THE EFFECT OF WATER STRESS ON [^{14}C]SUCROSE TRANSPORT IN BEAN PLANTS

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Summary

The passage of ^{14}C through stressed and control bean seedlings has been followed after supply of [^{14}C]sucrose to a primary leaf. The course of synthesis of [^{14}C]sucrose into non-ethanol-soluble compounds in the various plant parts was also investigated. Concomitant measurements of relative turgidity were made either on part of the ^{14}C-treated leaf or on the twin opposite leaf.

When the interval between ^{14}C application and assessment of transport exceeded 45 min, the amount of ^{14}C which moved out of the leaf was found to be much reduced by water stress. With increasing length of translocation interval the disparity in upwards transport between stressed and control plants increased. Downwards transport was also consistently greater in the controls, but the concentration of ethanol-soluble ^{14}C in the lower parts of stressed plants caught up with and eventually surpassed that in control plants. This was at least partly due to the superior rate of synthesis of [^{14}C]sucrose into non-ethanol-soluble compounds in the controls.

The same picture emerged whether absolute values were considered or whether results were expressed as a percentage of the total ^{14}C recovered in all fractions from midvein to root. Since the latter basis eliminates differences due to different rates of uptake and secretion into the phloem, it is concluded that the observed low turgor effects were largely due to an influence on movement within the phloem sieve-tubes themselves.

When the translocation period was shorter than 45 min a stimulating effect of stress was noted, in that a greater proportion of the ^{14}C that had entered the phloem system was found in the lower parts of stressed plants than was the case with controls. The disparity disappeared after 30–45 min. Experiments with steam-girdled plants suggested that ^{14}C movement during this early period in fact took place in the phloem.

The "logarithmic profile" of the distribution of ^{14}C down the plant 2 hr after [^{14}C]sucrose supply was much steeper in stressed than in control plants.

Within an hour of irrigation of wilting plants, a sharp acceleration in downwards transport was observed as compared with both fully irrigated and non-irrigated controls. This occurred long before the relative turgidity of the leaves had regained the control level: subsequently the value for downwards transport declined. [The translocation period itself was constant (45 min) for all treatments in these experiments.] The peak for ^{14}C content of the lower plant parts coincided with a trough in the curve for midvein and petiole. Investigation showed that the results could not be explained on the basis of a disturbance between rate of arrival of sugar and rate of synthesis.

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I. Introduction

Studies on the effect of water stress on translocation in the phloem have been very few in number. In the majority of cases sugar transport has not been measured directly, and the investigations, moreover, have produced conflicting results. While McCune (1958) reported that downward movement of ^{32}P was accelerated by soil moisture stress, Wilson and McKell (1961) on the contrary concluded that ^{32}P transport was decreased. Basler, Todd, and Meyer (1961) found retardation of 2,4-dichlorophenoxyacetic acid transport in plants of low turgidity. Some data derived from direct measurements of the relationship between diffusion pressure deficit and translocation of photosynthate in sunflower were presented by Wiebe and Wihrheim (1962); and Roberts (1964) has recently described similar experiments with a woody species, the yellow poplar. Though in some respects the observations to be reported here confirm, and extend, these last two investigations, there are some important differences. Moreover, our work contributes a number of new findings, notably in demonstrating the influence of length of translocation period on the nature of the observed effect of stress; and the interesting events that occur during the course of recovery from wilting.

II. Material and Methods

Bean plants (*Phaseolus vulgaris* cv. Brittle Wax) were grown in soil in a light room at 25°C (photoperiod 14 hr light, 10 hr dark). The fluorescent light source produced an intensity of 1000 f.c. at the level of the upper leaves. Daily irrigation maintained the soil moisture tension at a value below 0·8 atm in the case of control plants. Irrigation ceased 5 days before the experiment in the case of stressed plants.

A drop (0·01 ml) of uniformly labelled [^{14}C]sucrose solution (specific activity 10–13 mc/m-mole sucrose) containing a small amount of detergent and boric acid to assist in spreading and absorption (Nelson and Gorham 1957) was applied to the lower surface of a primary leaf within an area defined by a tygon ring, about 10 mm to one side of the midvein. The ring was covered with transparent tape to reduce evaporation. After various time intervals and treatments (during which light and temperature conditions were as described above) the leaf area within the ring was removed with a punch and discarded. The rest of the plant was divided into sections which were freeze-dried, ground, and extracted with three lots of boiling 85% ethanol. Aliquots of the extract were evaporated in planchets and counted, self-absorption being corrected for by means of a standard curve. The data presented are for *total* ^{14}C in each plant section.

In all experiments each treatment (or translocation period) was replicated four or five times, each replicate being analysed individually.

In certain experiments the residual plant material after ethanol extraction was examined for non-ethanol-soluble ^{14}C. It was first extracted three times with boiling 10% HCl for 1 hr, then washed and re-extracted with cold 24% KOH for 16 hr. After further washing the residue was extracted with acetolysing reagent according to the procedure of Schramm and Hestrin (1954). Each extract was examined for radioactivity by gas-flow counting.

Relative turgidity measurements were performed, either on the ^{14}C-treated leaf or on the leaf opposite, by the method of Barrs and Weatherley (1962).

III. Results

(a) *Effect of Stress on the Progress of Translocation*

(i) *Translocation Periods in Excess of 45 min*

When the translocation period exceeds 45 min, water stress drastically reduces the amount of applied [^{14}C]sucrose which is translocated out of the leaf. This emerges from the results for the experiments reported in Figure 1 and Tables 1 and 2. These

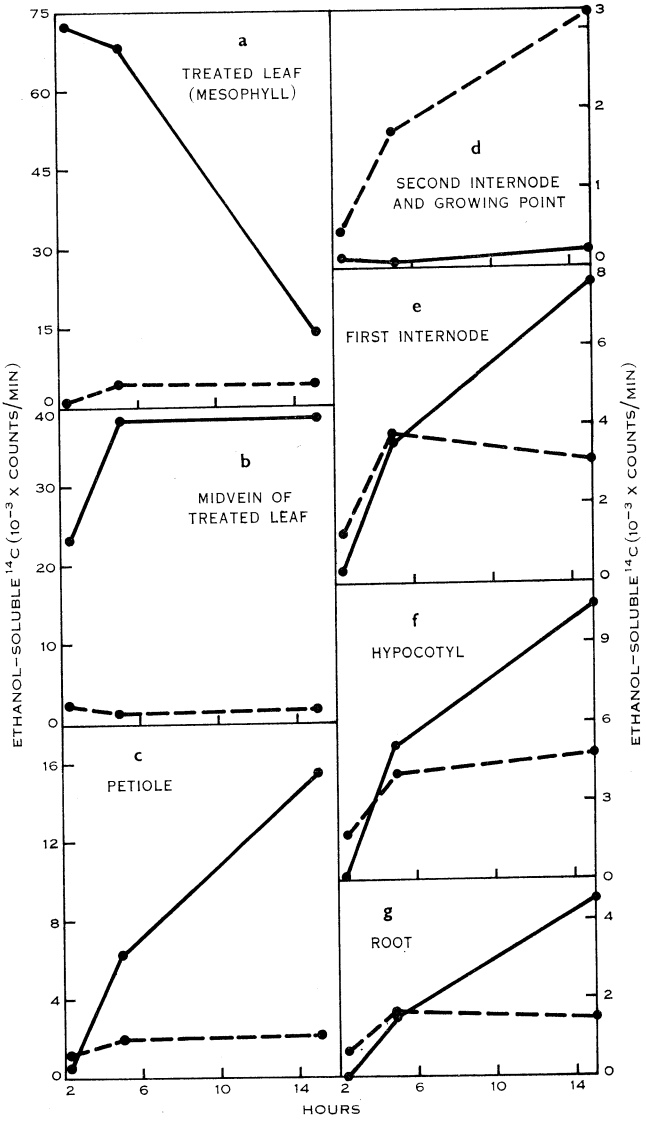

Fig. 1.—Changes with time in the distribution of ethanol-soluble ^{14}C through bean plants after treatment of primary leaf with [^{14}C]sucrose. The experiment was performed in quintuplicate. – – – – Fully irrigated. ——— Under water stress.

TABLE 1

INFLUENCE OF WATER STRESS ON THE DISTRIBUTION OF ETHANOL-SOLUBLE ^{14}C THROUGH BEAN PLANTS AT VARIOUS TIMES AFTER APPLICATION OF [^{14}C]SUCROSE TO PRIMARY LEAF

The experiments were performed in quintuplicate

1	2	3	4	5	6	7	8	9	10	11
			^{14}C as Percentage of Total ^{14}C in Midvein to Root							
Translocation Period (hr)	Treatment	^{14}C Translocated* (%)	Midvein	Petiole	Second Internode and Growing Point	First Indernode	Hypocotyl	Root	Relative Turgidity (%)	Soil Moisture Tension (atm)
Experiment 1										
2·5	Stressed	3·3	82·9	8·1	4·1	2·6	1·5	0·6	70·6	14·5
	Control	51·2	33·6	16·0	5·4	16·9	22·6	5·5	85·1	0·2
5·0	Stressed	29·3	57·4	11·5	0·1	10·4	18·4	7·9	71·2	11·2
	Control	69·4	13·8	13·4	6·4	25·2	33·9	15·5	86·6	0·3
15·0	Stressed	37·2	35·5	14·6	0·8	12·1	24·6	15·3	65·7	14·5
	Control	67·4	12·7	13·0	20·2	14·5	25·2	9·8	83·1	0·2
Standard error	Stressed Control	6·1	6·9	2·7	3·0	2·8	5·6	3·5	2·3	1·8 0·02
Experiment 2						First Internode plus Hypocotyl				
0·75	Stressed	30·7	34·3	8·4	18·0	10·5		28·7	67·8	17·0
	Control	33·6	31·3	15·9	17·2	24·8		10·5	89·7	0·6
3·0	Stressed	35·0	47·9	31·4	1·7	12·1		7·2	62·2	17·0
	Control	78·0	18·7	8·9	2·0	43·0		27·1	86·0	0·5
15·0	Stressed	67·2	15·2	18·5	4·2	28·0		33·9	67·9	16·7
	Control	86·0	7·9	13·6	15·6	35·2		27·5	90·3	0·5
Standard error	Stressed Control	6·4	5·3	4·8	4·3	4·5		3·0	3·0	0·7 0·1

* ^{14}C translocated out of leaf as percentage of total ^{14}C in plant.

experiments involved 30 plants each. Samples of five normal and five stressed plants were harvested at various intervals after treatment with [^{14}C]sucrose. At the moment of harvesting, relative turgidity measurements were performed on the leaves opposite to those treated. It will be seen (Table 1, column 10) that the relative turgidity of the stressed plants was consistently below that of the controls.

Figure 1 and Table 2, column 3, show the *absolute amounts of ethanol-soluble* ^{14}C recovered from the different plant parts after the various translocation periods.

TABLE 2

DISTRIBUTION OF ETHANOL-SOLUBLE, HCl-SOLUBLE, KOH-SOLUBLE, AND CELLULOSE ^{14}C THROUGH STRESSED AND NORMAL BEAN PLANTS AT VARIOUS INTERVALS AFTER APPLICATION OF [^{14}C]SUCROSE TO A PRIMARY LEAF

Values given are counts per minute. The experiment was performed in quintuplicate

1	2	3		4		5		6	
Plant Part	Translocation Period (hr)	Ethanol Extract		HCl Extract		KOH Extract		Cellulose	
		Stressed	Control	Stressed	Control	Stressed	Control	Stressed	Control
Leaf	0·75	1,240	890	0	0	165	260	0	0
	3·0	8,540	1,880	515	340	210	415	0	0
	15·0	3,220	3,330	690	1290	300	330	0	45
Standard error		1560		180		65		9	
Stem	0·75	76	471	0	0	175	190	0	0
	3·0	2,780	19,250	110	2,110	210	540	0	730
	15·0	19,190	20,350	450	16,900	490	3,790	340	9,680
Standard error		3060		1250		425		850	
Root	0·75	190	110	0	0	170	170	0	0
	3·0	190	11,690	0	2,600	170	530	0	680
	15·0	15,160	14,000	2,400	15,900	460	4,790	430	10,350
Standard error		1700		1740		430		940	

Several important points emerge. Firstly, entry of [^{14}C]sucrose from the treated spot into the rest of the leaf blade and midvein was apparently enormously greater in the stressed plants than in the controls (Figs. 1*a* and 1*b*). In the case of the mesophyll fraction the difference lessened with time. In spite of the apparently higher ^{14}C concentration in the leaves of stressed plants, translocation both upwards and downwards during the first $2\frac{1}{2}$ hr was much greater in the control plants (Figs. 1*d*, 1*e*, 1*f*, 1*g*).

With the passage of time the amount of ^{14}C recoverable from the lower parts of the stressed plants first drew level with, then actually exceeded that recoverable from the control plants (Figs. 1*e*, 1*f*, 1*g*). Translocation upwards, however, was

very much greater throughout in the control plants. Negligible upwards translocation occurred in the stressed plants (Fig. 1*d*).

Some of the effects brought out in Figure 1 might have been due to an influence of water stress on sugar uptake in the leaf and secretion into the phloem, rather than on movement within the phloem sieve-tubes themselves. In Table 1 the ^{14}C detected is expressed as a percentage of the total ^{14}C recovered from all the fractions midvein to root, i.e. as a percentage of the sugar that is either present within, or that has already been translocated through, the phloem. Differences due to different rates of uptake and secretion into the phloem have thus been eliminated.

It may be seen in Table 1 that the value for the midvein was consistently higher in the case of the stressed plants. Translocation to the upper stem was relatively greater in the control plants, and this disparity increased markedly with time. Translocation downwards was also relatively greater in the control plants at first. In this case, however, the disparity *decreased* with time, and in the final period the percentage of the [^{14}C]sucrose recovered from the root was actually higher in the stressed plants.

The picture obtained when the results are considered on this basis is thus very similar to that emerging from a consideration of the absolute values (Fig. 1). This would imply that the observed effects of low turgor are largely due to an influence on phloem translocation itself, and not on secretion into the phloem.

The figures for experiment 2 (Table 1) confirm those of experiment 1 with the interesting exception of the initial 45-min period, not examined in experiment 1. During this period significantly more ^{14}C appeared to reach the roots (column 9) of stressed than of normal plants [see Section III(*a*)(ii) below].

The possibility that different rates of synthesis of ethanol-soluble ^{14}C into polysaccharides might be contributing to the differences between stressed and normal plants was investigated in the second experiment. After ethanol extraction the residual plant material was further analysed for hot 10% HCl-soluble, cold 24% KOH-soluble, and acetolysed cellulose fractions. The results of the experiment are shown in Table 2.

It will be seen that, as far as the HCl-soluble and acetolysed cellulose fractions are concerned, there was virtually no synthesis during the first period. There is evidence for synthesis in all parts of the control plants during the second period, almost exclusively in the HCl-soluble fraction. During the third period synthesis is indicated in all plant parts in both groups of plants, but always more markedly in the non-stressed controls.

The figures for the KOH-soluble fraction suggest that there was, in fact, synthesis of some alkali-hydrolysable compound in all plant parts even during the first 45 min. In the leaf this fraction did not increase with time. Moreover, there was no difference between stressed and control plants. In stem and root there was a tendency for the fraction to increase with time, though marked synthesis is only evident in the figures for the control plant in the final period.

Inhibition of synthesis under water stress can thus account for the finding that the values for ethanol-soluble ^{14}C in the lower parts of stressed plants caught up with, and even outstripped, those for controls (Table 2, column 3, and Fig. 1).

(ii) *Translocation Periods under 45 min*

Table 3 gives the results of two experiments in which groups of plants, both stressed and control, were analysed at 15-min intervals after application of [^{14}C]sucrose to a primary leaf. The surprising result is demonstrated that, in contrast to the longer translocation periods discussed above, during the first 15–30 min a significantly larger proportion of the ^{14}C that entered the transport system appeared to reach the

TABLE 3

INFLUENCE OF WATER STRESS ON THE DISTRIBUTION OF ETHANOL-SOLUBLE ^{14}C THROUGH BEAN PLANTS AT SHORT INTERVALS AFTER APPLICATION OF [^{14}C]SUCROSE TO PRIMARY LEAF

The experiments were performed in quadruplicate

1	2	3	4	5	6	7	8
Translocation Period (min)	Treatment	^{14}C as Percentage of Total ^{14}C in Midvein to Root				Relative Turgidity (%)	Soil Moisture Tension (atm)
		Midvein	Petiole	Second Internode and Growing Point	First Internode plus Hypocotyl plus Root		
Experiment 1							
15	Stressed	42·0	1·1	1·5	55·5	70·3	14·1
	Control	68·8	4·0	3·9	20·4	95·7	0·2
30	Stressed	26·9	8·3	4·7	60·2	67·9	14·6
	Control	43·2	14·6	4·1	38·0	93·9	0·2
45	Stressed	52·1	3·8	16·0	25·6	66·9	14·9
	Control	42·2	22·4	6·7	28·8	94·8	0·2
Standard error	Stressed	9·3	3·2	4·0	8·4	1·4	0·5
	Control						0·07
Experiment 2							
15	Stressed	36·8	7·8	12·5	43·0	72·9	12·0
	Control	45·8	10·1	21·1	23·0	92·2	0·2
30	Stressed	58·4	6·0	17·0	18·7	68·5	11·9
	Control	32·1	4·6	18·0	45·3	92·5	0·3
Standard error	Stressed	6·7	1·5	4·5	6·6	3·1	0·3
	Control						0·04

lower parts of stressed plants as compared with controls. This is clearly shown in column 6, where the values for ^{14}C in lower stem and root, expressed as a percentage of total ^{14}C in all fractions midvein to root, were significantly higher in the case of stressed plants during the first two periods of experiment 1 and the first period of experiment 2. With passage of time the disparity disappeared.

Conversely, the amount of ^{14}C remaining in the midvein and petiole (columns 3 and 4) was higher in the case of the controls.

Since the effect of water stress on translocation thus seemed to be qualitatively different during the period immediately after ^{14}C application as compared with later

periods, girdling experiments were carried out to check whether ^{14}C movement during this early period did in fact take place in the phloem. A steam girdle was applied 30 min before ^{14}C treatment commenced. Translocation was assessed after 15 and 30 min. It was found that the girdle drastically reduced translocation into all the plant parts analysed. This result strongly suggests that the ^{14}C did indeed move in the phloem.

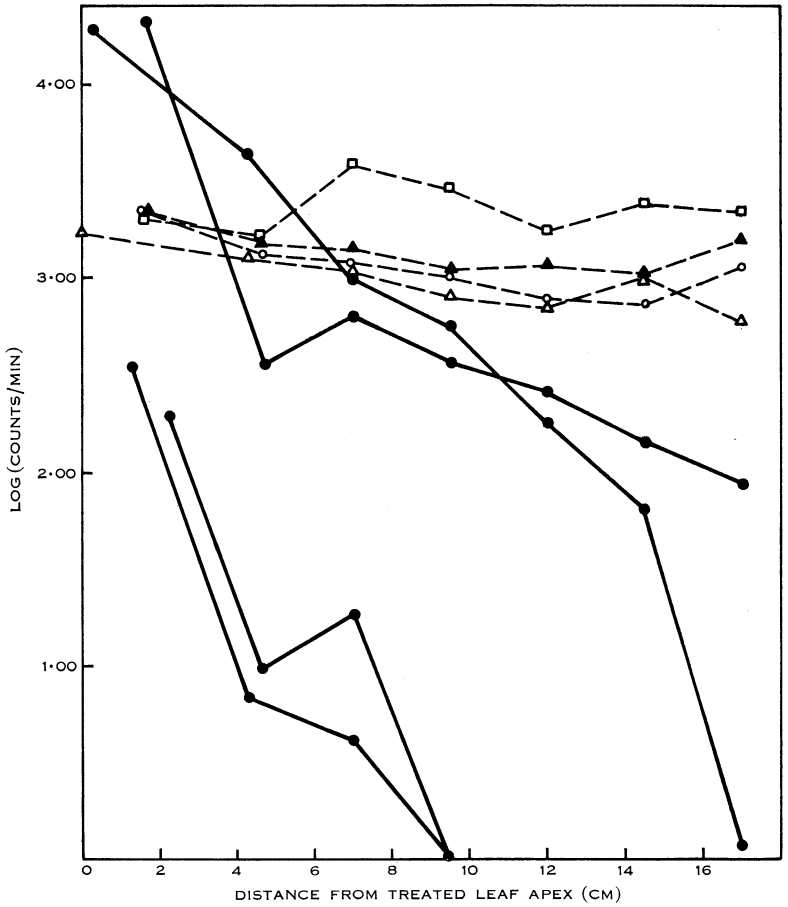

Fig. 2.—Logarithmic profiles of distribution of ^{14}C from midvein of treated leaf to root 2 hr after application of [^{14}C]sucrose to primary leaf of bean plants. – – – – Fully irrigated. ——— Under water stress.

It will be noticed in Table 3 that with the passage of time, the percentage of ^{14}C recovered from the stem and root (column 6) appeared to decrease in the stressed plants. Investigations showed that there was insufficient synthesis of ^{14}C into non-ethanol-soluble compounds to account for this effect.

(*b*) *Effect of Water Stress on the "Logarithmic Profile"*

Canny (1961) came to the conclusion that the "logarithmic profile" (i.e. the graph obtained if the logarithm of the ^{14}C concentration is plotted against distance from the site of application) is a fundamental symptom of the translocation process.

Figure 2 shows the results of an experiment in which we investigated the effect of water stress on this profile. For this purpose translocation was allowed to proceed for 2 hr after application of the radioactive drop. The midvein, petiole, stem, and hypocotyl were then divided into 1-cm sections and analysed. The profile obtained for the control was flat compared with others reported in the literature. Interestingly, stress caused a sharp steepening of the profile (see Fig. 2). This possibly reflects slower movement through the sieve-tubes.

(c) *Course of Recovery of the Phloem Transport System after Irrigation of Wilted Plants*

The results of two typical experiments which were carried out to study the course of recovery from water stress are given in Figure 3 and Table 4. In the first

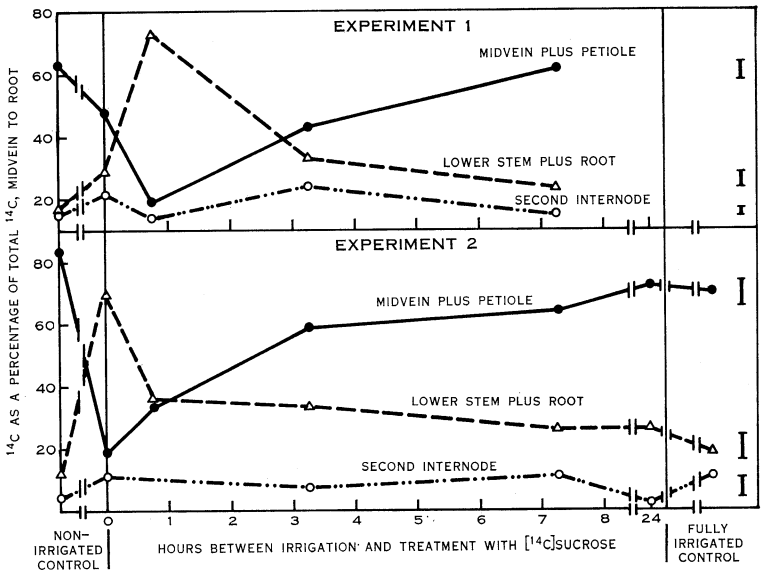

Fig. 3.—Effect of time interval between irrigation of wilting plants and ^{14}C treatment on the distribution of ^{14}C through bean seedlings. In all cases the plants were analysed 45 min after application of [^{14}C]sucrose to the primary leaf. The experiments were performed in quadruplicate. The vertical lines on the right indicate the standard error.

case irrigation of the bean plants had ceased 5 days before the experiment. The plants were in a wilting condition. [^{14}C]Sucrose was applied to one set of plants without further irrigation. These plants served as the stressed control. The other plants were watered, and [^{14}C]sucrose was applied at the following intervals after irrigation: 0 (i.e. simultaneously with irrigation), 45, 195, and 435 min. *In all cases the plants were analysed 45 min after treatment with ^{14}C.*

The second experiment was similar except that the treatments were extended to include an extra time interval for recovery—^{14}C application 24 hr after irrigation—and a second set of control plants which had never undergone water stress but had been fully irrigated throughout.

Since experiment had shown that negligible amounts of ^{14}C migrated across the midvein, relative turgidity measurements were made on the same leaf as that to which ^{14}C was applied, on the opposite side of the midvein. The results may be seen in Table 4, column 4.

TABLE 4

COURSE OF RECOVERY OF TRANSPORT SYSTEM AFTER IRRIGATION OF WILTED PLANTS

In all cases the bean plants were analysed 45 min after applications of [^{14}C]sucrose to the primary leaf. Relative turgidity was determined at the same time on the same leaf, on the opposite side of the midvein. The experiments were performed in quadruplicate

1	2	3	4
Time between Irrigation and Treatment with ^{14}C (min)	Total ^{14}C in Treated Leaf (including midvein) (counts/min)	Total ^{14}C in Rest of Plant (counts/min)	Relative Turgidity (%)
Experiment 1			
Non-irrigated control	52,070	740	60·6
0	705	606	68·0
45	365	2,826	68·3
195	387	605	89·0
435	3,684	801	86·9
Standard error		440	2·0
Experiment 2			
Non-irrigated control	11,450	288	64·3
0	619	457	65·3
45	1,418	353	76·6
195	293	116	86·1
435	498	278	91·6
1440	703	324	90·8
Fully-irrigated control	389	107	92·3
Standard error		77	2·2

Figure 3 shows the results plotted as a percentage of the total ^{14}C recovered from all the fractions midvein to root. A most interesting effect is clearly brought out: within a relatively short time after irrigation (second period in the case of the first experiment, first period in the second) transport to the lower stem and root apparently soared to a peak value. Subsequently, as relative turgidity climbed towards the value for fully irrigated plants (see Table 4, column 4), the value for downwards transport declined towards the level of the fully irrigated control. It should again be stressed that in all cases the translocation period itself was constant (45 min). The values for non-irrigated and fully irrigated controls are approximately equal, confirming that stress is not inhibitory during the first 45 min after ^{14}C application.

In both experiments this peak in translocation to the lower stem and root coincides with a trough in the curve for the midvein.

The peaks shown in Figure 3 depict ^{14}C translocated downwards relative to ^{14}C present in other parts of the plant. Table 4, column 3, gives *absolute* values for translocation, and it will be noted that the peaks are visible here too. The effect is especially marked in experiment 1 (45 min) but is also detectable in experiment 2 (0 min).

Table 4 also shows that, as before, very much more [^{14}C]sucrose was detected in the blade of the stressed leaves than in those of the plants at full turgor (column 2). Within the first period after irrigation, however, this effect of water stress had nearly disappeared. This result is the more striking in that the relative turgidity of the leaf was at this time still very low, and only regained the control value after 3–4 hr (see column 4).

No appreciable difference in amount of synthesis of [^{14}C]sucrose into non-ethanol-soluble substances could be detected between the groups of plants in this relatively short-term experiment.

IV. Discussion

One of the interesting results emerging from this investigation is that, during the period immediately after application of [^{14}C]sucrose to a leaf, the effect of low turgor on translocation is qualitatively different to that seen in subsequent translocation periods. During the first 30–45 min a larger proportion of the ethanol-soluble ^{14}C that had entered the transport system was found in the lower parts of stressed plants than was the case with controls. Different rates of synthesis of sucrose into non-ethanol-soluble compounds could not explain this effect, since analysis showed that no appreciable synthesis of supplied sucrose occurred within this time period either in control or in stressed plants. On the other hand, when the translocation period exceeded 45 min, the proportion of ^{14}C present in the lower plant parts was far less in the case of water stress. Further, the absolute amount of [^{14}C]sucrose transported out of stressed leaves was much less than in the case of controls (Fig. 1). The depressive effect of stress on carbohydrate transport over relatively long translocation periods is in agreement with the observations of Wiebe and Wihrheim (1962) and Roberts (1964).

The greater transport out of control leaves over the longer translocation periods is all the more striking in view of the fact that the absolute amount of [^{14}C]sucrose recoverable from the leaf, after removal of the ringed area where the drop was applied, was vastly higher in stressed plants. This latter effect is under detailed investigation, and will be discussed more fully in a further publication.

While in control plants [^{14}C]sucrose was translocated both upwards and downwards from the point of application, in stressed plants upwards movement was virtually abolished. A possible explanation is that the apical growing point, normally a very effective "sink" for translocated sugar, was highly sensitive to water stress. It is of considerable interest that Roberts (1963) reported a higher percentage of labelled photosynthate moving upwards in poplar trees subjected to water stress. He regarded this as the result of strong competition by the apical meristem for the products of

photosynthesis. Wilson and McKell's (1961) data for ^{32}P accord with ours in indicating inhibited upward movement in stressed sunflower plants.

In Figure 1 downwards transport in stressed plants appeared to catch up with, and eventually surpass, that in controls. After 15 hr more ethanol-soluble ^{14}C was detectable in the lower parts of the former group. Synthesis, however, was found to be much more active in the latter case. The flattening of the control curves for root, hypocotyl, and first internode after 5 hr in Figure 1 may represent the achievement of a steady state between rate of arrival and rate of synthesis. In the stressed plants [^{14}C]sucrose continued to accumulate. That the flattening of the control curves was not due to exhaustion of the ^{14}C supply in the leaf is indicated by Table 2—*total* ^{14}C in the lower plant parts continued to rise with time.

Translocation of applied sugar out of the leaf involves uptake of sugar, secretion into the phloem sieve-tubes, and movement *within* the sieve-tubes. Indications have been provided in several experiments that (in addition to any possible effects on uptake and secretion) the inhibitory effect of water stress seen in the longer translocation periods was exerted on movement in the sieve-tubes themselves. Firstly, approximately the same effects of stress emerged from *absolute* values for translocation as from ^{14}C distribution expressed relative to total ^{14}C present in all fractions from midvein to root. The latter basis eliminates differences due to uptake and secretion, since only ^{14}C that is within, or that has passed through, the phloem system is considered. Secondly, the "profile" of ^{14}C along the stem was very much steeper in stressed than in control plants. According to Canny (1961) events in the leaf, such as secretion, do not affect this profile.

Münch's pressure flow hypothesis, if correct, provides a ready explanation for the depressant effect of water stress on movement within the sieve-tubes. Lowered turgor in the leaf might well disturb the hydrostatic pressure gradient through the plant. It is less easy to account for the apparent acceleration of downwards transport observed in stressed plants during the first 30 min after [^{14}C]sucrose supply. The experiments with steam-girdled plants indicated that the ^{14}C was indeed moving in the phloem during this period. Perhaps more than one process is involved in sieve-tube transport (cf. Biddulph and Cory 1965). While mass flow may be depressed by low turgor, possibly another process is less so, and may even be stimulated. This latter process might appear to dominate during the period immediately following ^{14}C application if the sugar in the channel in which it operated became labelled to a detectable degree more quickly than did the sugar in the mass flow channel. Subsequently this process might be masked by the larger amounts of sugar moving by mass flow.

The loss in ^{14}C content seen in the values for the lower parts of stressed plants in Table 3 may have been due to upwards circulation of part of the ^{14}C (Harel and Reinhold, unpublished data).

A very strong acceleration of downwards transport as compared with fully irrigated controls seems to be an almost immediate response when wilted plants are irrigated. This emerges clearly both from absolute values for translocation (Table 4) and from values for the proportion of the ^{14}C within the transport system which reached the lower parts of the plant (Fig. 3). The effect was thus exerted on movement within the sieve-tubes, not on secretion into the latter. It is notable that the spurt

in translocation occurred before the leaves recovered their turgidity. A possibility to be considered was that the level of free sugar in stressed roots was high soon after irrigation because of a disturbance in the balance between rate of arrival of sugar and rate of synthesis. If the transport process recovered more rapidly than did synthesis (shown to be impaired under stress) the free sugar level in the root would rise. This possibility can be rejected, since no appreciable difference in amount of synthesis was detected between stressed and control plants during the first 45 min after ^{14}C application to the leaves. These striking events during the course of recovery from wilting invite further study.

V. Acknowledgment

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