TRANSLOCATION OF LABELLED ASSIMILATES IN THE SOYBEAN

IV. SOME EFFECTS OF LOW TEMPERATURE ON TRANSLOCATION

By Stella L. Thower*

[Manuscript received September 14, 1964]

Summary

Translocation of ¹⁴C-labelled assimilate within the plant ceased when the plant was held at 2–3°C. Chilling a short length of petiole to 1°C prevented translocation of labelled assimilate past the chilled section of petiole. When the petiole was again warmed, translocation through it was resumed. The time between warming the petiole and the resumption of translocation varied between 5 and 20 min.

The profile of labelled material developed in the stem 30 min after chilling and rewarming was shown to be of logarithmic shape. This shape was lost after 2 hr. A logarithmic profile was obtained for both mobile and fixed labelled material. The rate of movement of the front of detectable activity down the stem was of the order of 17 cm/hr.

Movement of labelled assimilate in the vascular tracts running downward from a particular leaf was inhibited when the leaf was isolated from the stem (by chilling), and enhanced when the root was deprived of assimilate from other leaves (by defoliation).

I. Introduction

Prior to the early 1950's there was considerable interest in the effects of temperature on translocation, and several opposing views were current. Hull's review in 1952 listed a number of workers who reported increased translocation with increased temperature up to 30°C. An almost equal number reported that translocation increased with decreased temperatures or was independent of temperature.

Esau, Currier, and Cheadle (1957) considered that a majority of the more recent studies supported the view that translocation of sugars was retarded at low temperatures. They considered that two explanations of this temperature effect were possible: either low temperature increased the viscosity of protoplasm and cell sap in sieve tubes, or low temperature had a direct effect on respiratory reactions supplying energy for the process of transport. These processes could both apply but there is at present insufficient evidence to decide conclusively in favour of either or both.

In the present decade little additional work has been published; however, the results which are available have lent support to the view that translocation is decreased at low temperatures. Mortimer (1961) has demonstrated that chilling sugar-beet petioles blocks translocation through them. Humphries (1963) used rooted Phaseolus leaves and compared translocation to the root at 12 and 24°C. He found that the rate of increase of dry matter of roots was significantly less at the lower temperature. Whittle (1964b) has shown that in Pteridium the apparent diffusion constant rose with temperature over the range 13–29°C.

* Department of Botany, University of Melbourne.

In the present work three aspects of the problem have been studied: (1) the effects of total chilling; (2) the effects of localized chilling; and (3) translocation after chilling.

II. METHODS AND MATERIALS

Biloxi soybean, Glycine max (L.) Merr. cv. Biloxi, was used for all experiments. Conditions of growth were as previously described (Thrower 1962).

Whole plants were chilled by placing them in a cold room at a temperature of 2–3°C. Short lengths of petioles or stems were chilled by application of crushed ice. The vessel used for chilling was slotted so that the petiole could be inserted in the slot and completely surrounded by crushed ice. During experiments the ice was replenished every 15 min. Preliminary tests showed that the petiole within the crushed ice was maintained at 1°C and the temperature of the petiole outside the chilling vessel rose to the greenhouse temperature (20°C) within 1·5 cm of the ice. The temperatures within the petiole were measured with an Electric Universal thermometer type T.E.3 (Electrolaboratiet, Copenhagen) fitted with fine needle probes of type K8. These needle probes, which have a diameter of 0·7 mm and whose points contain a thermocouple junction, were inserted into the petiole.

Single leaves were fed 14CO2 by “spot-feeding” and plants were subsequently dissected and dried. The presence of 14C in the plant was detected either by radioautography or by counting. Samples for counting were prepared by combustion and conversion to Ba14CO3 (cf. Thrower 1962) or else by a hot alcoholic extraction. This procedure was carried out by soaking short sections of dried stem in two successive aliquots (5 ml) of 80% ethanol at 56°C for 24 hr. The 10 ml of extract was pipetted on to metal planchets, dried, and counted.

A preliminary experiment showed that a 24-hr extraction was adequate for removal of all soluble label from the tissues. Following other workers (e.g. Canny 1961) it is assumed that the ethanol-soluble material extracted is largely sucrose.

III. EXPERIMENTAL AND RESULTS

(a) Effects of Chilling the Whole Plant

Four plants with two expanded leaves were used. These were held at 2–3°C for 2 hr prior to and during the 3 hr of 14CO2 feeding. 3 µc of 14CO2 was applied to the terminal leaflet of the upper expanded leaf by “spot-feeding”. This leaf was illuminated by a Photoflood 500-W globe 8 cm above the leaf surface, giving a light intensity of 750 f.c. and a temperature of 20°C at the surface of the leaf. The upper parts of the plant were screenerved from the lamp by a black paper screen and temperature at the apex was 3°C. After 3 hr the plants were dissected, air-dried, and radioautographs were made.

The radioautographs showed the presence of activity in the source leaves and petioles. No activity could be detected in apices, stems, or roots. Three replications of the experiment confirmed this result.

It was concluded that uptake of 14CO2 at the source leaf was adequate but that translocation from this leaf was inhibited by the temperatures of 2–3°C obtaining in the rest of the plant.
(b) Effects of Localized Chilling

(i) Experiment 1.—Petioles of the upper expanded leaves of four plants were chilled for 30 min and subsequently during a 3-hr application of $3\mu\text{c}$ of $^{14}\text{CO}_2$ to the leaf. Light intensity was 1000 f.c. and greenhouse temperature 27°C. At the conclusion of the application period the plants were dissected, dried, and radioautographs were made. In all cases the radioautographs showed the presence of a high level of radioactivity in the fed leaf and the distal length of petiole. No activity could be detected in either the chilled length of petiole or any proximal plant parts. Numerous repetitions of the treatment invariably gave the same result.

Lowering the temperature of a short length of petiole was thus shown to prevent movement of labelled assimilate through the chilled section. This is consistent with the results obtained when the whole plant was chilled and indicates that translocation ceases at 1–3°C, as far as the methods of detection can show. This behaviour of soybean is similar to the behaviour of sugar-beet as demonstrated by Mortimer (1961).

(ii) Experiment 2.—Experiment 1 was repeated with the difference that after 2 hr of $^{14}\text{CO}_2$ application the ice was removed from two of the petioles. These were quickly rinsed with water at greenhouse temperature and blotted dry. Preliminary measurements showed that the internal petiole temperature rose from 1 to 20°C in less than 2 min under these conditions. All plants were harvested at the end of 4 hr.

Radioautographs of the plants with petioles chilled throughout showed no movement past the chilled section. Radioautographs of plants with petioles warmed after 2 hr showed activity to be present in all parts of the petiole and for some distance down the stem (22 and 62 cm). Representative radioautographs of these plants are shown in Plate 1, Figures 1 and 2. Many replications of this treatment confirmed the findings.

These results show that the inhibition of translocation by low temperature is readily reversed when the temperature is again raised. It is significant that Czapek (1897) achieved a similar effect of stopping and restarting translocatory processes when he narcotized petioles with chloroform and then allowed them to recover. In this particular case narcotization might be expected to depress respiratory reactions rather than increase the viscosity of sieve-tube contents. It can therefore be argued that, under conditions of low temperature, the depression of respiratory reactions is important in the retardation of translocation irrespective of whether there is increased viscosity or not.

(c) Rate of Translocation following Chilling

Radioautographs of source leaves with chilled petioles show that after application of $^{14}\text{CO}_2$ for 2 hr the leaf contains considerable activity. When the petiole is again warmed, this accumulated isotope is free to move down the petiole and the rate of movement of this front of activity can be obtained simply by measuring the distance moved in a given time. Such a measurement of distance, by visual assessment of the radioautographic image, has the advantage that each measurement is
subject to the same limiting factors. These factors are inherent in the subjective assessment and the sensitivity of the radioautographic method. For this reason it can be assumed that in each case the front ceased to be detectable at approximately the same level of activity (the initial dose being, in each case, the same).

Fifty-six plants, each with stems 60–70 cm long, were used. All petioles were chilled prior to $^{14}$C administration for 30 min, and during application of $^{14}$CO$_2$ feeding for 2 hr. The ice was then removed from the petioles of all but four control plants. Harvesting was begun after 18 min and thereafter at c. 2-min intervals, the last plant being harvested 101 min after removing the ice. Stems were cut into short sections and radioautographs were made from the dried, dissected stems. The distance down the stem at which activity was detectable was measured on the radioautographs. As movement within the stem pieces may be expected during drying, the distances so measured are accurate only to within the length of a section (2–3 cm). However, it was commonly found that sections did not show an all-or-none content of activity and where activity was evident in only the upper part of a stem section the distance to the disappearance of activity was measured.

Radioautographs of the four control plants showed no translocation past the chilled zone. Results for the other 52 plants are shown in Figure 1 where a regression of distance on time has been plotted for the movement of the active front down the stem. At first sight the points show a wide scatter. However, a regression line of the form $y = a + bx$ was calculated for the points. The values for the constants were found to be:

$$a = -7.2, \text{ standard deviation} = 1.5; \quad b = 0.40, \text{ standard deviation} = 0.06.$$  

An analysis of variance was carried out by the method of Mather (1951) and the coefficient of regression was found to be highly significant (at the 0.1% level). This was taken as evidence that the line of best fit, i.e. $y = -7.2 + 0.40x$, is a reliable concept and inferences might justifiably be drawn from it.

Figure 1 shows that the scatter of points increases with higher values of $x$ and $y$. This introduces a difficulty in calculating whether the regression line can pass through the origin. To correct for this factor a regression of rate on time was constructed. The analysis of variance for this regression showed that the coefficient of regression of rate on time was significant at the 2% level, consequently the original regression line $y = -7.2 + 0.40x$ cannot pass through the origin and may be solved for $y = 0$. When this was done it was found that the line cuts the x-axis at $x = 18$, which suggests that there is a lag period of the order of 18 min between warming the petiole and the resumption of translocation.

Solution of the equation for $x = 60$ min gives $0.28 \pm 0.06$ cm/min for the rate of movement of the front. This is equivalent to 16·8 cm/hr. This value is somewhat lower than the generally quoted one of 50–150 cm/hr (Canny 1960), but Canny makes the point that this range is “rather an outline of the assumptions we are making than a statement of fact”. Canny (1961) found the surprisingly low value of 2 cm/hr for Salix. On the other hand, Porter (1959) found, after supplying a small, highly active dose of $^{14}$C for a few minutes, that activity could be followed in the stem as a band moving at c. 18 cm/hr.
A valid criticism of the method used in this study is that movement is investigated under conditions which themselves are likely to have an influence on its characteristics. A concentration of labelled assimilate is built up in the distal section of the source leaf petiole during chilling (cf. Plate 1). At the time of warming there may well be a very steep concentration gradient at the boundary of the previously chilled section and this gradient would be expected to have, at least, a local effect on the initial rate of movement.

![Graph](image-url)

**Fig. 1.**—Regression of distance down stem at which activity could be detected on time after removal of ice from source-leaf petiole. Equation of the regression line is \( y = -7.2 + 0.40x \).

Canny (1960) has reviewed methods of measuring the so-called rate or velocity of translocation and has pointed out three serious sources of error in methods where velocity is calculated from measurements of distance moved by a front of radioactivity in a given time. These sources are: (1) no estimate is usually made of the time taken for the active substance to penetrate from the site of application to the
transport system; (2) the distance measured from source to front of activity depends on the sensitivity of the detector or, alternatively, on the activity of the tracer dose—this is based on the fact that the profile of activity down a stem is logarithmic; (3) with long-continued application of the tracer the advance of the profile reflects not only the rate of transfer of labelled material but also the rate of entry of label into the system. This source of error is also based on the logarithmic nature of the profile of activity down the stem.

It is considered that the experimental method used in these experiments minimizes the errors due to sources (1) and (3) in that movement does not begin until active material is actually contained within the transport system. Consequently the time taken for it to penetrate from the exterior and its rate of penetration are not relevant to subsequent movement. Error due to source (2) is minimized when experimental conditions are standardized throughout and the final result is understood to apply under these particular conditions rather than assumed to be of general application.

(d) Profile of Activity in Petiole and Stem following Chilling

The profile of activity in the stem under conditions where label is entering at the leaf surface, penetrating to the phloem, and subsequently moving down the stem has been demonstrated as being logarithmic (Canny 1960). It was thus of interest to discover the form of the profile under the conditions of the present experiments. Twelve plants were used. These had seven fully expanded leaves and were carefully matched for size of plant and for stage of development of the apical expanding leaves. The uppermost expanded leaf was used as the source leaf in all plants and received 6.4 μc of 14CO2 over a period of 2 hr. For 30 min prior to the application of 14C, and throughout the 2-hr application period, the petioles of all source leaves were chilled. The experiment was done in the morning, under greenhouse conditions. Temperature was 25–33°C, light intensity 1500–2000 f.c.

At the end of the period of 14C application the ice was removed from the petioles, the petioles rinsed in water at greenhouse temperature, and blotted dry. Plants were harvested after either a further 30 min (10 plants) or 2 hr (two plants). At harvesting the petioles and stems were laid along lengths of cellulose tape and cut into measured 1-cm lengths with a sharp razor-blade. They were then air-dried under pressure. The tissue pieces remained in situ on the cellulose tape during drying which ensured that they remained in serial order.

The dried tissue was checked for activity by direct counting of the surface of the pieces with a Philips electronic counter and scaler, type PW4035. The petiole and stem pieces were then extracted in hot ethanol and re-dried under pressure. The dried extracts and the tissue pieces were then counted. Figure 2 shows typical graphs of the distance–translocation profiles for 30-min and 2-hr periods of translocation.

Logarithmic values of the radioactivity in the petiole sections were plotted against distance and regression lines of the form \( y = a + bx \) were fitted. Analyses of variance showed that the logarithmic graphs of the 30-min profile were linear (at the 1% level) but that those of the 2-hr profile were not so. It is concluded that the
Fig. 2.—(a) and (c) Profiles of activity of hot ethanolic extracts of successive 1-cm sections of petioles and stems 30 min and 2 hr, respectively, after warming the petioles of the source leaves which had been previously supplied with 6.4 μc 14CO2. (b) and (d) Corresponding profiles of activity of these tissue pieces after extraction. U, stem above the source-leaf node. D, stem below the source-leaf node.
distance–translocation profile developed during the first 30 min of movement has a logarithmic form but that this form is lost after 2 hr of translocation. The distance–profile of ethanol-insoluble, active material fixed in the petiole has also a logarithmic shape after 30 min and again this is lost after 2 hr.

These results show that the distribution in the petiole, of both material mobile in the phloem and material used by the phloem cells in metabolic processes or lost by lateral movement to adjacent cells, may present a logarithmic profile. The change of this profile in the ethanol-insoluble fraction with time suggests that the very rapid exchange between mobile material and storage cells shown for willow by Peel and Weatherley (1962) is also typical of soybean.

The 30-min and 2-hr profiles for mobile material approximate in shape those shown by Whittle (1964a) for Pteridium, and seem to conform to the “wave” and “diffusion” profiles discussed by Canny and Phillips (1963). The results show the same type of variability which was recorded by Whittle (1964a) for Pteridium rachis. It is not known whether this variability is due to the experimental method or represents the true state in the phloem.

Comparison of 30-min profiles in upper and lower stem shows that the main front of downward-moving material has moved further in 30 min than that moving upward. This observation suggests that these fronts are moving at different velocities which may be associated with differences in the sizes of the sinks to which they are moving. In a previously reported experiment (Thrower 1962) the effective “size” of the radical sink was increased when deprived of source of translocate by defoliation. Under these conditions the velocity of downward-moving label was also increased.

(e) **Lag Period associated with Resumption of Translocation following Chilling**

Calculations of the regression of distance on time (Fig. 1) suggested that a lag period of the order of 18 min existed between warming the petiole and the resumption of translocation. This was experimentally tested by feeding plants with $^{14}$CO$_2$ whilst the petioles were chilled, then warming the petioles, and harvesting at short intervals thereafter.

Forty plants, each with five fully expanded leaves, were used in this experiment. These plants were treated in eight groups. All source-leaf petioles were first chilled for 30 min, and chilling was continued throughout a 2-hr period when $^{14}$CO$_2$ (5 μc per plant) was supplied to the source leaves. The petioles were then warmed and, after allowing translocation to proceed for short periods ranging from 5 to 20 min, were harvested and radioautographed. Table 1 gives details of the light intensities and air temperatures prevailing during the experiment. Movement of labelled assimilate was assessed visually by inspection of the radioautographs and was found to occur in 50, 90, 30, and 70% of petioles for periods of translocation of 5, 10, 15, and 20 min, respectively.

These results show that resumption of translocation after warming may be rapid and occur within 5 min. They also show that the response is markedly variable. This variability is similar to that occurring in the measurement of rate of translocation and indeed will be a contributing factor. The degree of variability suggests
that factors such as temperature or humidity may be influencing results. Table 1 shows that during treatment of some groups temperatures of 41-42°C obtained and, although there seems to be no direct relationship between the values for the lag period and the temperatures recorded during the experiment, it is felt that at such high temperatures translocation may well be erratic.

Clor, Crafts, and Yamaguchi (1962, 1963) have shown that translocation and movement of assimilate from phloem to xylem may be considerably affected by high humidity and again this may well be a factor playing a part in the production of the present results.

**Table 1**

**CONDITIONS OBTAINING DURING INVESTIGATION OF THE LAG PERIOD ASSOCIATED WITH RESUMPTION OF TRANSLLOCATION AFTER A CHILLED PETIOLE WAS BROUGHT TO AIR TEMPERATURE**

<table>
<thead>
<tr>
<th>No. of Plants Treated in Each Group</th>
<th>Time Allowed for Translocation after Warming the Chilled Petiole (min)</th>
<th>$10^{-3} \times \text{Light Intensity during Experiment (f.c.)}$</th>
<th>Air Temperature during Experiment ($^\circ$C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>5</td>
<td>2-3</td>
<td>29·5</td>
</tr>
<tr>
<td>6</td>
<td>5</td>
<td>2-3</td>
<td>29·0</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
<td>2-3</td>
<td>38·5</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
<td>2-3</td>
<td>35·0-41·5</td>
</tr>
<tr>
<td>5</td>
<td>15</td>
<td>2-3</td>
<td>34·0</td>
</tr>
<tr>
<td>5</td>
<td>15</td>
<td>2-3</td>
<td>38·0-42·0</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>2-3</td>
<td>35·0-38·0</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>1·3-1·5</td>
<td>28·0-29·0</td>
</tr>
</tbody>
</table>

In three plants a check was made for completeness of utilization of the $^{14}$CO$_2$. At the end of a 125-min exposure period the experimental leaves were taken from the bottles in which they had been exposed to $^{14}$CO$_2$, and the bottle mouths quickly covered with aluminium foil. These bottles were then immediately applied to fresh leaves on other plants. After 30 min these leaves were harvested and dried for radioautography.

The radioautographs showed that after 2 hr a small but constant amount of radioactive gas remained unused. Previously it has been shown (Thaine, Ovenden, and Turner 1959) that under normal conditions the labelled CO$_2$ from 1 mg of Ba$^{14}$CO$_3$ is all used within 2 hr. The present result suggests that prevention of translocation of labelled assimilate from the leaf resulted in reduced photosynthetic incorporation of $^{14}$CO$_2$.

*(f)* Influence of the Source Leaf on Translocation following Chilling

The technique of chilling and warming was further used in an experiment designed to discover the influence of the source leaf upon movement of assimilate in the stem. If a section of stem were chilled whilst $^{14}$CO$_2$ was being supplied, labelled assimilate should move out of the leaf and down the stem to the chilled section. If
the source leaf were then cut off and the stem warmed, any activity subsequently found below the previously chilled region would have moved there in the absence of the source leaf. This was tested in a preliminary experiment with 12 plants, and it was found that there was no further movement down the stem of plants from which the source leaf had been removed. This result was in contrast to the control plants in which movement was manifest in five out of six plants. The wounding effect of cutting off the source leaf possibly may have been responsible for this result.

<table>
<thead>
<tr>
<th>Treatment Group</th>
<th>Treatment</th>
<th>Plants showing Activity in Stem (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Stem warmed, 1 hr allowed for translocation, then plants harvested, dissected, and dried for radioautography</td>
<td>Immediately above Chilled Region: 100, Below Chilled Region: 70</td>
</tr>
<tr>
<td>Source leaf cut off</td>
<td>Source leaf cut off immediately before stem was warmed; 1 hr then allowed for translocation before plants were harvested</td>
<td>Immediately above Chilled Region: 100, Below Chilled Region: 20</td>
</tr>
<tr>
<td>“Defoliated”</td>
<td>All leaves removed except uppermost source leaf, which was isolated by chilling for 30 min and during the following 1 hr translocation period when the stem was warmed</td>
<td>Immediately above Chilled Region: 100, Below Chilled Region: 80</td>
</tr>
<tr>
<td>“Leafy”</td>
<td>Treatment as above, with all leaves intact</td>
<td>Immediately above Chilled Region: 100, Below Chilled Region: 10</td>
</tr>
</tbody>
</table>

rather than the absence of the source leaf. To obviate this possibility the source leaf was left intact when the experiment was repeated, but its petiole was chilled to prevent further movement out of the leaf into the stem. Finally, the effect of differing concentration gradients in the stem was tested by defoliating one group of plants (with the exception of the uppermost, source leaf) 24 hr prior to applying $^{14}$CO$_2$. Forty plants with five expanded leaves were used. Ten of these plants had all mature leaves but the uppermost removed 24 hr before treatment. In all plants the stem for a distance of 10 cm below the source leaf node was chilled for 30 min then throughout a 2-hr application of $^{14}$CO$_2$ to the source leaf. Subsequent treatments given in each case to 10 plants and the distribution of activity in these plants as a result of the treatments are set out in Table 2. All the plants were harvested at the conclusion of the hour allowed for translocation, dissected, dried, and radioautographed. Movement past the chilled section was assessed visually from the radioautographs.

Uptake of labelled assimilate and movement down to the chilled region occurred in all plants. Cutting off the source leaf prevented further movement in 80% of
plants so treated. When the source-leaf petiole was chilled ("leafy" treatment group) 90% of the plants showed no further movement, suggesting that it is the absence of the source leaf rather than a wounding effect of cutting which has inhibited movement. In the "defoliated" plants, however, the inhibitory effect of isolating the source leaf is shown by only 20% of plants, and is thus comparable with the "control" group with source leaf intact. This result strongly suggests that the effect of increasing the concentration gradient between upper stem and root by cutting off the four lower leaves has cancelled the effect of isolating the source leaf from the upper stem. As the source leaf is the only expanded leaf left on these plants an alternate sucrose supply is necessary if continued movement of sugars down the stem is to occur after isolation of the source leaf. The suggestion of Peel and Weatherley (1962) that storage carbohydrates may be rapidly mobilized and moved to the phloem provides a possible means by which the sucrose content of the phloem might be maintained. Apparently a steep concentration gradient mediates the changeover to the alternate sucrose source. Transections of soybean stem and petiole reveal copious starch so that the supply of storage carbohydrate would be adequate for the operation of this mechanism.

The inhibition of translocation in "leafy" plants with the source leaf isolated suggests that a propulsive effect of the accumulated sugars in the source leaf is important to the movement of sugars already in the vascular traces originating from this leaf under conditions where the concentration gradient in these traces is not abnormally increased. The promotion of translocation (to "control" levels) in "defoliated" plants with source leaf isolated suggests that the attractive effect of the root is an equally strong force in moving material down the vascular tracts of the stem.

IV. Discussion

The results presented here support the view that translocation of sugars is retarded at low temperatures. The low-temperature effect has been shown to be reversible, and translocatory processes are resumed after only a short period at the higher temperature. This prompt reversibility would be expected if either or both of the possible processes postulated by Esau, Currier, and Cheadle (1957), namely increased viscosity or depressed respiratory activity, were operative in retarding translocation at low temperatures.

The logarithmic shape of the profile of activity of labelled material in the stem after application of label for short terms appears to be well established. It is significant that the profile after chilling also takes this form and that the distribution of fixed label in the stem should be of similar shape.

The difference in velocity of the upward- and downward-moving components of the labelled translocation stream from the source leaf emphasizes the importance of sink size in determining velocity of movement. Additional evidence for this concept comes from defoliation experiments such as that reported previously (Thrower 1962) and that described in this paper. Nelson and Gorham (1957) and Nelson (1962) have demonstrated both for soybean and Pinus the association between greater root fresh weight and increased translocation. The present results suggest that the sink size is more important than a continued photosynthetic supply of carbohydrate in determining the characteristics of movement to a sink under normal
conditions. Rapid mobilization of storage carbohydrate can apparently replace the source leaf as the effective supply of translocate.

The degree to which experiments on rate of translocation are meaningful has been discussed by Canny (1960) and the necessity for critical interpretation of such experiments is very apparent. However, the observation that labelled molecules travel a certain distance within the plant in a certain time requires an explanation of the mechanism whereby they do so, even though it is inadvisable to draw any general conclusions about translocatory processes from such data.

There appears to be no evidence that translocated molecules move at any particular steady velocity over short distances, and indeed the variability of observed results suggests that such molecules may well move at widely differing velocities, possibly dependent on the energy relationships in the particular sieve-tube through which they are passing. Whilst profiles of activity of labelled material in stems show an over-all trend, they also show fluctuations in activity over short distances. Such fluctuations may be due to varying velocities. The variation due to sink size are manifest over relatively long distances and would thus be superimposed on such short-term effects.

The supposition that rate of movement of translocate is to some extent connected with sink size suggests a possible explanation for some of the variation in reported values for rate in experiments where the sinks may vary from a colony of aphids (e.g. Canny 1961) to rapidly developing fruits (e.g. Clements 1940; Crafts and Lorenz 1944).

V. Acknowledgments

The author is indebted to Professor J. S. Turner for experimental facilities and to Dr. H. A. Borthwick, United States Department of Agriculture, for continued supply of soybean seed. Thanks are also due to Dr. G. H. Jowett, Statistics Department, University of Melbourne, for advice on statistical procedures.

VI. References


Fig. 1.—Radioautographs showing activity in source leaves and distal parts of petioles of two plants. The sections of these petioles indicated were chilled during $^{14}$CO$_2$ administration for 4 hr. $\times 0.25$.

Fig. 2.—Radioautographs showing activity in source leaves, whole petioles, apices, and stem sections of two plants. The sections of the petioles indicated were chilled during $^{14}$CO$_2$ administration for 2 hr then warmed to air temperature for 2 hr. $\times 0.25$.


