect of roots removal on the distribution of radioactivity in bean plants, after 30 min. assimilation of $^{14}\text{CO}_2$

12-13 June, 1962

t phot. 27-32°C

Average of two plants

Trans- location period	Plant organs Plants	Primary leaves		Petiole		Stem		Roots		Apical part		Total trans- location × 10 ³ cpm	% of trans- location
		10 ³ cpm	% of total ¹⁴ C	10 ³ cpm	% of ¹⁴ C transl.	10 ³ cpm	% of ¹⁴ C transl.	10 ³ cpm	% of ¹⁴ C transl.	10 ³ cpm	% of ¹⁴ C transl.		
2 hrs	intact	96.378	72.5	6.747	18.5	23.442	64.2	5.456	14.9	0.886	2.4	36.531	27.5
	derooted	68.473	77.9	4.416	22.8*	14.000	72.3	—	—	0.959	4.9	19.375	22.1
8 hrs	intact	48.231	41.3	6.768	9.9	42.477	61.9	17.410	25.4	1.934	2.8	68.589	58.7
	derooted	49.396	67.2	4.393	18.2**	18.105	75.2**	—	—	1.591	6.6	24.089	32.8**
24 hrs	intact	25.323	37.9	1.986	4.8	25.324	61.0	12.661	30.5	1.547	3.7	41.518	62.1
	derooted	28.322	48.8	4.254	14.3**	23.475	79.0	—	—	1.969	6.7	29.698	51.2*

* Significant differences ($p = 0.05$).** Significant differences ($p = 0.01$).

of intact and derooted plants are insignificant, because both values are very close to the limit of detection.

Experiment II was performed in condition similar to experiment one, only temperature during ^{14}C -exposure was higher in comparison with that in experiment I. This may be the reason for a higher relative radioactivity translocated in experiment II during the same period of time (Table 2). Total ^{14}C -translocation in derooted plants was lower than that in intact ones (the differences are statistically significant). There was no interaction between time and derootment as it was observed in experiment I. After derootment the share of petioles in the total radioactivity translocated from the "feeding" leaf is significantly higher than in intact ones, especially after 24-hour translocation. In this experiment (unlike experiment I), the interaction between time and derootment is significant. The distribution of radioactivity in the stem of intact and derooted plants was very similar after two hour period of translocation (Fig. 2).

After eight and twenty-four hour translocation periods, the gradient of radioactivity in the stem of intact plants is positive due to accumulation of radioactivity in the lower part of the stem. As regard derooted seedlings, the situation is different. After an eight hour period of translocation the radioactivity in derooted plants was distributed almost uniformly along the stem and after twenty-four hours the gradient was decreasing in downward direction again, due to a rise of radioactivity in the upper segments (Fig. 2).

All these observations suggest, that the examined factors interact and this is statistically significant.

Fig. 2. The effect of derootment on the distribution of ^{14}C -assimilates in the stem of bean plant (Radioactivity expressed as in fig. 1).

The effect of roots removal on the distribution of radioactivity

30—31 July, 1962

(Average of

Translocation period	Treatments	Source organs			Petiole			
		radioactivity × 10 ³ cpm			10 ³ cpm	% of ¹⁴ C transl.	% of ¹⁴ C in etha- nol insol.	% of total ¹⁴ C
		leaves	cotyle- dons	total				
2 hrs	intact	220.74	23.63	244.37	9.10	11.8	14.8	2.8
	derooted	265.81	24.50	290.31	12.68	19.1	11.0	3.5
4 hrs	intact	267.98	20.00	287.98	14.20	16.4	17.0	3.8
	derooted	277.52	20.41	297.93	27.12	23.1	18.5	6.5
8 hrs	intact	290.14	21.50	311.64	12.58	10.3	33.8	2.9
	derooted	213.75	13.18	226.93	26.25	23.4	26.1	7.7
	partially derooted	243.20	12.96	256.16	18.94	16.3	—	5.1
24 hrs	intact	158.18	12.42	170.60	17.90	10.1	39.4	5.2
	derooted	202.83	10.37	213.20	41.47	24.9	28.8	10.9
	partially derooted	156.94	14.63	171.57	26.50	17.0	—	8.1
L.S.D.					10.48			

The radioactivity distance diagram in both experiments did not conform exactly to a linear function. This may be due to the anatomical structure of the stem. The part of stem near the cotyledon node is much thicker and may store more photosynthates (Biddulph 1959). The accumulation of radioactivity in this part of stem may be also due to the thickening of the vascular bundles due to increase of sieve tubes number, originated from the cotyledons.

Translocation into the apical part of the plant was very low, as it was observed in previous experiment. Assimilates from the primary leaves may move mainly in downward direction, as Biddulph suggested (1959). A similar fact was observed in experiment with labelled sucrose exported from the trifoliate leaf of bean plant (Turnowska-Starck 1960), as well as from the petioles of primary leaves of soybean (Nelson *et al.* 1957).

Lupine experiment. In this experiment 23-days old seedlings were used. The plants had still green cotyledons, which were also ¹⁴C-supplying organs. After 30 minutes long photosynthesis followed by 30 minutes of removal the air (containing radioactive traces), from the chamber, the plants were divided into three experimental series: intact plants, derooted plants and plants partially derooted (about 1/3 of roots, mainly lateral ones, were cut off). Then all the plants were allowed to

le 3

in lupine after 30 min. assimilation of $^{14}\text{CO}_2$

two plants)

t phot. 23—25°C

Apical parts			Stem			Roots			Total radio-activity 10 ³ cpm	Total trans- location 10 ³ cpm	% of ^{14}C transl.	Fresh weight of plant in g
10 ³ cpm	% of ^{14}C transl.	% of ^{14}C in ethanol insol.	10 ³ cpm	% of ^{14}C transl.	% of ^{14}C in ethanol insol.	10 ³ cpm	% of ^{14}C transl.	fresh weight in g				
21.72	28.2	—	30.80	40.1	10.0	15.30	19.9	1.262	321.29	76.92	23.9	2.841
20.12	30.3	—	33.66	50.6	10.6	—	—	—	356.77	66.46	18.6	2.007
22.39	25.9	37.9	32.53	37.6	19.9	17.38	20.1	0.779	374.48	86.50	23.1	2.444
40.30	34.4	30.8	49.75	42.5	19.8	—	—	—	415.10	117.17	28.2	1.673
34.40	28.1	50.3	40.35	32.9	33.7	35.04	28.7	0.981	434.01	122.37	28.2	3.020
30.02	26.8	40.4	55.77	49.8*	28.7	—	—	—	338.97	112.04	33.0	1.640
29.34	25.3	—	46.96	40.5*	—	20.63	17.9	0.325	372.03	115.87	31.1	2.224
31.41	17.7	54.7	41.96	23.8	52.0	85.17	48.4	1.054	347.04	176.44	50.8	3.078
37.04	22.2	46.2	88.20	52.9**	30.8	—	—	—	379.91	166.71	43.9	1.588
25.22	16.2	—	70.60	45.3**	—	33.46	21.5	0.290	327.35	155.78	47.6	1.933
			27.65						107.37			

translocate ^{14}C -assimilates during a period of two, four, eight and twenty — four hours. The results are presented in the Table 3 and Fig. 3.

Total translocation calculated as cpm and expressed in relative value, was similar in intact and derooted plants (the differences are insignificant). However, the distribution of radioactivity depended on the roots. In all cases the total radioactivity of petioles in derooted plants was significantly higher than that in intact plants. Similar accumulation of ^{14}C -photosynthates was observed in the stem of derooted plants, especially after a 24-hour period of translocation. The curves represent not only distribution of radioactivity in the stem, but also in the main root. The second or the third segment corresponds approximately to the position of cotyledons, which are also ^{14}C -supplying organ.

In both experimental series, the radioactivity of the upper part of stem of derooted and intact plants was uniformly distributed along the stem, already after two-hour long translocation, but radioactivity decreased in the lower segments in downward direction. After four- and eight-hour translocation, in intact plants radioactivity was still uniformly distributed in the stem, but decreased along the main root. In the stem of derooted plants the share for upper segments in the total radioactivity increased in comparison with the same segments of intact plants, but only some of these differences are significant. After a longer period of

translocation the picture completely changed. Radioactivity of the stem of derooted plants increased significantly downward (Fig. 3), without changing the share of upper segments in the total radioactivity. The share increased in the intact plants only for the upper segments. The level of radioactivity of the whole stem for the intact plants was much lower than that for derooted plants. The pattern of distribution of radioactivity in the stem of plants after excision of a part of roots was similar to that in completely derooted ones. The differences between radioactivity of this series and intact plants, found after 24-hour long translocation, are statistically significant ($P = 0.01$).

After a 24-hour period of translocation, almost half of ^{14}C -substances was translocated to the roots similarly as in an experiment previously described (Starck 1963), but only half of that — to the roots in the series of partially derooted plants.

Almost in all the parts of the plants investigated, the degree of ^{14}C -incorporation into ethanol insoluble fraction, was slightly lower in

Fig. 3. The effect of derootment on the distribution of ^{14}C -assimilates in the lupine stem (Radioactivity expressed as in fig. 1).

derooted plants than in the intact ones, especially after a longer period of translocation (8 and 24 hours) — see Table 3.

Sunflower experiments. In these experiments only leaves (located 3—4 cm below the top of shoot) were the source of radioactive assimilates, formed during 40-minutes of $^{14}\text{CO}_2$ -photosynthesis. Coty-

Fig. 4. The effect of derootment on the distribution of ^{14}C -assimilates in the stem (Radioactivity expressed as in fig. 1).

ledons were kept all the time in darkness, except for intact plants*. One hour after the beginning of ^{14}C -exposure, the plants were divided into intact and derooted ones and sampled at different times.

* The intact plants in this experiment are the same as intact ones in next experiment (plants with roots immersed in solution at 20°).

The effect of roots removal on the distribution of radioactivity in

30—31 July, 1962

Average of

Translocation period	Treatment	Leaves 10 ³ cpm	Petiole				Cotyledons		
			10 ³ cpm	% of ¹⁴ C transl.	% of total ¹⁴ C	% of ¹⁴ C in etha- nol insol.	10 ³ cpm	% of ¹⁴ C transl.	% of ¹⁴ C in etha- nol intol.
2 hrs	intact	680.05	23.32	8.0	2.4	52.1	22.45	7.7	31.0
	derooted	922.00	41.66	9.0	3.0	24.9	21.87	4.7	37.3
4 hrs	intact	1155.40	55.74	10.2	3.3	52.2	27.17	5.0	44.4
	derooted	711.50	39.32	7.8	3.2	50.5	11.00	2.2	52.0
8 hrs	intact	1222.30	46.93	10.3	2.8	61.2	4.60	0.9	37.7
	derooted	662.10	33.03	6.8	2.9	54.2	15.52	3.2	52.3
24 hrs	intact	655.77	44.25	7.5	3.6	56.7	18.53	3.1	31.0
	derooted	466.10	33.00	8.1	3.8	55.2	5.76	1.4	55.0

* Significant differences ($p = 0.05$).** Significant differences ($p = 0.01$).

Total radioactivity of whole plants, as well as total translocation were highly variable for the respective replications. In this experiment also the differences between replications were much smaller in relative value.

All the revelant data are presented in Table 4 and Fig. 4. In most cases root removal decreased neither total translocation nor relative translocation except for 8-hour long translocation where derootment increased translocation significantly. Nevertheless the effect of derootment is insignificant in calculation done for the whole experiment.

The general pattern of ¹⁴C-distribution in intact and derooted plants was very similar but in derooted plants after 4 and 8 hours of translocation a slightly higher level of radioactivity in the stem, especially above source leaves (Fig. 4) was observed.

All the other differences between particular curves are not significant (except for the differences between the third segments of intact and derooted plants after 24 hr translocation). Interaction between roots removal, time and radioactivity of particular segment as well as time $\times$ $\times$ derootment and time $\times$ segment is significant.

The distribution of ¹⁴C-photosynthates in the particular organs differed very much in sunflower from that in bean plant and lupine.

le 4

sunflower after 40 min assimilation of $^{14}\text{CO}_2$

two plants

t phot. 23–25°C

Apical part			Stem			Roots			Total radio-activity $\times 10^3$ cpm	Total trans-location $\times 10^3$ cpm	% of ^{14}C transl.	Fresh weight in g
10^3 cpm	% of ^{14}C transl.	% ^{14}C in etha- nol insol.	10^3 cpm	% of ^{14}C transl.	% of ^{14}C in etha- nol insol.	10^3 cpm	% of ^{14}C transl.	fresh weight in g				
24.76	8.6	61.5	213.07	73.6	30.3	5.84	2.1	2.27	969.49	289.44	29.9	9.331
31.37	6.8	37.9	365.95	79.5	28.3	—	—	—	1382.85	460.85	33.3	6.662
52.25	9.5	49.9	408.15	74.4	35.7	5.23	0.9	2.25	1703.94	548.54	32.2	10.698
45.18	8.9	45.7	411.20	81.1**	42.2	—	—	—	1218.20	506.70	41.6	4.566
50.59	10.9	46.4	355.40	76.5	45.8	6.95	1.4	2.46	1686.77	464.47	27.5	10.186
48.49	9.9	49.2	391.08	80.1**	36.4	—	—	—	1150.22	488.12	42.4*	3.799
64.47	10.9	61.8	453.01	76.3	57.3	12.71	2.2	2.18	1248.74	592.97	47.4	9.111
36.71	9.1	60.6	330.70	81.4*	53.0	—	—	—	872.27	406.17	46.5	3.129

In sunflower most of the radioactivity was found in the stem. Already after 2 hours, the share for the stem in the total translocation was about 80%. To the contrary, roots accumulated a very low amount of ^{14}C (only 2% of total translocation). Comparing this fact with the result of previous experiments (Stark 1963) roots accumulated about 25% of assimilates, translocated in the four hours period.

The degree of incorporation of ^{14}C into the fraction insoluble in 80% ethanol is very high in the stem, petioles and also in the apical part. The degree of incorporation of ^{14}C into ethanol insoluble fraction in petioles and apical part was smaller in derooted plants than in intact ones, after the period of 2 hours translocation. The curve representing the total radioactivity and that of ethanol soluble fraction have almost parallel course in both experimental series.

The high degree of incorporation of ^{14}C into ethanol insoluble fraction may cause a rapid decrease of the amount of substances available for translocation and consequently a rate of translocation diminishing with the lapse of time.

Another experiment was carried out with 25-day old sunflower. Photosynthesis of $^{14}\text{CO}_2$ lasted 40 minutes. One hour after the beginning of exposure, plants were divided into four experimental series: 1. intact plants, 2. part of roots cut off (mainly basal part), 3. about half of roots

Table 5

The effect of removal part of roots on the distribution of radioactivity in sunflower after 40 min. assimilation of $^{14}\text{CO}_2$

6-7 September, 1962

t phot. 21°C. Periods of translocation — 10 hrs.

Average of four plants calculated per 1 plant

Root's treatment Part of plant	Intact plant			Part of roots cut off (youngest)			Part of roots cut off (young and old)			3/4 roots cut off		
	10^3 cpm	% of ^{14}C transl.	fresh weight in g	10^3 cpm	% of ^{14}C transl.	fresh weight in g	10^3 cpm	% of ^{14}C transl.	fresh weight in g	10^3 cpm	% of ^{14}C transl.	fresh weight in g
Leaves	349.90	—	3.16	467.10	—	2.96	324.10	—	2.12	428.10	—	2.76
Cotyledons	34.62	—	0.69	2.19	0.6	0.80	2.97	1.1	0.75	3.66	1.1	0.76
Petiole	18.48	7.0	0.60	21.55	6.0	0.54	17.86	6.6	0.37	19.54	6.0	0.44
Apical part with youngest leaves	30.84	11.5	0.21	42.38	11.9	0.17	40.37	14.8	0.16	47.68	14.5	0.18
Roots	27.32	10.2	3.75	30.13	8.5	1.96	17.31	6.3**	2.30	18.04	5.5**	0.97
Stem	190.54	71.3	6.78	259.43	73.0	6.45	194.02	71.2	5.80	238.34	72.9	5.72
Total transloc.	267.18	40.9	—	355.68	43.2	—	272.53	45.7	—	327.26	43.3	—
Total plant	651.70	—	15.19	822.78	—	12.88	596.63	—	11.50	755.36	—	10.83

* Significant differences ($p = 0.01$).

cut off (young and old ones) and 4. about 3/4 of roots (both young and old ones) removed. All the plants were collected after 10 hours translocation (Table 5). No. special effect of removing part of roots was observed in this cases. The only difference recorded was that the radioactivity of roots of plants after excision of 3/4 of roots and also after excision of about half of young and old ones (cut off vertically on the side of the stem) was lower than in the intact series. All the other differences were insignificant. The roots accumulated a low percentage of the total radioactivity and most of ^{14}C was detected in the stem. The derootment did not affected the degree of ^{14}C -incorporation into the ethanol insoluble fraction (these figures are not presented in the tables).

II. The effect of different root temperature on the translocation

Experiments were carried out with 25-days old sunflower.

After 40 minutes of $^{14}\text{CO}_2$ assimilation and 20 minutes of removing the residual $^{14}\text{CO}_2$, the plants were divided into three experimental series: roots were immersed in the nutrient solution at 5° , 20° or 35° , for 9 hours. The plants were sampled after 10 hours (feeding time included). The results are presented in Table 6 and Fig. 5. In this experiment both leaves and cotyledons assimilated radioactive carbon. The distribution of radioactivity has a slightly different pattern in the particular series (Fig. 5). The highest radioactivity was found in the upper three and one before the last segment of the stem, because of two supplying organs (leaves and cotyledons). In all series radioactive compounds moved from the leaves mainly upward, especially in 5° and

Fig. 5. The effect of different temperatures of the roots on the distribution of ^{14}C -assimilates in the sunflower stem (Radioactivity expressed as in fig. 1).

Table 6

The effect of treatment the roots with different temperature on the distribution of radioactivity after 40 min assimilation of $^{14}\text{CO}_2$ in sunflower 6--7 September, 1962

Period of translocation — 10 hrs; t phot. 21°C

Root's treatment Part of plant		5°			20°			35°		
		fresh weight in g	10^3 cpm	% of ^{14}C transl.	fresh weight in g	10^3 cpm	% of ^{14}C transl.	fresh weight in g	10^3 cpm	% of ^{14}C transl.
Leaves		2.39	405.00	—	3.16	349.90	—	3.53	385.90	—
Cotyledons		0.74	43.48	—	0.69	34.62	—	0.75	41.77	—
Petiole		0.40	14.95	4.2	0.60	18.48	7.0	0.48	17.49	6.0
Apical part with youngest leaves		0.17	33.90	9.4	0.21	30.84	11.5	0.22	43.25	14.9
Roots		3.35	40.58	11.3	3.75	27.32	10.2	2.90	35.84	12.4
Stem		5.61	269.21**	75.1	6.78	190.54	71.3	6.81	193.43	66.7
Total transloc.		—	358.64	44.4	—	267.18	40.9	—	290.01	40.4
Total plant		12.66	807.12	—	15.19	651.70	—	14.69	717.68	—

35°-series. (The differences between radioactivity of the stem above source leaves in plants, treated at 5°C and that treated at 20°C are statistically significant). Radioactive substances moved from the cotyledons both upward and downward (radioactivity decreased in similar degree in both direction). Relatively the highest level of radioactivity was found in the stem near cotyledons at 5°-series suggesting, that movement of assimilates from this organ was lower in chilled plants. (These differences are statistically significant). Similar differences between particular series were observed in the distribution of ethanol soluble fraction in the stem.

The radioactivity of roots which were immersed in nutrient solution of low temperature was the highest, and the lowest — in plants belonging to the series at 20°C. This may be connected with the different rate of root respiration depending on temperature. The differences in the total translocation in particular series are insignificant.

DISCUSSION

No simple interpretation of the effect of root excision on the translocation of photosynthates is possible on the basis of the experiments described above. This effect depended on the species or even on the stage of plant development. Many uncontrolled factors might have influenced the investigated process. The great difficulty in drawing the conclusion from the experimental facts is due to a great variation between the replications. The cause of these considerable discrepancies, may be due either to variability in the investigated plants or to the different conditions influencing particular plants during experiment or to both.

The plants used in individual experiments were selected taking into account their total weight, leaf area, length and thickness of petioles and stems as well as the size of roots. However, it is very difficult to choose a rather great number of plants similar in respect to seven different features. Nevertheless one can expect that the rate of physiological processes in particular plants was similar, because all of them were grown in the same conditions and their physiological stage was the same. The fact that the distribution of radioactivity calculated in relative value, gave much smaller variability, can be considered as a proof for that supposition. Therefore the reason for the observed discrepancies would be connected rather with the condition of exposure to $^{14}\text{CO}_2$. The first source of error may be the ununiform distribution of $^{14}\text{CO}_2$ in the experimental chamber, in spite of mixing the air by the use of rotation fan. Besides particular leaves might not have been illuminated uniformly enough, because some of them were partially shaded by the others.

Comparing the translocation process in intact and derooted plants by the use of radioactive carbon, some objections have to be considered.

The first one is connected with the greater loss of radioactive substances in respiration by intact plants as compared with the derooted ones, especially when the roots contributed a great deal to the total weight of the plant.

In derooted plants a decrease of the rate of photosynthesis was observed already a few hours after root excision (Starck *et al.* 1962), therefore the degree of dilution of photosynthates by ^{12}C -photosynthesis products could have been lower in derooted than in intact plants, especially in the long term experiments.

The other objection to be taken into account is the possibility of leakage of radioactive substances to the nutrient solution after excision of the roots*.

In same experiments the decrease of degree of incorporation of ^{14}C into the ethanol insoluble fraction in plants after excision of the roots was observed. Therefore the amount of substances available for translocation can be hardly compared in both series after long period of translocation.

The distribution gradient of radioactivity in the stem, represents the total amount of ^{14}C -compounds inside and outside the translocation channel. This fact should be also taken into account especially in experiments with rather long term translocation (more than one hour). All the above mentioned facts suggest, that the short term experiments give the most objective results of distribution of assimilates along the stem in conducting channel. But on the other hand, too short a period of translocation may be not long enough to observe the effect of root excision.

In experiments, where the share of roots in the total translocation was very low (the sunflower experiments) removal or cooling of the roots did not reduce the total amount of ^{14}C translocated and only slightly changed the distribution of radioactivity in the whole plant. The stem of sunflower seems to be a very important acceptor of assimilates, probably in connection with its lateral growth, typical for this species. Conversely to the other examined species, sunflower petioles are very small and do not accumulate a great deal of assimilates.

In all experiments, where roots accumulated a great percentage of translocated carbon (experiments on bean and lupine plants), derootment greatly changed the pattern of ^{14}C -distribution, and in some cases caused also a decrease of translocation. The reason for difference in the accumulation of labelled assimilates in roots are not known sufficiently. This may depend on the metabolic activity of growing cells or even on their amount.

* This possibility was tested (unpublished data). In the nutrient solution only traces of radioactivity were found.

Excision of some roots accumulating a great portion of ^{14}C -assimilates (experiment with lupine), caused changes in radioactivity distribution in similar way to which it was observed in completely derooted plants. Only the degree of these changes was smaller. This may suggest that the weight of roots influence at least quantitatively the translocation. A similar effect of root weight on the translocation process was observed by Shiroya *et al.* (1962).

Nelson (1959) presumed, that "roots exert a strong demand" which caused a downward translocation of assimilates. This supposition as well as the facts observed in experiments described above, may point to the role of roots in translocation of organic substances, which act merely as an acceptor of assimilates, but not as an organ controlling the mechanism of translocation.

The further step in the investigation of role the of roots in translocation is to answer the following question: what is the organ, in which the changes of translocation after derootment take place if a change is produced, how quickly is this manifested? It may throw some light on the nature of interaction between organs-acceptors of asimilates and its donors and conducting channels.

The effect of derootment was observed in the shortest translocation period examined — two hours after "feeding" time. Diminishing of translocation after excision of the roots maintains for many hours, but after longer period of translocation, the differences between intact and derooted plants did not increase markedly. This may be the result of 1) a great loss of radioactivity in respiration of intact plants, 2) higher degree of incorporation of ^{14}C into the ethanol insoluble fraction in plants with roots and consequently higher conversion of assimilates into substances unavailable for translocation.

Some further informations on the role of roots in the migration of assimilates may provide the distribution of ^{14}C -assimilates in intact and derooted plants. The character of changes observed after excision of roots, depends on the plant. In the case when total amount of translocated ^{14}C -photosynthates did not change after derootment, but the roots accumulated relatively a great deal of ^{14}C , an increase of relative radioactivity of the petioles was observed already after a two-hour period of translocation (experiment with lupine). In these cases radioactivity of the stem of derooted plants increased as compared with intact plants. After a short period of translocation (4 and 8 hrs), the differences between both series were registrated mainly in the upper part of stem and after a longer time (24 hrs) — in the lower segments. It seems therefore, that the changes of the character of translocation caused by derootment, starts in the upper part of plant and then are transmitted down.

In the case when excision of the roots also produced a decrease of translocation, the changes of distribution occurred at first in the lower

part of stem, and began to shift upward after a few hours, in some cases to the upper part of stem and in all cases — to the petioles. All the changes of translocation observed after derootment may be due either 1) to the change in the rate of penetration of assimilates from the parenchymatic tissue into the conducting channel or 2) to the change in the rate of movement in the conducting tissue itself or 3) to the change of the rate of leakage from the phloem into the surrounding tissue, or in some other way. The first possibility will have to be proved in more detail in future experiments, because described experiment can not explain this question. Nevertheless the total amount of radioactive compounds, exported from the leaves, in many experiments did not depend on the presence of roots, therefore this first possibility can not be the only reason for the changes in translocation pattern due to derootment. The leakage from the conducting tissue was not investigated in the reported experiments. As regards the second possibility, it seems quite reasonable to presume that roots removal may influence the velocity of movement of organic substances in the conducting channel.

The measurement of velocity of translocation, with the use of radioactive elements is very difficult to interpret (see discussion of Canny 1960). Nevertheless it seems to be possible to compare the velocity of translocation in intact and derooted plants, because in both cases measurement was made under similar condition. The constant slope of curves representing distribution of radioactivity in petioles and stem, may be calculated according to Canny's equation:

$$\log r = \log a - bd$$

r = radioactivity at any point

b = slope constant

a = radioactivity of the site of ^{14}C -supplying organ

d = distance from the site of ^{14}C -supplying organ to the point of radioactivity = r

With the aid of this formula, one can compare the velocity of translocation in particular plants, assimilating even different amounts of $^{14}\text{CO}_2$. The smaller numerically is b , the less steep is the curve and consequently translocation proceeds more rapidly. With the use of the above mentioned formula, slope constant b , for the curve representing ^{14}C -distribution in the stem of intact and derooted lupine and bean plants was calculated (Table 7). In these experiments, a expresses the total radioactivity of the plant, assuming, that at the very beginning all radioactivity is located in source leaves.

The stem of intact plants of both species had the slope constant closer to 0.11, which was calculated by Canny (1960) as an average for several experiments, done by many authors.

Table 7

Slope constance „b” of the curves of ^{14}C -distribution in the stem of lupine and bean plants

Bean plant — 2 hrs translocation; Lupine — 4 hrs translocation

Experiment Replication	Bean plant				Lupine	
	Exp. I		Exp. II		intact	derooted
	intact	derooted	intact	derooted		
I	0.14	0.24	0.14	0.16	0.18	0.22
II	0.19	0.35	0.11	—	0.15	0.21
Average	0.16	0.30	0.12	0.16	0.16	0.21

The derooted plants had a higher value for slope constant in all the cases. This may support the assumption that the excision of roots, being the main acceptor of assimilates in young seedlings, may produce a decrease of velocity of downward translocation of photosynthates. However, this does not exclude other possibilities as regards the influence of roots on the translocation process. The above — mentioned suppositions have to be further investigated in more detailed experiments.

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SUMMARY AND CONCLUSIONS

The reported work was undertaken to obtain some further information concerning the role of roots in the process of translocation of assimilates. The translocation of ^{14}C -photosynthates in intact and derooted plants after different period of translocation (2 to 24 hrs) was compared.

In all cases, when the share of roots in the total translocation was very low (sunflower experiments) removal or cooling of the roots did not reduce the total amount of ^{14}C -translocation but only slightly changed the distribution of radioactivity in the whole plant.

In all experiments, where roots accumulated a great percentage of labelled assimilates (experiments with lupine and bean plant), derootment greatly changed the pattern of distribution. The share for petioles as well as for the stem in the total radioactivity of the plant was increasing. Excision of a part of roots actively accumulating ^{14}C -assimilates caused similar character of changes in the pattern of ^{14}C -distri-

bution, but to a lesser degree than observed in completely derooted plants.

In bean plant experiments, root removal changed not only the ^{14}C -distribution but also decreased the percentage of translocated assimilates from the feeding leaves.

All these data seem to suggest, that roots exert some influence on the translocation process acting as an acceptor of assimilates. The possibility of a decrease of movement velocity as a consequence of decotment was discussed.

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Wpływ korzeni na przemieszczanie asymilatów. I.

Streszczenie

Przeprowadzono szereg doświadczeń mających na celu bliższe wyjaśnienie roli korzeni w procesie przemieszczania asymilatów, powstających w czasie kilkunastominutowej fotosyntezy w atmosferze $^{14}\text{CO}_2$. Porównywano przemieszczanie asymilatów w nie uszkodzonych roślinach i w roślinach po odcięciu korzeni. Pomiary przeprowadzano po 2, 4, 8, 12 i 24 godzinach.

We wszystkich przypadkach, w których udział korzeni w ogólnej ilości przemieszczanych asymilatów był mały (doświadczenia ze słonecznikiem), odcięcie korzeni lub ich oziębienie do 5°C nie wpływało na ogólną ilość przemieszczonych radioaktywnych asymilatów i tylko nieznacznie modyfikowało charakter rozmieszczenia radioaktywności w całej roślinie.

We wszystkich doświadczeniach, w których korzenie gromadziły duży procent asymilatów, usunięcie korzeni wpływało w dużym stopniu na ogólny charakter rozmieszczenia ^{14}C . W tych przypadkach wzrastał udział ogonków liściowych, jak również łodygi, w ogólnej ilości przemieszczonych, znakowanych asymilatów oraz w ogólnej radioaktywności całej rośliny.

Odcinanie części korzeni powodowało zmiany w procesie przemieszczania tego samego charakteru, co odcięcie całego systemu korzeniowego. Ilościowo zmiany te były jednak mniejsze.

W doświadczeniach przeprowadzonych na fasoli usunięcie korzeni wpływało nie tylko na zmianę charakteru rozmieszczenia znakowanych związków, lecz również obniżało ogólny procent przemieszczania z liści.

Wszystkie powyższe dane zdają się wskazywać, że korzenie wywierają pewien wpływ na przemieszczanie substancji organicznych, który można zaobserwować już po stosunkowo krótkim czasie (kilku godzin). Wpływ korzeni na proces przemieszczania jest najprawdopodobniej związany z ich działalnością jako akceptora asymilatów. Dlatego też wielkość tego wpływu uzależniona jest od stanu fizjologicznego korzeni.

Przedyskutowano możliwość wpływu odcięcia korzeni na szybkość przemieszczania asymilatów.