Evaluation of Selected Parameters in a Sugar Beet Translocation System[1, 2]

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In a previous paper (3), we reported on the kinetics of C^{14} translocation in sugar beet as measured in a conventional short-term labeling experiment. Evidence was presented that the rate of C^{14} translocation is linearly related to the specific activity of the sucrose in the source leaf, as would be anticipated in a steady-state system if sucrose were the dominant source of the transport molecule.

In the present study we have extended our information on sucrose translocation by long-term labeling experiments in which both the partial pressure and specific activity of the administered $C^{14}O_2$ were maintained at constant known values for the total duration of the translocation period. Specifically we have sought answers to the following questions: 1) For beet plants of specified geometry, functioning under essentially steady-state conditions[4], what is the required length of time from the start of labeling for isotopic saturation of the translocate [presumably sucrose (3)]? 2) How does the isotopic saturation time for the translocate compare with the isotopic saturation time for the sucrose pool in the source leaf? 3) Is there more than one reservoir or pool of sucrose in the source leaf (7)? If so, what fraction of the total cellular concentration of sucrose in the source leaf comprises the active pool (the transport sucrose as distinguished from the nontransport or storage sucrose)? 4) What is the rate of translocation in mass units per unit time (μg translocate-carbon min^{-1} dm^{-2} source-leaf area) from source leaf to sink leaf under specified conditions?

Materials and Methods

Sugar beet plants (*Beta vulgaris* var. Klein Wanzleben), pruned to a simplified source-path-sink system (3, fig 1), were used in these experiments. Culture methods, treatment of plants prior to the labeling period, and analytical procedures were essentially the same as those used in the short-term labeling experiments previously reported (3), the only significant difference being that labeled CO_2 was maintained in the supply-leaf cuvette at a constant partial pressure of 0.38 mm Hg (usually within the range of $\pm$ 0.08 mm Hg) and at a constant known value of specific activity (2.5–6.7 μc C^{14} $mg^{-1}C$, depending on the duration of the experiment) throughout the entire translocation period. A Sigmamotor peristaltic pump provided a circulation flow rate of 800 cm^3 min^{-1}, giving an average turnover time of about 20 seconds for the gas volume in the leaf cuvette. Total CO_2 concentration and $C^{14}O_2$ concentration in the system were continuously monitored by a Model 15-A Beckman infrared gas analyzer and a Nuclear-Chicago Dynacon-6000 ionization electrometer, respectively (fig 1). Labeled CO_2 from the CO_2 reservoir was introduced into the system by mercury displacement at a rate sufficient to compensate for photosynthetic uptake (approximately 14 ml CO_2 hr^{-1} dm^{-2} source-leaf area), the bleed-in rate being manually regulated by varying either the pressure head on the CO_2 reservoir or the setting on a microcontrol valve. Proper regulation of the bleed-in rate proved somewhat difficult, and significant deviations in the partial pressure of CO_2 from the normative value of 0.38 mm Hg occasionally occurred. It should be noted, however, that a pressure change would not affect the specific activity of the CO_2 in the system.

During the experimental periods (of up to 8-hours duration), heat input, principally from the

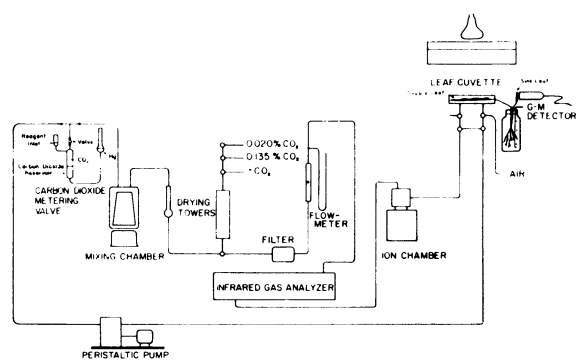

FIG. 1. Monitoring system for supplying CO_2 of constant concentration and specific activity to source leaf. C^{14} accumulation in sink leaf measured by G-M detector.

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[4] The term steady-state is not used in the strictest sense because there is a steady increase in the assimilate content of the source leaf. This fact is taken into consideration in the model and in the discussions which follow.

pump and the 50°-thermostated sample cell of the infrared gas analyzer, resulted in a differential pressure increase within the closed system (fig 1), thus changing the calibration constants for the electrometer and gas analyzer. All critical measurements were made, therefore, after regulating the gas in the system to a constant reference pressure by appropriate adjustments of the temperature within the mixing chamber. (In the present design of our equipment, the mixing chamber is thermostated at below-ambient temperatures, and serves, therefore, as a heat exchanger as well.)

As in the short-term labeling experiments (3), the time-course curve for the entry of labeled translocate into the sink (all parts distal to source blade) was derived from ratemeter data obtained with a D-34 G-M detector positioned against the sink leaf (fig 1). The assumptions and precautions required in such analyses have been discussed in the above paper. In the present experiments, the investigations were carried a step further: by permitting metabolic pools to reach asymptotically a constant level of radioactivity (isotopic saturation), the values of several important parameters of the translocation system could be readily determined. Thus, given isotopic saturation of the transport molecules (considered in the present experiments to obtain when the rate of C^{14} accumulation in the sink leaf reached a constant value) as well as the counting efficiency in μc per cpm and the specific activity of the supplied CO_2, then the rate of C^{14} arrival at the sink leaf in cpm min^{-1} is directly convertible to the total quantity of carbon translocated in μg min^{-1} (or the equivalent in μmoles min^{-1} of sucrose or other molecular species). The method permits, therefore, a quantitative, nondestructive evaluation of the translocation rate in units of mass per unit time (for a general discussion of terminology pertaining to translocation rates, cf. Canny, 2). A more general advantage of the method is that for any pool at isotopic saturation in which the total quantity of C^{14} in μc can be measured, the equivalent moles or weight of that compound can be readily determined.

Results and Discussion

Figure 2 presents the data from an experiment showing the change with time in the rate of C^{14} accumulation in the sink leaf, measured with a G-M counter, when the partial pressure and specific activity of the CO_2 provided to the source leaf were held constant for the total time course of the translocation period. Since export of the labeled translocate is known to be negligible from immature leaves (4, 8, 9), the sink leaf functions as a terminal trap, and the rate of accumulation is equivalent, therefore, to the rate of translocation to this site.

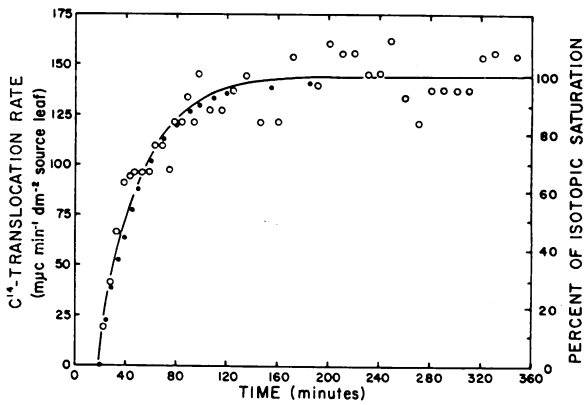

FIG. 2. Rate of C^{14} translocation (normalized to total sink) as a function of time. Translocate within 95 % of isotopic saturation at about 100 minutes. Rate at isotopic saturation = 145 mμc min^{-1}, equivalent to 58 μg translocate-carbon or 137 μg sucrose min^{-1}, normalized to total sink and a source-leaf area of 1 dm^2. Open circles, experimental points; closed circles, predicted points based on mathematical model.

As may be noted from the smoothed curve (fig 2), the C^{14}-translocation rate rapidly increased to an equilibrium rate of approximately 145 mμc min^{-1} dm^{-2}, attaining about 95 % of this rate in 100 minutes from the start of labeling (time 0). Under the steady-state conditions presumed to obtain in these experiments, this curve may be considered to depict the rate of approach of the translocate to isotopic saturation. In this experiment the slope constant at steady state translocation was 124 cpm min^{-1}, the counting efficiency was 1.21×10^{-4} μc/cpm (the ratio of the C^{14} in μc in the sink leaf at the end of the run relative to the final count rate corrected for coincidence losses) and the specific activity of the administered CO_2 was 400 μg total carbon/μc C^{14} (table I: 360-min expt). On this basis, the translocation rate from the source leaf (0.60 dm^2) to the sink leaf was approximately 15.0 mμc C^{14} or 6.0 μg total carbon min^{-1}. In terms of sucrose, this rate converts to 14.2 μg or 0.042 μmoles min^{-1} (124 cpm $min^{-1} \times 1.21 \times 10^{-4}$ μc/cpm $\times$ 400 μg $\mu c^{-1} \times 342/144$ = 14.2 μg sucrose min^{-1}). Normalized to a standard source-leaf area of 1 dm^2 and to the total sink, on the basis that the partition coefficient remained constant throughout the translocation period (3), this rate converts to 137 μg sucrose min^{-1} dm^{-2}. Data for this experiment and 3 similar experiments of shorter duration are summarized in table I.

The average rate of dry weight increase in a sink leaf within a given size range was estimated from the regression of dry weight on sink-leaf size (area) obtained by measuring the dry weight increase (based on increase in sink-leaf area) over a 1-day interval. By this method it was established that a sink leaf of 17-mg average dry weight would be expected to accumulate 17.6 $\pm$ 1.8 μg dry weight min^{-1} from a

Table I. *Data from Long-Term Labeling Experiments*

Both the partial pressure and specific activity of the administered CO_2 were maintained constant for the duration of the labeled translocation period.

Exptl data	Duration of translocation period (min)				Avg ± standard deviation
	80	120	240	360	
Source leaf area (dm^2)	0.52	0.63	0.61	0.60	
Specific activity of CO_2 $\left(\frac{\mu g \text{ carbon}}{\mu c\ C^{14}}\right)$	149	222	370	400	
Yield factor $\left(\frac{\mu c \text{ in sink leaf}}{\text{final cpm corr.}}\right)$	1.57×10^{-4}	0.59×10^{-4}	0.68×10^{-4}	1.21×10^{-4}	
μc Translocate in sink leaf: μc in total sink	0.156	0.185	0.117	0.173	
Slope constant at steady-state translocation (Δ cpm min^{-1})	263*	310	136	124	
Carbon translocation rate normalized to total sink and standard source-leaf area (μg C min^{-1} dm^{-2})	76*	36	48	58	55 ± 17
Ditto but calculated in sucrose equivalents (μg sucrose min^{-1} dm^{-2})	180*	85	114	137	130 ± 40
Carbon fixation rate (μg C min^{-1} dm^{-2})	150	108	125	133	126 ± 17
Sucrose in source leaf (μg sucrose dm^{-2})	4500	4740	5700	6650	

* Rough estimate; calculated for the 75- to 80-minute interval.

source leaf of 1 dm^2 (95 % confidence level) while steady-state labeling yielded a value of 6.6 μg C or 15.7 μg sucrose min^{-1} import rate from a 1-dm^2 source leaf into a 17-mg dry weight sink leaf. The agreement between the methods suggests that the influx of labeled sucrose from the source leaf was of sufficient magnitude to account for the dry weight increase noted in the sink leaf, and counters any possible argument that a significant fraction of the translocate consisted of nonlabeled molecular species.

The open circles in figure 2 represent rate calculations (Δ cpm/Δ t) for selected intervals on the C^{14} accumulation-time curve. The scatter in these points results primarily from difficulties in reading small increases in cpm against a large background count rate. Thus, for a ratemeter operating on the 30,000 full scale range (the usual mode in the present studies), the optimum read-out precision is ± 50 cpm (disregarding possible dead-zone uncertainties on a 5-inch strip chart. Hence for a C^{14}-translocation rate of 100 cpm min^{-1}, a Δ t greater than 5 minutes would be required to provide a read-out precision better than ± 10 %. In evaluating the rate increments, therefore, sliding averages were used over portions of the curve where rapid changes in rate necessitated using small count and time increments; for relatively constant rates, larger time and count increments allowed the value of Δ cpm/Δ t to be determined to a much higher degree of accuracy.

Whether the scatter in the points after 100 minutes (fig 2), equivalent to about ± 20 cpm min^{-1}, represented real fluctuations in the translocation rate, or a noise level induced by minor changes in the yield factor (geometry) resulting from small nutational movements of the sink leaf in the holder positioned against the G-M detector, is not known with certainty. We are of the opinion that variations in the translocation rates were the major factor, for, as mentioned in the section on Material and Methods, fluctuations in the CO_2-concentration level in the supply-leaf cuvette occasionally occurred, and these fluctuations undoubtedly induced minor perturbations in the rates of various physiological processes including translocation. On the assumption that, given steady-state assimilation, the rate of translocation would itself be constant, the equilibrium rate is shown as an average constant value. In studies now in progress on the effect of temperature on sucrose translocation, an improved system design has made possible a more precise control of the CO_2-concentration level, and data thus far accumulated have indicated greater constancy for the translocation rate as well.

The average time required for isotopic saturation (to within 95 %) of the translocate arriving at the sink leaf, based on smoothed data for 8 plants, was 99 ± 8.6 minutes. Allowing for a 15-minute lead time for events in the source leaf (note from fig 2 that C^{14} was not detectable at the sink leaf until 15 min from time 0) it may be inferred that the sucrose pool in the source leaf became isotopically saturated in 84 ± 8.6 minutes.

A reasonable assurance of the validity of this conclusion is provided by chromatographic analyses of the amount of C^{14}-labeled sugars in the source leaf of 5 comparable plants, supplied with $C^{14}O_2$ under steady-state conditions for respectively 10, 80, 120, 240 and 360 minutes. The results are shown in figure 3 (sucrose curve, open circles). It is apparent that the sucrose-C^{14} fraction increased rapidly at first, and then leveled off after about 80 minutes to a constant rate of increase of about 8.3×10^{-3} μc min^{-1} dm^{-2} (normalized to a standard specific activity of 2.5 μc/mg C) for the duration of the translocation period. On the basis that constancy of slope may be taken to indicate isotopic saturation, the predicted time course for isotopic saturation of the source-leaf sucrose, requiring attainment of saturation at about 80 minutes, appears established. A recently completed direct test of this inference by measurements of the absolute specific activity of sucrose supports the same conclusion (1).

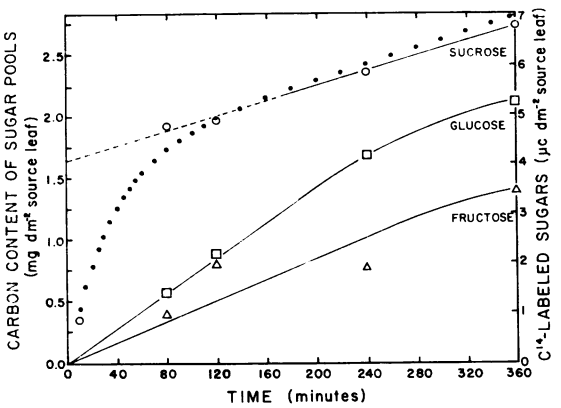

FIG. 3. Time course of C^{14} content in μc normalized to specific activity of 2.5 μc $mg^{-1}C$ (right-hand ordinate) of sugars in source leaf. Open circles, sucrose; triangles, fructose; rectangles, glucose; closed circles, predicted time course for approach of sucrose pool in source leaf to isotopic saturation. Left-hand ordinate applicable only to sucrose after isotopic saturation. Extrapolated value for intercept on y axis = 1640 μg carbon or 3900 μg sucrose dm^{-2} source-leaf area (value of S in equation II).

The rate of accumulation of sucrose in the source leaf, calculated from the steady-state slope following isotopic saturation, amounted to 3.3 μg carbon min^{-1} dm^{-2} leaf area (fig 3) or, calculated as sucrose, 7.8 μg min^{-1} dm^{-2}. The net rate of sucrose synthesis, therefore, in the 360-minute experiment may be estimated at approximately 145 μg min^{-1} dm^{-2}, which is the sum of the rate of outflow (translocation) of 137 μg sucrose min^{-1} dm^{-2} and the rate of accumulation of 7.8 μg sucrose min^{-1} dm^{-2}. Glucose and fructose pools did not reach isotopic saturation within a time period of 6 hours (fig 3), hence quantitative estimates of these fractions by tracer methods were not possible.

The fact that the translocate (sucrose) and the active sucrose pool in the source leaf appear to have reached isotopic saturation simultaneously (corrected for transport time between source leaf and sink leaf) suggests that the active sucrose pool is essentially equivalent to the total sucrose content of the source leaf, for otherwise the time required for isotopic saturation of the sucrose in the source leaf would have been longer than that required for the sucrose-translocate. To test this inference, a mathematical model was set up based on the following assumptions: 1) the translocate is composed exclusively of sucrose; and 2) the newly synthesized sucrose mixes immediately and uniformly with the total pool of indigenous sucrose.

The net increase in the amount of labeled sucrose in the source leaf in time dt is given by the equation:

$$\frac{dL}{dt} = F - T\left(\frac{L}{S + At}\right) \qquad \text{I}$$

Rate of increase of radioactive sucrose in leaf	=	Rate of production of radioactive sucrose by leaf	−	Rate of removal of total sucrose	×	Radioactive sucrose as a proportion of total sucrose in pool

where: L = Amount of radioactive sucrose in the source leaf at time t (the influent sucrose is considered to have the same specific activity as the administered CO_2). S = Amount of sucrose in source leaf at time 0 (start of labeling). t = Time in minutes after start of labeling. A = Rate of sucrose accumulation in source leaf. T = Rate of translocation of sucrose from source leaf. F = Net rate of sucrose synthesis in the source leaf.

Solving the differential equation (I) by method of separation of variables one obtains:

$$L = S + At - S\left(\frac{S}{S + At}\right)^{T/A} \qquad \text{II}$$

that is, the amount of radioactive sucrose in the source leaf (L) expressed as a function of time (t).

Evaluating L as a function of time gives the predicted time course for the increase in the amount of labeled sucrose (shown in fig 3, closed circles), based on the following experimentally determined values (360-min experiment) for the defining parameters: S = 3900 μg dm^{-2} (extrapolated intercept on ordinate at $t = 0$), A = 7.8 μg min^{-1} dm^{-2}, T = 137 μg min^{-1} dm^{-2}, and F = 145 μg min^{-1} dm^{-2}. The values used for the model calculations are representative of those obtained in several sets of experiments. For example, the average value of T from 4 plants for which radiochemical analyses of the sucrose pool in the source leaves are available is 130 ± 40 μg min^{-1} dm^{-2}; if 4 additional plants from an experiment conducted about a year later are included, the average is 119 ± 29 μg min^{-1} dm^{-2}.

Similarly, in figure 2 (closed circles) is shown the predicted time course for the rate of approach of

the translocate to isotopic saturation. The degree of saturation was calculated by computer using the following relationship:

$$\text{Percent isotopic saturation} = \left(\frac{L}{S + At}\right) \times 100. \quad \text{III}$$

The excellent quantitative fit of the experimentally measured data to the mathematically derived curves, based on the model of a single source leaf sucrose pool substantiates the view that, within the limits of accuracy of the method, all of the sucrose in the source leaf is about equally available for translocation, and hence the sucrose pool is not divisible into a transport pool and a storage pool [in the short-term labeling experiments (3, fig 5), the data suggest that a small fraction of the sucrose may be irreversibly sequestered in the source leaf]. The fit also provides an independent check on the reliability of the analytical procedures used in measuring the values of the specified parameters.

To demonstrate the deviation of fit when an incorrect value is used for one of the parameters in the mathematical model, the time required to reach 90 % saturation was calculated by computer while systematically varying the translocation rate computationally. For a 70 μg sucrose min^{-1} dm^{-2} rate, 142 minutes would be required; for a 190 μg sucrose min^{-1} dm^{-2} rate, 50 minutes. This contrasts with a predicted time of 80 minutes (the time experimentally determined, as noted above) when the observed average translocation rate of 130 μg sucrose min^{-1} dm^{-2} is used. Similarly, the size of the supply-leaf sucrose pool at $t = 0$ was varied computationally, and again the time for 90 % saturation was calculated, based on the observed average translocation rate of 130 μg min^{-1} dm^{-2}. For a pool size of 2840 μg sucrose dm^{-2}, 56 minutes would be required; for a pool size of 5700 μg sucrose dm^{-2}, 111 minutes. This contrasts with a predicted time of 75 minutes when the observed initial pool size of 3900 μg sucrose dm^{-2} is used. Allowing for a possible inaccuracy of 15 minutes in determining the isotopic saturation time, a pool size of about 750 μg sucrose, equivalent to about 15 % of the 5200 μg pool size (average size during the 360 minutes of photosynthesis) could be nonactive in translocation. Inasmuch as an error of this magnitude is probably a maximum, it is evident that most if not all of the source-leaf sucrose constitutes the active translocate pool. Because of different sized sucrose pools in different source leaves, the dilution effect will cause the specific activity of the sucrose-translocate to differ between plants in short-term experiments. Consequently the use of relative rates of C^{14} export in short-term labeling experiments as a measure of translocation rates must be interpreted with caution.

The reliability of the steady-state labeling method for quantitizing translocation rates thus appears reasonably confirmed. Studies are currently in progress to determine the effect of temperature and light on various parameters of translocation using this method. An example of a preliminary experiment showing the rapid change in translocation rate incident upon darkening the source leaf is given in figure 4. In this experiment the source leaf was subjected to steady-state labeling for 8 hours in the light, darkened for 16 hours, and then resubjected to steady-state labeling for 2.3 hours in the light. In the initial light period, the translocation rate was 52 μg sucrose min^{-1} dm^{-2}; in the dark, 26 μg min^{-1} dm^{-2}; and in the second light period, 48 μg min^{-1} dm^{-2} (the source leaf in this plant system was 2 weeks older than those used in the earlier experiments, and this fact may account for the considerably lower rates of translocation observed in the light).

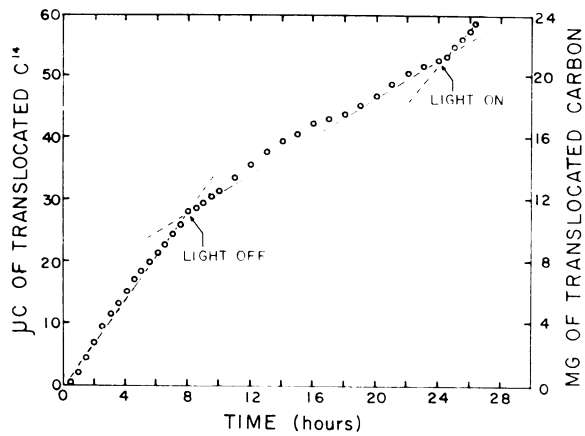

FIG. 4. Accumulation of translocate in sink in μc C^{14} and mg carbon, normalized to total sink and 1 dm^2 source-leaf area.

Of interest is the observation that the transition to the dark rate, which remained fairly constant during the ensuing 16 hours, occurred rapidly. Because of uncertainties in determining the translocation rate over short periods of time, as explained above, the precise time required for transition to the dark rate cannot be established. If the transition time is 15 minutes (the transit time for sucrose from the source leaf to the sink leaf, as noted above) a possible inference would be that the lower rate in the dark results from a reduction in loading rate at the source rather than from a reduction in carrier velocity. If the transition time is more rapid than this, a possibility suggested by some data of Butcher (1), a reduction in carrier velocity would be indicated as well. Further studies of this question are now in progress.

A sucrose pool of 7100 μg dm^{-2} (a probable maximum value after 8 hours of photosynthesis) would be completely depleted by a translocation rate of 26 μg sucrose min^{-1} dm^{-2} in about 6 hours. Of necessity, therefore, most of the translocated carbon was derived from reserve polysaccharides. Mortimer and

Wylam (5) have shown that the polysaccharide fraction formed in sugar beet leaves during the light is derived from early photosynthetic intermediates. Consequently, the polysaccharide increment synthesized during the 8-hour light period should have had the same specific activity as the sucrose pool, and if this increment is used to maintain the sucrose pool in the dark, no decrease in the specific activity of the translocate would be anticipated (provided that deposition of the polysaccharide fraction is by apposition and not by intussusception). The rapid response upon resumption of light at 24 hours further supports the view that the specific activities of both the sucrose pool and the reserve polysaccharides supplying the translocate (presumably via sucrose) in the dark were the same. This interpretation is consistent with the findings of Porter et al. (6), who studied starch conversion in darkened leaves. It would be of interest to determine over what range the size of the sucrose pool in the source leaf can vary without affecting the rate of translocation.

Summary

The rate of translocation, in units of micrograms of translocate-carbon min^{-1} dm^{-2} area of source leaf, was determined in beet plants (*Beta vulgaris*, var. Klein Wanzleben) pruned to a simplified source leaf-sink leaf system. Carbon dioxide of specified concentration and specific activity was supplied to the source leaf and concurrently the rate of accumulation of C^{14} in the sink leaf was measured with a G-M detector positioned against the leaf. A constant rate of C^{14} accumulation in the monitored sink was attained after about 100 minutes. Under the steady state conditions of these experiments, a constant rate of C^{14} accumulation is considered to signify isotopic saturation of the translocate. From the physical constants for the experiment [the steady-state slope constant, the counting efficiency (μc/cpm), and the specific activity of the administered CO_2] an average translocation rate of 55 μg translocate-carbon min^{-1} dm^{-2} was determined, equal to 130 μg sucrose-equivalents min^{-1} dm^{-2}.

By similar analyses, the net rate of sucrose synthesis, the size of the sucrose pool, and its rate of approach to isotopic saturation in the source leaf, were also evaluated. These values were used in a mathematical model to generate a predicted time course for approach to isotopic saturation of the source-leaf sucrose pool and the sucrose-translocate, based on the hypothesis that the total sucrose concentration of the source leaf constituted the active pool for translocation. Good agreement was obtained between predicted and observed values. These results suggest that the use of short-term C^{14} labeling experiments to evaluate the relative contribution of different leaves in supplying translocate to nutritionally dependent plant parts must be interpreted with caution unless corrections are made for different sucrose-pool sizes.

Acknowledgments

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