ACTA SOCIETATIS
BOTANICORUM POLONIAE
vol. XXXVI — nr 2
1967

Translocation of ^{14}C-photosynthates in bean plants deprived of blades and roots

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The concept of translocation, as movement of substances towards sinks has been popular for many years.

Mobilization may involve some sort of pulling forces, located mainly in organs importing assimilates or pushing forces, situated in organs exporting organic substances.

The present work was undertaken in order to obtain some information concerning translocation of photosynthates in young bean plants deprived of all mature blades — the main donor of assimilates, and roots — one of the most important acceptors.

MATERIAL AND METHODS

Bean plants were grown under natural light and temperature conditions, in water culture on nutrient solution, as previously described (Starck 1963, 1964 a).

The plants used in both experiments (1964 and 1965) had fully expanded primary leaves and the first very young trifoliate leaf.

Exposure to $^{14}CO_2$ was done in a plexiglass chamber, under natural light. Only primary leaves were allowed to carry on $^{14}CO_2$-photosynthesis for 1 hour. All the other organs (including the apical part with the first trifoliate leaf), were shaded. The conditions during exposure to $^{14}CO_2$ are presented in table 1.

After exposure to $^{14}CO_2$, the plants were divided into experimental series. One of them was collected as a control (intact plants, 1-hr translocation). All the other plants were placed on 4-time diluted nutrient solution. One series were allowed to continue translocation over the next 2 hrs as intact plants, the others were deprived of blades of primary leaves or both blades and roots (experiments No. 1 and 2). Experiment No. 2 included also an additional series — plants deprived of roots. The removed organs were analysed for radioactivity. All the plants translocated ^{14}C-photosynthates in the next two hours, (that is, they translocated for 1 hour as intact plants and for the next 2 hrs as plants deprived of certain organs). After the above metioned experimental procedure plants were collected and immediately frozen in dry ice. At the same time the second control (intact plants, translocating ^{14}C-substances for 3 hrs) were also harvested. The frozen plants were separated

into the particular organs. Total radioactivity as well as radioactivity of the 80% ethanol-soluble fraction was determined by means of a G—M counter, with about 5% efficiency, as described in previous papers (Starck 1963, 1964 a). By subtracting the radioactivity of the 80% ethanol-soluble fraction from the total, the radioactivity of the fraction insoluble in 80% ethanol was calculated.

RESULTS

To compare the plants used in both experiments, the relative contribution of particular organs to the total fresh weight of the plant was calculated (table 2). The plants of experiment No. 1 were bigger, probably as a consequence of age differences (see table 1).

Table 1

The conditions during $^{14}CO_2$ exposure

Data of experiment	Age of plants (days)	Conditions of $^{14}CO_2$-exposure				Period of translocation
		time	t (°C)	spec. rad. μc/mg CO_2	conc. of CO_2 % (v/v)	
No. 1 9 May 1964	25	11^{30} —12^{10}	20—22	0.6	0.1	1 hr and 3 hrs
No. 2 18 June 1965	21	10^{20} —11^{00}	16—18	1.27	0.1	1 hr and 3 hrs

Table 2

The contribution of fresh weight of particular organs into the total weight of whole plant (in percentage)

Organs		Expt. No. 1 1964	Expt. No. 2 1965
Blades of leaves		27.7	30.5
Petioles		4.9	6.7
Apical part		7.9	9.4
Stem		10.1	12.7
Roots		49.4	40.7
Total plant	(%)	100.0	100.0
	(g.f.w.)	7.75	5,62

The distribution of labelled substances in bean plants of experiment No. 1 is presented in table 3 and fig 1.

Total translocation of ^{14}C-substances in experiment No. 1 was not intensive as compared with that of experiment No. 2 (table 4). Most ^{14}C-assimilates in intact plants were translocated to the apical part, (about one half of the ^{14}C-substances

Table 3

Effect of blades and roots removal on translocation of ^{14}C-assimilates. Expt. No 1.
Radioactivity in 10^2 cpm; total and 80% ethanol insoluble fraction

No.	Treatment	Blades of leaves		Petioles		Apical part		Stem		Roots	Total radioactivity		% of transloca-tion
		total	insoluble	total	insoluble	total	insoluble	total	insoluble	total	total plant	total transloc.	
1	Intract plant (1 hr translocation)	2149,2	984.0	26.9	10.8	59.4	28.5	44.9	16.0	trace	2280.4	131.2	5,8
2	Intact plant (3 hrs transloc.)	2608.2	1355.3	30.9	10.3	229.5	116.4	68.3	20.7	31.5	2968.4	360,2	12.1
3	blades removed	(2185.3	1053.1)	8.0	2.2	109.1	63.3	20.8	1.6	7.0	2330.2	144.9	6.2
4	blades and roots removed	(2705.4	1652.3)	23.8	7.6	70.4	34.5	46.2	12.9	—	2845.8	140.4	4.9
5 5	Effect of blades removal (difference between Nr 3 and 1)	—	—	—18.9	—8.6	+49.7	+34.8	—24.1	—14.4	+7.0	—	—	—
6	Effect of blades and roots removal (differences between Nr 4 and 1)	—	—	—3.1	—3.2	+11.0	+6.0	+1.3	—3.1	—	—	—	—

Table 4

Effect of blades and roots removal on translocation of ^{14}C-assimilates (expt. No. 2) Radioactivity in 10^2 cpm

Average of 3 replications, two plants in each, recalculated per one plant

No	Treatments	Blades of leaves		Petioles		Apical part		Stem		Roots		Total radioact.		% of translocation
		total	insoluble	total	insoluble	total	insoluble	total	insoluble	total	insoluble	total plant	total translocation	
1	Intact plant (1 hr translocation)	2698.8	978.2	134.6	54.9	78.6	36.1	191.6	73.7	95.1	55.1	3198.7	499.9	15.6
2	Intact plant (3 hrs translocation)	1484.8	1007.2	71.8	42.5	678.2	350.2	255.7	138.2	622.0	175.1	3112.5	1627.7	52.3
3	Roots removed	1505.3	942.2	162.6	54.5	962.6	424.0	417.2	123.0	(125.1	34.1)	3172.8	1667.5	52.6
4	Blades removed	(2507.9	989.4)	50.4	17.4	221.5	121.8	77.4	34.3	68.5	20.2	2925.7	417.8	14.3
5	Blades and roots removed	(2351.9	810.5)	59.0	13.7	131.6	66.3	101.5	25.8	(125.1	34.1)	2769.1	417.2	15.1

D. c. tabeli 4

6	Effect of roots removal (Difference between No. 3 and 2)		+20.5	—65.0	+90.8	+12.0	+284.4	+73.8	+161.5	—15.2	—	—	+60.3	+39.8	0.3
7	Effect of blades removal (Difference between No 4 and 1)		—	—	—84.2	—37.5	+142.9	+85.7	—114.2	—39.4	—26.6	—34.9	—273.0	—82.1	—1.3
8	Effect of blades and roots removal (diff. No. 5 and 1)		—	—	—75.6	—41.2	+53.0	+30.2	—90.1	—47.9	—	—	—429.6	—82.7	—0,5
	L.S.D.	p=0.05			62.5	20.7	143.8* 56.5**	76.0	117.2* 73.4**	35.6					
		p=0.01			88.8	29.5	204.7* 87.1**	108.1	166. * 111.2**	50.7					

Figures in bracets illustrate the radioactivity of organs, removed after 1 hr translocation. Radioactivity of roots in treatments Nr. 3 and 5 was estimated for both treatments together in roots cut after 1 hr translocation.

* L.S.D. calculladed for all treatments.

** L.S.D. calculladed for treatments No. 1, 4, 5. only.

translocated in a 1-hr period and about 60%, after 3-hrs migration). Nevertheless this constitutes a very low percentage of the total radioactivity of the whole plant. Roots accumulated less than 10 percent of labelled substances, translocated during 3 hrs, constituting about 1 % of the total radioactivity of the whole plant. The ra-

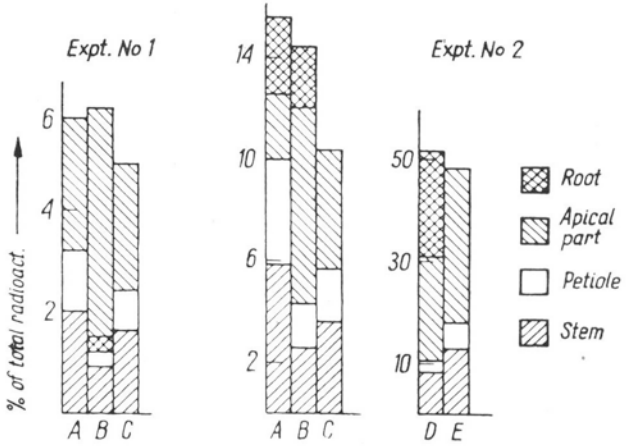

Fig. 1. Distribution of ^{14}-assymilates in bean plants after roots, blades or roots and blades removal.

A — intact plant, 1 hr translocation; *B* — blades removed; *C* — blades and roots removed; *D* — intact plant, 3 hrs translocation; *E* — roots removed.

dioactivity of petioles, did not vary so much in intact plants independently of the period of translocation.

In the plants deprived of blades, translocation of ^{14}C-photosynthates was still observed. Total and "insoluble" radioactivity of the stem and petioles markedly decreased in contrast to the increment of radioactivity of the apical part. Some labelled substances migrated also to the roots.

Translocation in plants deprived of blades and roots was very slow or ceased completely (the changes in radioactivity of the apical part, stem and petioles seem to be within the limit of experimental errors).

The distribution of ^{14}C-substances in the stem is illustrated in fig. 2 (expt. No. 1). After 1 hr of translocation, both total and 80% ethanol-soluble substances were located mainly in the epicotyl. In the next period of translocation, ^{14}C-compounds migrated mostly upwards.

The distribution of ^{14}C-photosynthates in the plants used in experiment No. 2 is presented in table 4 and fig. 1.

The percentage of ^{14}C-photosynthates translocated in 1 and 3 hrs periods was much higher than in expt. No. 1. In experiment No. 2 labelled substances were translocated both to the apical part and to the roots in comparable amounts (fig. 1). Removal of roots caused an increment of translocation to the apical part in comparison with that in intact plants. Total translocation of ^{14}C-substances did not change as a consequence of root removal. In this series, radioactivity of petioles was higher than in control plants.

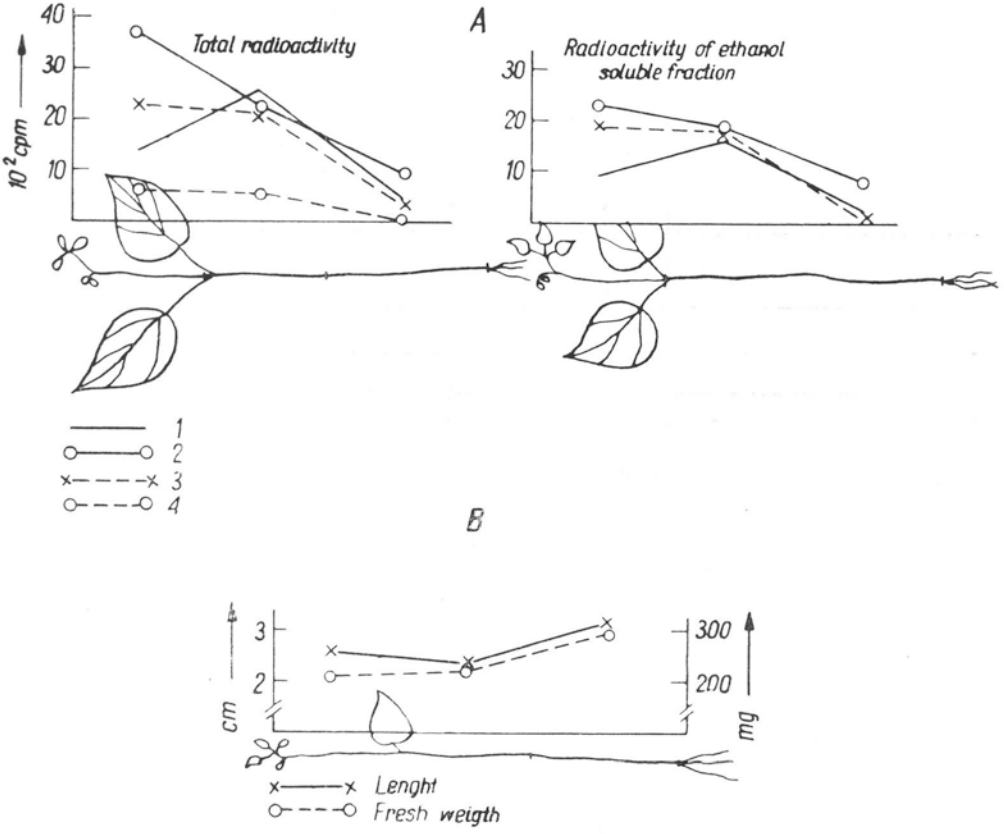

Fig. 2. The distribution of ^{14}C-substances in the bean plant stem (*A*), and fresh weight and the length of particular parts of the stem (*B*). Experiment No. 1.

1 — intact plant (1 hr transloc.); *2* — intact plant (3 hrs transloc.); *3* — blades and roots removed; *4* — blades removed.

In 2 hours after removal of the labelled blades, migration of ^{14}C-photosynthates continued. During this time, radioactivity of the apical part increased in contrast to the stem and petioles, where radioactivity markedly decreased. Radioactivity of roots decreased sightly, but probably as an consequence of expire in respiration. The decrease of radioactivity in all the organs mentioned concerned not only total radioactivity, but also that of the 80% ethanol insoluble fraction, (table 4).

After roots and blades removal, a very low migration of ^{14}C-photosynthates to the apical part from the stem and petioles was observed, (the increase of total radioactivity of the apical part is at the limit of experimental errors; the decrease of the stem and petioles radioactivity is significant).

In table 5, the radioactivity of the insoluble fraction is expressed as percentage of total radioactivity, estimated in separate organs (Experiment No. 1 and 2). The contribution of the radioactivity of the 80% ethanol insoluble fraction, to total radioactivity, was lower in the stem and petioles of plants, deprived of blades, blades and roots or only roots, as compared with that in intact plants

Table 5

Percentage of 80% ethanol insoluble fraction in experiments No. 1 and 2
(Radioactivity of particular organ is assumed as 100%)

Experimental series	Petioles		Apical part		Stem	
	No. 1	No. 2	No. 1	No. 2	No. 1	No. 2
Intact plant 1hr translocation	40.1	40.8	48.0	44.8	35.6	38.5
Intact plant 3 hrs translocation	33.3	59.2**	50.7	50.4	30.3	53.9
Roots removed	—	34.5**	—	44.4	—	29.5*
Blades removed	27.5	35.2**	58.0	54.6	7.7	44.4
Leaves and roots removed	31.9	22.5**	49.0	49.9	27.9	25.4**

* Differences significant at $p = 0.05$

** Differences significant at $p = 0.01$

Table 6

The changes in upward and downward translocation as an consequence of roots and blade's removal
Radioactivity 10^2 cpm

Expt.	No. 1 1964				No. 2 1965				
percent of total radioactivity	Intact 1 hr	Intact 3 hrs	With--out blades	With--out blades and roots	Intact 1 hr	Intact 3 hrs	With--out roots	With--out blades	With--out blades and roots
translocation up*	3.25	9.00	5.11	3.24	3.77	23.73	33.02	8.47	5.59
translocation down**	1.32	2.11	0.76	0.86	7.66	26.27	13.41	4.13	7.35
up / down	2.5	4.3	6.7	3.8	0.49	0.90	2.5	2.1	0.76

* Radioactivity of apical part and stem above labelled leaves.

** Radioactivity of stem belowe labelled leaves (epicotyl and hypocotyl) and roots.

allowed 3 hrs translocation. This may suggest, that in the petioles and stem of plants deprived of blades, some part of ^{14}C-substances previously incorporated into the ethanol-insoluble fraction was exported to other organs.

The distribution of ^{14}C-substances in the stem, (expt No. 2) is illustrated in figure 3. After 1-hr translocation, the radioactivity of the stem was located mainly

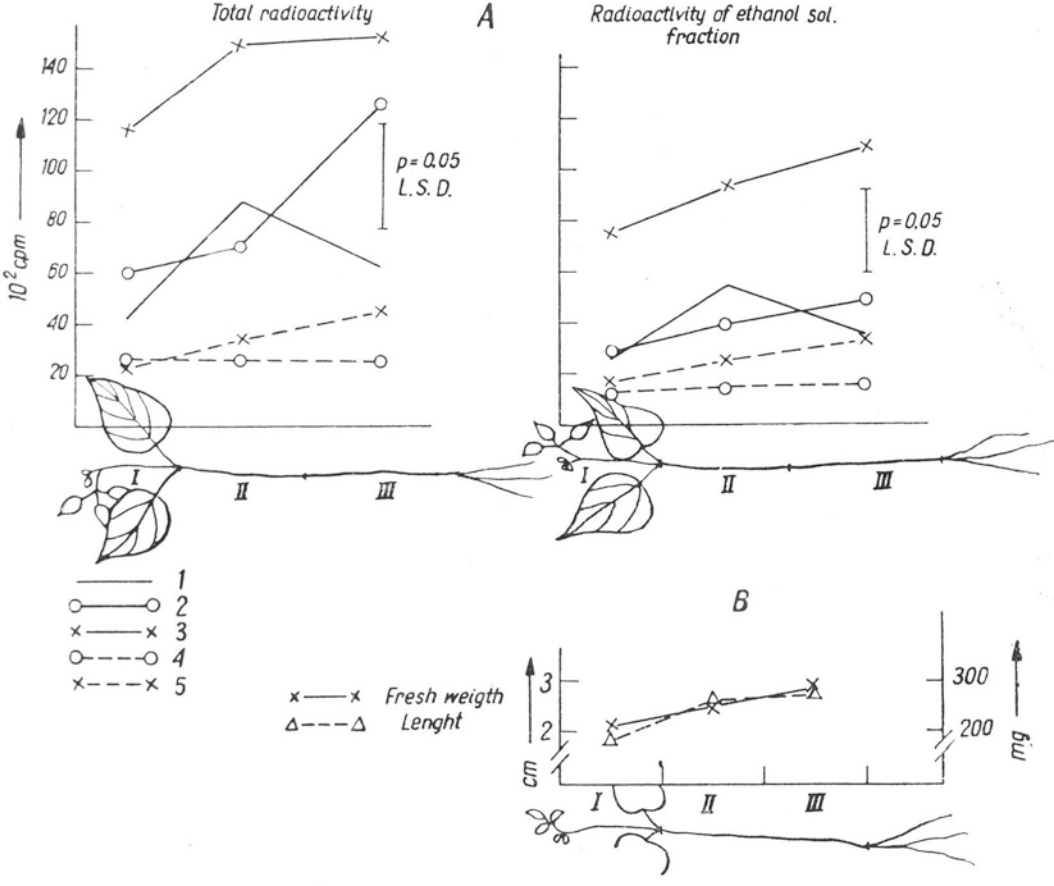

Fig. 3. Distribution of ^{14}C-substances in the bean plant stem (*A*), and fresh weight and the length of particular parts of the stem (*B*). Experiment No. 2.

1 — intact plant (1 hr translocation); *2* — intact plant (3 hrs translocation); *3* — roots removed; *4* — blades removed; *5* — blades and roots removed.

in the epicotyl, as it was observed in expt. No. 1, but after 3-hrs translocation — an increasing gradient towards the roots was established.

Derootment caused accumulation of labelled compounds in the whole stem. Radioactivity of all segments in the stem of plants deprived of blades and blades as well as roots, was much lower as compared to that of intact plants. But even in this series the stem of plants deprived of roots and blades was a little more radioactive than that of plants deprived of blades only.

The differences in radioactivity of the ethanol soluble fraction, especially in the hypocotyl of intact plants after 1 and 3 hours translocation are less pronounced, but radioactivity of the 80% ethanol soluble fraction was also the highest in the stem of plants without roots.

DISCUSSION

The object of this investigation was to determine translocation of ^{14}C-photosynthates in plants deprived of roots and blades. Removal of roots may cause elimination of some pulling forces, whereas in plants deprived of mature blades, pushing forces seems to be reduced.

In the experiments reported, translocation of assimilates in bean plants was continued at least for 2 hours after removal of the blades — the main donor of photosynthates. Migration took place also in plants deprived of roots, as has already been described before (Gage and Aronoff 1960; Hartt 1964 a; Starck 1964 a, b). The main effect of blades and roots removal was similar in both experiments, independently of the differences in the distribution of ^{14}C-photosynthates in the whole plant.

In plants deprived of blades the stem, especially the epicotyl, as well as the petioles, seem to take over the function of main donors of assimilates. These organs exported ^{14}C-assimilates of the ethanol-soluble fraction and partly the ^{14}C-substances previously incorporated in the insoluble fraction. These assimilates were translocated to the apical part and to the roots.

Derootment of plants caused a marked increase of upward and decrease of downward translocation, probably as consequence of diminution of competition for organic substances between various organs, importing assimilates. The cumulation of ^{14}C-substances in the petioles of plants deprived of roots seems to support the suggestion mentioned previously, that removal of some acceptor-organs decreases the velocity (or rate) of translocation of organic substances (Starck 1964b, 1966a) from the blades to the stem through the petioles. Derootment also caused a decrease in ^{14}C-incorporation into the 80% ethanol-insoluble fraction, as it was reported before (Starck 1964b). This fact may, in some degree, be the reason of plant wilting after root removal.

In plants deprived of blades as well as roots, translocation was diminished, in spite of the presence of the apical part, which in intact plant accumulated a great part of ^{14}C-assimilates. This seems to support the previous observation, that removal of one organ (e.g. roots or daughter plants in strawberry, Starck 1964 a, 1966a), interferes in some way with the migration of photosynthates to the other sinks. This agrees also with supposition, that the demand for assimilates is not a sufficient condition for translocation to acceptor-organs, (Nelson 1959; Czajłachjan 1957; Thrower 1964). It suggests a very complex and still unknown interaction between particular organs in the plant.

In expt. No. 2, most ^{14}C-photosynthates migrated toward the roots and in expt. No. 1 to the apical part of the plant, what attests to different "sink power" of these organs. The reason of "sink power" differences is still unknown and may depend, among other factors, on the rate of growth (Ribideau, Burr 1945; Starck 1966b).

The "sink power" of particular organs seems to influence distinctly the distribution of assimilates in the stem. In plants, where the apical part was the region most actively importing assimilates, ^{14}C-substances were translocated mainly to

the part of the stem, above the labelled leaves (fig. 2). Similar results were obtained in the previous investigations with bean plants, (Starck 1966a). On the contrary, when the roots were the dominant acceptor of assimilates, radioactivity of the stem increased in downward direction (see fig. 3) Such a pattern of ^{14}C-distribution was observed also in other experiments with bean plants (Starck 1964 a) and lupine (Starck 1966 b). Therefore in the first hour of translocation in exp. No. 1 the dominant migration of assimilates was upward, but in expt. No. 2 mainly downward.

In the light of Biddulph's recent experiments (1965), one may assume that even ^{14}C-assimilates, translocating to the apical part, may be found in the stem below the labelled leaves owing to the anatomical connection of the conducting bundles and localization of leaf traces. Nevertheless the comparison of the up/down ratio of ^{14}C-translocation in particular experimental series, may throw some light on the interaction between donor and acceptor organs.

The up/down ratio of translocation is different in both experiments (table 6). In plants deprived of blades ^{14}C-assimilates migrated acropetally from the epicotyl and the radioactivity of the lower part of the stem (belowe labelled leaves) decreased, as compared with intact plants. Therefore in these series in both experiments the up/down ratio of translocation increased.

As mentioned before, roots removal caused an increase of upward translocation and consequently an increase of the up/down ratio. Plants deprived of blades and roots translocated assimilates mainly to the apical part, therefore up/down ratio also increased as compared again with that in intact plants (1-hr translocation).

The problem of the character and localization of driving forces of translocation in plants is still open to discussion. Bauer (1953) and Hartt) 1964 a, b, 1965) suggest, that the driving forces of organic substances migration are located within the blade itself. They observed translocation in detached leaves. Aronoff assumes, that the driving forces of translocation in soybean are located in the stem below the cotyledons.

Mortimer (1961) reported some migration of ^{14}C-photosynthates even in isolated petioles of sugar beat leaves. It may suggest that removal of the blades does not stop immediately translocation even in the isolated petiole.

All these observations seem to indicate, that mobilization of organic substances may involve some sort of pulling as well as of pushing forces. The distribution of photosynthates would depend on the interaction between these driving forces, but this problem reguires some further investigations.

The author wishes to thank Professor dr H. Birecka for a helpfull discussion in the course of this study.

SUMMARY

In young seedlings of bean plants translocation of ^{14}C-assimilates continued at least for 2 hrs after ^{14}C-blades removal. In this period the stem, (especially the epicotyl), and petioles, become the main donor of ^{14}C-assimilates. These organs exported ^{14}C-photosynthates mainly to the apical part of the stem with the youngest leaf and to the roots. Petioles and stem exported 80% of the

ethanol soluble compounds and also some part of the ^{14}C-substances previously incorporated into the 80%-ethanol insoluble fraction.

Derootment caused: 1) an increase of upward and decrease of downward translocation, 2) an accumulation of ^{14}C-substances in the petioles and 3) decrease of ^{14}C-incorporation into the ethanol insoluble fraction, as has been already observed in a previous paper.

In plants deprived both: of blades and roots, translocation of organic substances was greatly diminished.

The results obtained seem to suggest, that mobilisation of organic substances may involve some sort of pulling as well as pushing forces.

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Przemieszczanie ^{14}C-asymilatów w siewkach fasoli pozbawionych blaszek liściowych i korzeni

STRESZCZENIE

Ze względu na dużą rozbieżność poglądów, dotyczących lokalizacji siły motorycznej asymilatów, badano wpływ odcięcia blaszek liściowych i korzeni na transport asymilatów w siewkach fasoli.

Stwierdzono, że po odcięciu znakowanych blaszek liściowych, transport ^{14}C-asymilatów odbywał się w dalszym ciągu co najmniej przez następne 2 godz. W tym przypadku łodyga, (a szczególnie epikotyl) i ogonki liściowe, które pozostały po odcięciu blaszek, przejęły funkcje głównych donorów asymilatów. Organy te eksportowały ^{14}C-asymilaty do wierzchołkowej części pędu i do korzeni. Eksport dotyczył głównie ^{14}C-substancji, rozpuszczalnych w 80% etanolu, lecz częściowo również związków, uprzednio inkorporowanych do frakcji substancji nierozpuszczalnych w etanolu.

Odcięcie korzeni powodowało wzrost transportu w kierunku akropetalnym i spadek w kierunku bazipetalnym. Ponadto u roślin pozbawionych korzeni, stwierdzono większe gromadzenie ^{14}C-asymilatów w ogonkach, w porównaniu z roślinami kontrolnymi, oraz spadek procentowego udziału frakcji nierozpuszczalnej w 80% etanolu w ogólnej radioaktywności organów, co wielokrotnie obserwowano w poprzednich badaniach.

W roślinach pozbawionych zarówno korzeni, jak i blaszek liściowych, transport był bardzo wyraźnie zwolniony.

Wyniki przytoczonych badań zdają się wskazywać, że o przemieszczaniu substancji organicznych decyduje szereg sił współdziałających ze sobą i zlokalizowanych w różnych organach. Wymaga to jednak dalszych, szczegółowych badań.