SELECTIVE TRANSLOCATION OF PRODUCTS OF PHOTOSYNTHESIS IN SOYBEAN [1, 2]

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INTRODUCTION

There is general agreement among plant physiologists that sucrose is the principal sugar of translocation in many species (9, 17, 19). Since a number of investigators have demonstrated that compounds other than sucrose may be translocated (7, 21), it is possible that the compound translocated varies significantly with species and also with environmental conditions. In soybean, Vernon and Aronoff (19) demonstrated that the C^{14} fixed in the first trifoliate leaf during 20 minute photosynthesis was translocated down the stem as sucrose. Small amounts of C^{14}-labelled glucose and fructose were isolated at shorter distances down the stem than sucrose. They concluded that the hexoses were translocated along with sucrose but at a lower velocity.

Many workers have shown that the radioactive compounds accumulating in leaves during photosynthesis in $C^{14}O_2$ may be qualitatively and quantitatively different depending on the environmental conditions such as drought (20), mineral nutrition (16), light intensity (5), and carbon dioxide concentration (10). It is possible, therefore, that a change in the environment bringing about a change in the products of photosynthesis may influence which compounds are translocated. By using soybean plants of different ages grown under different conditions of nutrient, light, and temperature, and different concentrations of CO_2 during photosynthesis, the present work demonstrates that several compounds can be translocated. Part of this work has been previously reported (6).

MATERIALS

Plants of *Glycine max* (L.) var. Comet were grown under three different sets of conditions:

I. In aerated nutrient solution especially designed for the culture of legumes (15). Illumination was approximately 2,000 ft–c. (tungsten, water-filtered) for a 16-hour day. Temperature of the growth chamber was maintained at 21 ± 0.5 C. Figure 1A shows a Stage I (11) plant, (i.e. the first trifoliate leaf fully expanded) 14 days old grown under these conditions. Stems were thick and woody and the foliage light green.

II. In a growth chamber maintained as described above, seeds were germinated and grown in coarse exploded mica (vermiculite) in 5-inch pots irrigated from below with tap water. Stage I plants, 15 days old, (fig 1B) had elongated stems and light green foliage.

III. In a greenhouse in aerated nutrient solution. Illumination was supplemented with unfiltered tungsten light as needed especially at the beginning and end of the photoperiod to give at least 1,000 ft–c. for a 16-hour day. Although the greenhouse was maintained at 21 ± 1 C, leaf temperatures were raised about eight degrees by the unfiltered lamps. Figure 1C shows a 14-day old plant with one partly expanded trifoliate leaf (Stage I). Under these conditions stems were elongated and foliage was dark green.

METHODS

About 30 minutes prior to the experiment, plants were transferred to the laboratory where they were illuminated in air with tungsten light filtered through 5 cm of water. The illumination was 2,000 ft–c. measured at the height of the primary leaves (15). At zero time $C^{14}O_2$ was injected from a hypodermic syringe into a 50 ml polyethylene bag which was sealed around one of the primary leaves of the plant. The concentration of $C^{14}O_2$ inside the bag was 0.04 % and the specific activity 38.5 mc per mmole. After 10 minutes the plant was divided into pieces (table I) and the stem between the primary node and the root was further divided into pieces 3 cm long. Each piece was killed immediately by freezing in liquid nitrogen and extracted with hot 80 % ethanol as previously described (11). Ethanol extracts were assayed for C^{14} content after plating on aluminum planchets. Insoluble residues were burned to CO_2 by the method of Baker et al. (1) and counted as $BaCO_3$. Counting was done to within 3 % standard error in a windowless methane gas flow proportional counter (14).

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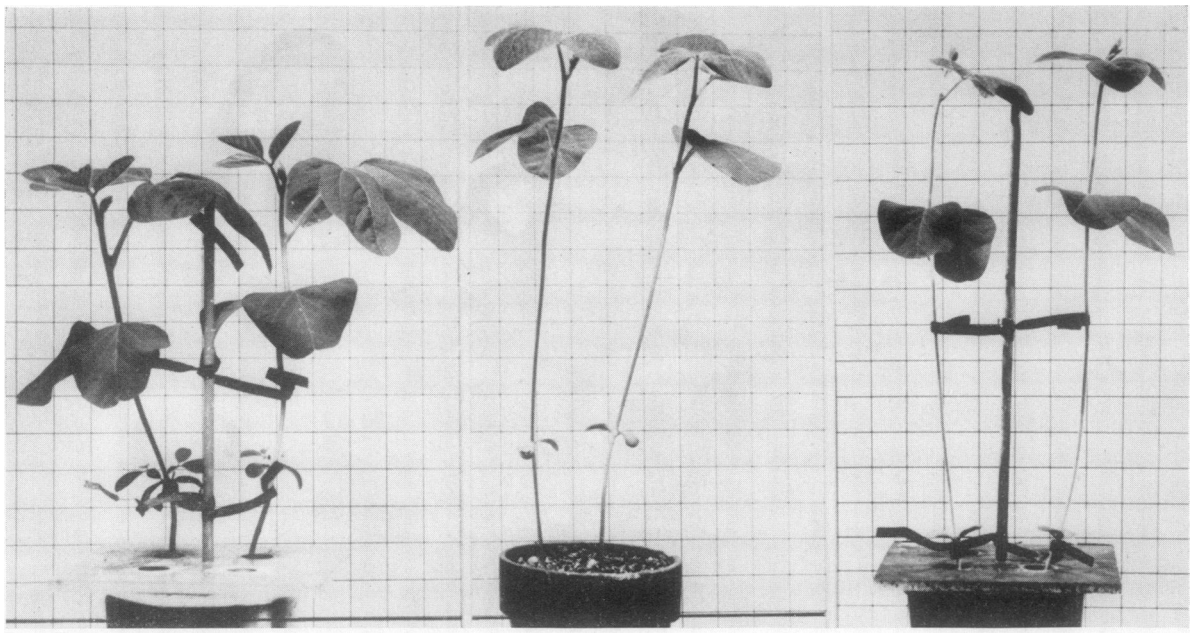

FIG. 1. Soybeans, 2 weeks old, grown under the following conditions: A (*left*): in solution culture in the growth chamber maintained at 21 C under water-filtered, tungsten illumination of 2,000 ft-c for 16 hours daily; B (*center*): in vermiculite irrigated with tap water only but otherwise the same conditions as A; C (*right*): in solution culture in the greenhouse maintained at 21 C supplemented with unfiltered tungsten illumination as needed to give at least 1,000 ft-c for 16 hours daily. The plants were photographed against a grid of 1-inch squares.

Ethanol extracts were examined by two dimensional paper chromatography in two different solvent systems (13). Radioactive areas on the chromatograms, located by radioautography, were counted with a gas flow counter fitted with a Micromil window (4).

The experiments in which the CO_2 concentration in the tagging chamber was varied were carried out under conditions of steady state photosynthesis. One primary leaf of a plant was sealed into a Lucite chamber connected to a circulating system (13, 18). Leaves were allowed to carry on photosynthesis for 30 minutes in 0.03, 0.15, or 0.3 % $C^{12}O_2$ followed by photosynthesis for 10 minutes in $C^{14}O_2$ (specific activity, 1 mc per mM) at the same total CO_2 concentrations.

RESULTS

EFFECTS OF AGE ON TRANSLOCATION OF PRODUCTS OF PHOTOSYNTHESIS. The plants used in these experiments were grown in aerated nutrient solution in the growth chamber (fig 1A). In order to reduce the variability each experiment was carried out at the same time of day (10:00 AM — 4 hours after beginning of daily light period) with three plants in the same pot at each of the following ages: 11, 14, 17, 20, and 24 days old. Because of difficulties of extraction, accurate counting data were obtained from only one of the 24-day old plants. The C^{14} content of the ethanol-insoluble residue of the treated leaf was about 50 % of the total C^{14} assimilated in the 10 minute period. The ethanol-insoluble residues of all other parts of the plant contained no C^{14}.

In spite of the fact that the area of the treated primary leaf more than doubled between 11 and 17 days (13 & 29 sq cm) and remained unchanged between 17 and 24 days, the total C^{14} assimilated was similar (tables I, II). The total C^{14} translocated out of the primary leaves of plants of the same age and also of different ages was extremely variable and represented no more than about one per cent of the total assimilated in the ethanol-soluble fraction (table I). One of the 11-day old plants (No. II) and one of the 20-day old plants (No. II) translocated the most C^{14}. Another one of the 20-day old plants (No. III) translocated the least C^{14}. Seven out of thirteen plants translocated less than 40 mμc out of the primary leaf. All but one of these (17 days, I) translocated a high proportion to the opposite primary leaf. Only one of the six plants that translocated more than 46 mμc (14 days, I) had a high proportion of C^{14} in the opposite primary leaf. There was thus a tendency for a high proportion of C^{14} in this leaf to be correlated with a low total translocation of C^{14}. In all plants even after the very short time of 10 minutes, C^{14} was recovered from the roots. The constancy of the total C^{14} assimilated contrasted with the low and variable amount translocated and the differences in destination suggest that translocation is not directly controlled by assimilation.

The concentration of C^{14} in the 3-cm pieces of stem, sectioned after the 10-minute photosynthetic

TABLE I

FIXATION & TRANSLOCATION OF C^{14} IN ETHANOL-SOLUBLE FRACTION OF SOYBEAN PLANTS OF INCREASING AGE*

ETHANOL-SOLUBLE C^{14}	11 DAYS			14 DAYS			17 DAYS			20 DAYS			24 DAYS
	I	II	III	I	II	III	I	II	III	I	II	III	I
Total fixed, μc**	5.8	6.3	6.3	5.9	8.2	8.2	6.6	7.5	6.1	7.2	7.3	6.2	7.4
Total translocated, mμc	46.0	68.8	22.4	65.4	38.2	65.7	17.7	17.6	22.0	60.6	68.3	15.3	35.2
Plant Part	*Distribution of translocated* C^{14}, %												
Tops	6.5	1.4	4.7	5.1	8.7	7.0	4.9	6.6	11.9	10.4	26.9	22.7	0.2
Opp. primary leaf	0.6	9.7	28.0	18.2	37.0	4.3	5.5	77.5	11.9	3.7	2.7	15.2	10.9
Lower stem	92.5	84.7	67.2	76.4	52.8	88.6	89.2	13.6	75.6	86.0	70.0	55.0	88.7
Root	0.4	4.2	0.1	0.3	0.5	0.1	0.4	2.3	0.6	Trace	0.5	7.1	0.2

* Plants grown in nutrient solution in the growth chamber. 0.04 % CO_2, 38.5 mc $C^{14}O_2$ per mmole offered to primary leaf for 10 minutes.

** An additional 3–5μc of C^{14} was fixed in the ethanol-insoluble fraction of the primary leaf treated with $C^{14}O_2$, no C^{14} was fixed in this fraction in other parts of the plant. The distribution of ethanol-soluble C^{14} was therefore a measure of the total translocation.

period, decreased logarithmically from the primary node downward. Although the general pattern was the same with all of the plants and similar to that described earlier (15, fig 1), the slopes of the log plots varied from plant to plant within each and between different age groups. These curves did, however, extrapolate back to a common y-intercept. The average values for slope and y-intercept within each age group shown in table II illustrate both the variability of slope and the constancy of intercept. The common intercept may reflect the relatively constant assimilation of C^{14} by all the treated primary leaves, or it may indicate a control mechanism vested in the node where the petiole is connected to the stem. The latter possibility is consistent with the observation that variable amounts of C^{14} were also moved to the opposite primary leaf and upper part of the plant. The variations in slope indicate differences in the rate of translocation (i.e., quantity of C^{14} moved per unit time). This view fits with the observations drawn from tissue radioautographic studies conducted in parallel experiments (15) that the regions of high activity near the top of the stem have C^{14} distributed throughout many more phloem bundles than do regions of lower activity further down the stem.

Although the total C^{14} fixed by the primary leaf was about the same in plants of different ages, the distribution of C^{14} among the ethanol-soluble compounds of this leaf was different (fig 2). The proportion of C^{14} in sucrose increased from 22 % in the 11-day old plant to 55 % in the 24-day old plant. This increase was greater between 11 and 14 days than between 20 and 24 days. The proportion of C^{14} in serine decreased more or less steadily from 31 % in the youngest plant to 12 % in the oldest plant. The proportion of C^{14} in other compounds such as malic acid, alanine, aspartic acid, and glutamic acid was much lower than in either sucrose or serine and decreased with age. Note that the data for sucrose in figure 2 include about five per cent hexose and for serine from five to ten per cent glycine. In addition, small amounts of glyceric acid and glycollic acid were isolated from leaves of all ages.

Sucrose and serine accounted for at least 95 % of the total radioactivity isolated from the stems. Alanine, aspartic acid, glutamic acid, malic acid, and an unknown compound accounted for the remaining 5 %. The relative importance of serine and sucrose in translocation can be determined by examining the ratio of total C^{14} in serine to total C^{14} in sucrose for

TABLE II

CHARACTERISTICS OF C^{14} DISTRIBUTION IN STEMS OF SOYBEANS OF DIFFERENT AGES SHOWN IN TABLE I.

AGE DAYS	NO. PLANTS	TOTAL C^{14} RECOVERED IN ETHANOL-SOLUBLE FRACTION OF PLANT μC	Y INTERCEPT OF LOGARITHMIC PLOT dpm/cm × 10^3	SLOPE OF LOGARITHMIC PLOT
11	3	6.18 ± 0.23*	21.0 ± 0*	0.64 ± 0.36*
14	3	7.51 ± 1.09	21.5 ± 1.3	0.58 ± 0.25
17	2	6.36 ± 0.24	20.8 ± 0.2	1.01 ± 0.13
20	3	6.77 ± 0.56	20.8 ± 0.5	0.77 ± 0.33

* Standard deviation.

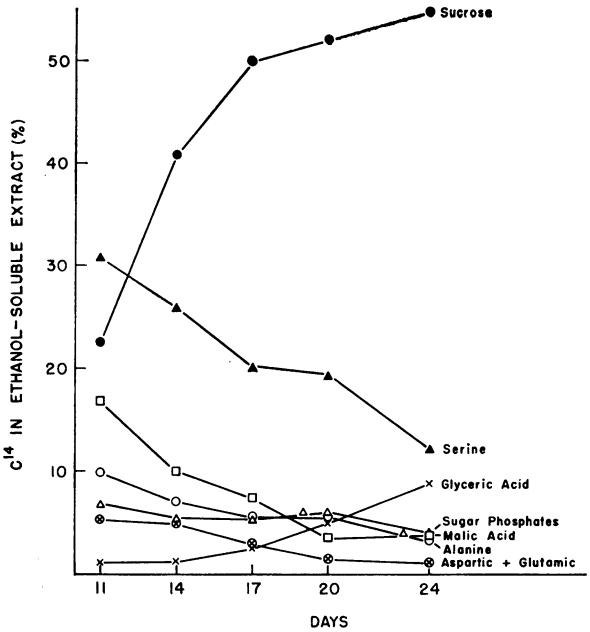

FIG. 2. Distribution of C^{14} among the ethanol-soluble compounds of primary leaves of different ages after 10 minute photosynthesis.

both the treated primary leaf and the 4-cm section of stem below this leaf (table III). Although the ratio was greater than one in the leaves of the 11-day old plants (cf. fig 2) it was less than one and very small in the stems. In other words, much less serine-C^{14} than sucrose-C^{14} was translocated, even though there was much more serine-C^{14} than sucrose-C^{14} in the leaves. In the leaves of the older plants the ratios varied considerably. In all cases they were less than one and tended to decrease with age. In the stems of the older plants the ratios were also less than one (except 17 day, II) and varied considerably. They were highest (more serine) in the 14-and 17-day old plants. With but one exception, 14 day, II, they were higher than the corresponding ratios in the leaves.

The serine-C^{14}/sucrose-C^{14} ratios in successive pieces of stem below the primary node were determined for a number of plants (table IV). An increase in the ratio from the top section downward would indicate that serine was translocated faster than sucrose while a decrease in the ratio would suggest the opposite. The data show increasing, decreasing, and constant ratios with different plants. The range of variation of the ratios in any one plant was not large. The results suggest, therefore, that both C^{14}-labelled compounds were translocated at more or less the same velocity.

Biddulph (3) has studied the translocation of S^{35} and P^{32} introduced into a bean leaf by means of a flap cut so that the initial movement was toward the periphery of the leaf and from there through intact veins into the petiole (2). After a migration period of 1 hour she found that in the stem below the treated leaf, both isotopes were concentrated in the phloem. It is probable that sucrose-C^{14} introduced into the primary leaf by the flap technique would also be localized in the phloem of the stem below. On the basis of this assumption a direct check was made of the rate of conversion of sucrose to serine that is to be expected in a soybean stem during the translocation of photosynthate.

TABLE IV

RATIO TOTAL C^{14} IN SERINE/TOTAL C^{14} IN SUCROSE IN SOYBEAN STEMS

PLANT	DISTANCE FROM PRIMARY NODE			
	0–3 cm	3–6 cm	6–9 cm	9–12 cm
I, 11 days	0.27	0.28	0.27	0.25
III, 14 days	0.68	0.52	0.49	...
II, 14 days	0.39	0.48	0.58	...

Radioactive sucrose was introduced through a flap containing the mid-vein of one primary leaf of a 12-day old plant which had been grown in nutrient solution in the growth chamber. In 2½ hours 18 % of the total sucrose introduced was translocated out of the tip of the leaf and recovered in all parts of the plant. Table V shows that there was considerable metabolism of the introduced sucrose, especially in

TABLE III

RATIO TOTAL C^{14} IN SERINE/TOTAL C^{14} IN SUCROSE IN TREATED PRIMARY LEAF & FIRST PIECE OF STEM BELOW PRIMARY NODE OF PLANTS OF VARIOUS AGES SHOWN IN TABLE I

PLANTS	11 DAYS		14 DAYS		17 DAYS		20 DAYS	
	LEAF	STEM	LEAF	STEM	LEAF	STEM	LEAF	STEM
I	1.43	0.27	0.51	0.66	0.19	0.65	0.17	0.28
II	1.30	0.10	0.62	0.39	0.39	1.08	0.36	0.40
III	1.42	...	0.37	0.68	0.25	0.50	0.23	0.44
Mean	1.38	0.18	0.50	0.58	0.27	0.74	0.25	0.37

TABLE V

DISTRIBUTION OF C^{14} AMONG ETHANOL-SOLUBLE COMPOUNDS IN DIFFERENT PARTS OF PLANT ADMINISTERED SUCROSE-C^{14} FOR 2½ HOURS THROUGH MID VEIN OF 1 PRIMARY LEAF BY BIDDULPH'S FLAP TECHNIQUE *

	TREATED PRIMARY LEAF		3 cm PIECE OF STEM BELOW PRIMARY NODE	ROOT
	TIP** %	BASE %	%	%
Sucrose	81.5	89.5	88	70.5
Serine	1.0	0.7	0**	1.0
Alanine	0.7	0.9	Trace	1.7
Aspartic & glutamic acid	1.65	1.25	3.8	2.65
Malic acid	2.6	1.75	1.5	3.2
Sugar phosphates	1.1	1.75	2.8	17.3
Glucose-1,2-phosphate	0***	Trace	Trace	3.0
Total C^{14} (mμc)	762.0	85.7	7.7	54.3

* Plants grown in nutrient solution in the growth chamber.
** Region of leaf distal to flap.
*** Less than 0.01 mμc.

the roots. Small amounts of serine-C^{14} were formed in both the leaf and root but none would be detected in the stem below the primary node. That is, there was less than 0.01 mμc (0.1 % of the total C^{14}) in serine in the 3-cm piece below the primary node. In the photosynthesis experiments using plants of the same age and grown under the same conditions at least 20 % of the total C^{14} in the stem was recovered as serine. Since sucrose is converted to serine much too slowly if at all in those tissues of the stem in which products of photosynthesis are translocated and accumulated, it is concluded that serine was translocated as such from the leaf.

EFFECT OF OTHER GROWING CONDITIONS ON TRANSLOCATION OF PRODUCTS OF PHOTOSYNTHESIS. Plants that were grown in vermiculite and tap water showed all the signs of nitrogen deficiency (fig 1B). From these plants at least 95 % of the C^{14} in the stem was recovered as sucrose while serine was seldom detected. In fact, in most plants sucrose was the only radioactive compound isolated from the stem. One example is shown in table VII. This absence of translocation of serine in these plants is a reflection of the distribution of the products of fixation in the leaf. The amount of C^{14} fixed in serine in the leaf was never above 5 % of the total ethanol-soluble C^{14} in a 10 minute experiment with nitrogen deficient plants while the amount of C^{14} fixed in serine was from 10 to 30 % in plants grown with adequate nitrogen (fig 2).

From young plants grown in nutrient solution under partially controlled greenhouse conditions (fig 1C), a high proportion of the C^{14} in the stems was isolated as malic acid (table VI). The unusually high proportion of assimilated C^{14} in malic acid in the leaves of these plants again points to a relation between the products of assimilation and the compounds translocated. Although the proportion of C^{14} in malic acid was the same in the leaves of both plants, its proportion in the compounds isolated from the stems was very different in the two plants. Since malic acid was the only compound isolated from the stem of plant II, it must have been translocated as such and could not have arisen by metabolism of translocated sucrose.

If malic acid can be translocated in plants grown under these conditions it is probable that the malic acid isolated in traces from the stems of plants grown with sufficient nitrogen was also in transit and did not arise by conversion of translocated sucrose. Such an interpretation is strengthened by the experiment showing that sucrose introduced by the flap

TABLE VI

DITRIBUTION OF RADIOACTIVITY AMONG ETHANOL-SOLUBLE COMPOUNDS OF PRIMARY LEAF & 1ST SECTION OF STEM BELOW PRIMARY NODE *

	PLANT I, 11 DAYS OLD		PLANT II, 10 DAYS OLD	
	LEAF %	STEM %	LEAF %	STEM %
Sucrose	21	18	29	0
Malic acid	22	29	22	100
Serine	27	22	9	0
Aspartic & glutamic acids	10	0	7	0
Leucines	4	0	10	0
Alanine	3	15	3	0
Hexose	2	0	3	0
Others	11	16	14	0
Total C^{14} in ethanol extract	5.8 μc	2.06 mμc	6.8 μc	1.35 mμc

* Plants grown in nutrient solution in the greenhouse. 0.04 % $C^{14}O_2$, 38.5 μc per mmole offered to primary leaf for 10 minutes.

technique is only slowing metabolism in the stems of soybean. Indeed, in short-term photosynthesis experiments the other radioactive compounds isolated from the stem, such as alanine, aspartic acid, glutamic acid, and an unknown compound, may have been in transit.

Effect of CO_2 Concentration on Translocation of Products of Photosynthesis. Plants grown in tap water in the growth chamber were used under steady state conditions (10). This was arranged by supplying large enough volumes of air mixture so that less than 5 % of the total $C^{12}O_2$ was removed during the 30 minute pretreatment, and less than 5 % of $C^{14}O_2$ during the 10 minute treatment.

In figure 3 is shown typical data for the distribution of C^{14} in the stems. In the three plants shown, the logarithmic decrease in C^{14} content down the stem was observed. Although the total C^{14} fixed by the leaf increased a factor of 3 over the tenfold increase in concentration of CO_2 (table VII), the total C^{14} translocated did not increase and was in fact lowest at the highest concentrations. This latter point is reflected in the more negative slope of the curve for the 0.3 % level in figure 3. The data in table VII also show that sucrose-C^{14} was the main radioactive compound accumulated in the ethanol-soluble fraction of the leaves and was also the main compound translocated. Although the amount of serine-C^{14} present in the leaves was about the same at all concentrations of CO_2, it was not translocated in the plant treated with 0.03 % CO_2. Since serine-C^{14} was isolated from the stems of other plants treated with 0.03 % CO_2, it is concluded that the absence of serine translocation in this case was due to variability in plant material rather than to CO_2 concentration.

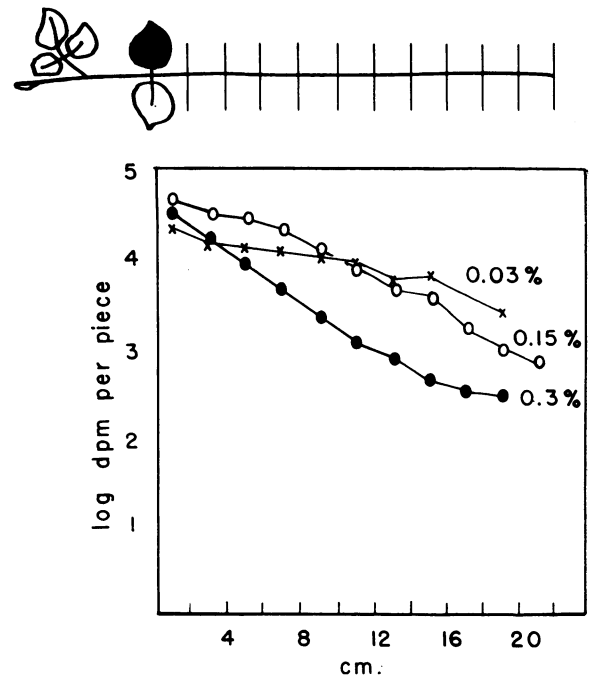

Fig. 3. Distribution of radioactivity in the stems of soybeans, 15 days old, after photosynthesis for 10 minutes by one primary leaf in 0.03, 0.15, or 0.3 % $C^{14}O_2$.

Varying the concentration of CO_2 in the photosynthesis atmosphere as a means of influencing translocation did not, in the present study, effect sufficient change in the distribution of C^{14} among the products of photosynthesis, or in the kind and quantity of C^{14}-labelled compounds translocated to warrant further study.

Table VII

Distribution of Radioactivity in Primary Leaf & Stem Between Primary Node & Root of Plants 15 Days Old Treated With Various Concentrations of $C^{14}O_2$ *

	Conc of $C^{14}O_2$ in air		
	0.03 %	0.15 %	0.30 %
C^{14} In treated leaf (μc)	4.0	9.8	13.0
Ethanol insoluble	0.56	3.8	4.9
Ethanol soluble	3.4	6.0	8.1
Serine	0.13	0.16	0.12
Sucrose	2.7	5.3	7.1
C^{14} In lower stem (mμc)	88.4	148.0	63.3
Ethanol insoluble	0	11.5	2.0
Ethanol soluble	88.4	136.5	61.3
Serine	0	1.4	2.1
Sucrose	88.4	132.5	58.3

* Plants grown in tap water in the growth chamber. $C^{14}O_2$, 1 mc per mmole offered to primary leaf for 10 minutes.

Discussion

The translocation of a C^{14}-labelled product of photosynthesis from its site of synthesis in the leaf, into and down the stem, may be influenced by the rate of operation of any one or more of several sequential processes: A: carbon dioxide assimiliation, B: synthesis of labelled compound, C: mixing of labelled with endogenous unlabelled compound, D: local utilization of the mixed endogenous pool, E: translocation of the compound from the site of synthesis to the vein, F: longitudinal translocation of the compound through the vein, petiole, and stem, G: radial translocation of the compound from the conducting elements to surrounding tissues, H: accumulation and metabolism of the compound in the conducting and surrounding tissues. In the experiments described above, cultural and experimental conditions were altered in attempts to modify the relative rates of these individual processes and thereby evaluate their importance in the overall translocation system.

The radioactive compounds observed in translocation were, in these experiments, drawn from the products of photosynthesis in $C^{14}O_2$. The experiments demonstrate that assimilation and translocation are not directly coupled. In the age series the total amount of C^{14} assimilated was relatively constant inspite of changes in leaf size and age, whereas the amount of C^{14} translocated was variable and represented at best only 1 % of that assimilated. When an increase in the amount of C^{14} assimilated was induced by increasing the total CO_2 concentration in the atmosphere, the amount of C^{14} translocated was not significantly correlated with the increase.

In all of the experiments, sucrose and serine were the principal products of assimilation and in most of the experiments they were the principal compounds that were translocated. The analysis of C^{14}-labelled serine and sucrose in the stem, when compared with those in the leaf, suggest that the amount of newly-formed compound that is translocated does not directly reflect the amount that is synthesized in the leaf. Similarly, translocation of serine or of serine and sucrose was suppressed despite substantial synthesis in the leaf by altering cultural conditions. In certain of these modified conditions, biosynthesis of labelled malic acid in the leaf was greater than usual, and the amount that was translocated was also greater than usual. On the other hand, labelled glyceric acid and sugar phosphate were always synthesized in substantial amounts but were never detected among the compounds translocated. All these results lead to the conclusion that certain selected products of photosythetic assimilation are translocated, and that the selection is modified in response to environmental conditions.

The most likely processes in the sequence listed above for a selective step are probably the mixing of labelled with unlabelled compound, local utilization, and translocation from site of synthesis (Nos. C, D, & E). A change in cultural conditions, such as limiting nitrogen, might, for example, cause a reduction in the endogenous serine pool (see table VIII). Newly-formed serine, in mixing with this pool, would be utilized so rapidly within the leaf that it would be virtually unavailable for translocation. The additional selectivity which discriminates against translocation of compounds in apparently good supply is not easily pictured but might be ascribed to membrane permeability.

Vernon and Aronoff (19) reported that in Hawkeye soybeans grown in pots in a growth chamber at 800 ft–c. and 26 to 30 C, glucose and fructose were translocated from the first trifoliate leaf in addition to sucrose. The hexoses did not move as far down the stem as sucrose. An examination of their data shows that the two hexoses were isolated in approximately equal amounts. This suggests that the hexoses were formed by inversion of sucrose in the conducting and surrounding tissues (process No. H). It is, however, possible that the hexoses were translocated and that the failure to observe them in the present work simply reflects the differences in plant variety, and in cultural and experimental conditions used in the two studies.

Since this work was completed, a paper by Kursanov, Brovchenko, and Pariiskaya has appeared (8) which deals with the selective flow of products of assimilation to the conducting tissue in rhubarb leaves. These workers allowed a small area of a leaf to assimilate $C^{14}O_2$ photosynthetically for 2 minutes, then waited 3 minutes for translocation and during a final 2 minutes cut out the mesophyll between the fourth and fifth order veins in the treated area, and the prolongation of these veins into the region outside the treated area. Tissues from these three zones were immediately extracted and the total C^{14} and the distribution of C^{14} in various sugars, amino acids, organic acids and unknowns were determined for each. Kursanov et al. concluded that several products of assimilation in addition to sucrose entered the translocation stream during the first few minutes. They also concluded that entrance is of a selective nature, that some compounds do not appear to enter at all, while others enter very slowly. Specifically, they found that of the compounds most strongly labelled during their experiments, sucrose, threonine, alanine, serine, malic acid, and citric acid entered with the greatest ease, while aspartic acid, proline, γ-amino butyric acid, fumaric, succinic, and oxalic acids entered with difficulty or not at all.

These findings with a different plant species and with a different experimental approach are in good agreement with those reported above for soybean. They further indicate that one of the sites of action of the selective mechanism is in the step involving translocation of compounds from the site of synthesis to the veins.

Summary

Translocation of the C^{14}-labelled products of 10 minute photosynthesis in $C^{14}O_2$ by primary leaves of soybean, *Glycine max,* was studied with plants grown under controlled conditions (16 hr day, 2,000 ft-c. Mazda, 21 C). The results from these plants were compared with those from plants grown under modified conditions. In plants grown in an adequate nutrient solution, C^{14} was recovered from the stem in both serine and sucrose. In nitrogen-deficient plants, from 95 to 100 % of the C^{14} in the stem was recovered in sucrose. In plants grown in the adequate nutrient solution but under partially controlled greenhouse conditions, malic acid was the only C^{14}-labelled compound detected in the stem. When the carbon dioxide concentration in the photosynthesis atmosphere was changed from 0.03 to 0.15 or 0.3 %, the total carbon dioxide assimilated increased, but this had little effect on the products of assimilation and no direct effect of translocation.

Analysis of a series of plants of different ages showed that serine was translocated with sucrose but in proportions not directly related to the proportions

of these compounds in the leaf. Metabolic conversion of sucrose to serine in the stem was too slow to account for the serine isolated. We conclude that translocation of the products of assimilation is selective. While sucrose and serine are the principal products translocated in the soybean, malic acid and possibly other compounds can also be translocated under suitable conditions.

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