Alterations in Source-Sink Patterns by Modifications of Source Strength[1]

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ABSTRACT

Bean plants, trimmed to a simplified "double source, double sink" translocation system (the paired primary leaves serving as the double source and the paired lateral leaflets of the immature first trifoliate leaf as the double sink) were used to study the magnitude and short-term time course of change in the allocation ratio (partition ratio) of assimilates translocated from the labeled primary leaf to its respective "near" and "far leaflet" sinks in response to an increase or decrease in the source strength of the opposite primary leaf (the "control" leaf). If the rates of net photosynthesis in the two primary leaves were similar, assimilates from the labeled source leaf partitioned to the leaflet sinks in the ratio of 5:1 or higher, the dominant sink being the leaflet "nearer" to the labeled source leaf. If the rate of net photosynthesis in the control leaf was increased substantially above that of the labeled source leaf, the rate of translocation from the labeled source to either the near leaflet sink or far leaflet sink remained unaffected, despite, presumably, a higher translocation rate from the control leaf, and hence a higher phloem pressure gradient (or increased cross-sectional area) in the transport pathway from the control leaf to the leaflet sinks. If the control leaf was excised, thus reducing the source leaf area by about a half, the translocation rate from the remaining source leaf rapidly doubled, the partition ratio becoming equal to unity. If the control leaf was darkened, the partition ratio adjusted to an intermediate value. Although export rates from the labeled source leaf were increased either by excising or darkening the control leaf, the rate of net photosynthesis in the labeled leaf remained constant.

The rate of acropetal translocation from a source leaf to a sink leaf varies with the position of the sink leaf in the phyllotactic sequence and with the ontogenetic stage of both the source leaf and the sink leaf. Complicating the dynamics of this export pattern is the fact that source leaves in orthostichies adjacent to that of the principal source leaf may also contribute assimilates to this leaf, though as may be expected their major export is normally directed to sink leaves in their own respective orthostichies (3, 13, 16, 18).

As part of a series of studies on nutritional traffic patterns in plants, we have investigated the magnitude and time course of change in the patterns of assimilate transport by systematically varying source-sink parameters. For these studies we have used bean plants pruned to a simplified "double source, double sink" translocation system, as shown schematically in Figure 1. Leaflets of the immature first trifoliate leaf usually differ in the amounts of assimilates imported from a given primary leaf. Mullins (16) showed that about 65% of the total assimilates translocated from source leaf A to the immature trifoliate leaf was allocated to the "near leaflet" (A'), 25% to the central leaflet (C'), and the remaining 10% to the "far leaflet" (B'). For trifoliate leaf sinks which were minus the central leaflet, the allocation ratio (or partition ratio) was about 9:1. Thus the partition ratio of assimilates from a given primary leaf is strongly biased to the leaflet sink in the nearer or nearest orthostichy.

What are the controlling parameters of this ratio? To what extent and how rapidly can this ratio be altered by varying the respective source strengths of A and B? Since the putative control which leaf B exerts on the distribution pattern of translocates from A may be expected to be mediated through changes in the export rate from B, to what extent does this rate vary with the photosynthetic rate? The present experiments were carried out to examine some of these relationships.

For purposes of this paper, source strength is equated with the net photosynthesis rate and sink strength with the import rate (22, 23).

MATERIALS AND METHODS

Bean plants (*Phaseolus vulgaris* L., cv. Black Valentine) were grown hydroponically as previously described (20), and were selected for use when 12–13 days old. At this stage, the primary leaves were at or near mature size and maximum export capacity, and the first trifoliate leaf was 5–7% of its fully expanded size and nearing its maximum sink strength (20).

The design of the test plants is shown schematically in Figure 1. On the day prior to an experiment the test plants were pruned to the "double source, double sink" format as shown, the pair of primary leaves constituting the "double source" and the pair of lateral leaflets of the first trifoliate leaf constituting the "double sink". In plants designated as "girdled", the stem was heat-girdled 1 cm below the primary leaf node. The central leaflet of the trifoliate leaf and the apical shoot growth above this leaf were both removed. Thus the translocation system in the girdled plants consisted principally of a pair of source-sink couples: source leaf A to its major and minor sinks A' and B', and source leaf B to its major and minor sinks B' and A'. In the nongirdled plants, these transport couples competed with the mobilizing ability of the root and lower stem sinks. Thus, various levels of sink competition and interaction were explored. Most of our studies to date have been carried out with the more simplified of these systems, namely, the girdled plants.

Translocation rates from A to A' and from A to B' are desig-

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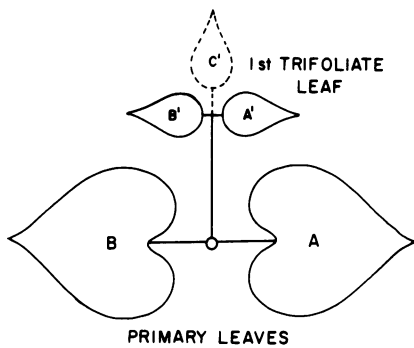[5] To whom correspondence should be addressed.

FIG. 1. Schematic of "double source, double sink" test plant as viewed from above. Plants 12–13 days old. Primary leaves constituted the source leaves A and B; lateral leaflets of the immature first trifoliate leaf constituted the sinks A' and B'. Central leaflets, C', removed. Sinks A' and B', respectively, designated the "near" and "far leaflet" sinks of source leaf A, and B' and A', respectively, the "near" and "far leaflet" sinks of source leaf B.
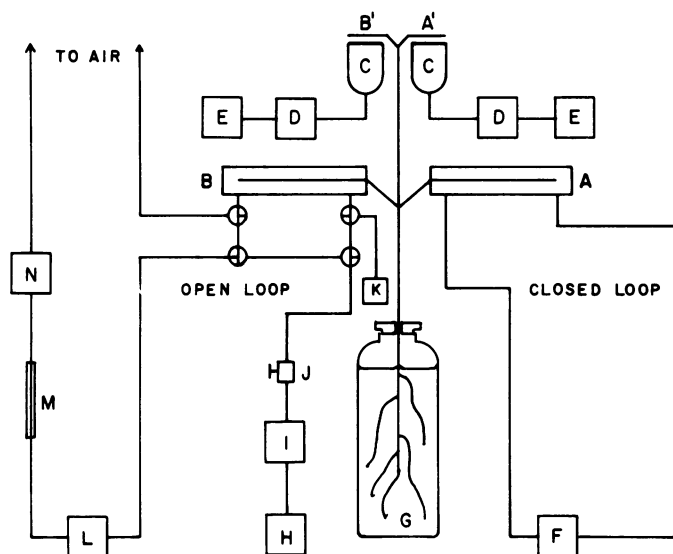

FIG. 2. Schematic of analytical train. Test plant trimmed as in Figure 1. A, cuvette for source leaf A in closed loop; B, cuvette for source-leaf B in open loop; C, Geiger tubes subtending sinks A' and B'; D, ratemeter; E, potentiometric recorder; F, analytical train for maintaining concentration and specific activity of CO_2 constant; G, Hoagland solution, aerated; H, compressed air tank; I, low pressure line regulator; J, microcontrol valve; K, manometer; L, IR gas analyzer; M, flowmeter; N, wet-test flowmeter.

nated $T_{AA'}$ and $T_{AB'}$, respectively, and are given in units of μg carbon transported min^{-1} under steady-rate or near steady-rate conditions. The respective ratio of these rates, the partition ratio, is designated $T_{AA'}:T_{AB'}$. Designation of the source leaves as A or B was strictly arbitrary.

Two series of experiments were carried out. In series 1, the effect of removing leaf B on the rates $T_{AA'}$ and $T_{AB'}$ and on the corresponding partition ratios was studied, holding the net photosynthetic rate of leaf A (P_A) constant. In series 2, the rate of net photosynthesis in leaf B (P_B) was varied relative to P_A, which, as in series 1, was held constant throughout the time course of each experiment. Data relative to the cuvette environments of leaves A and B and the respective rates of photosynthesis established in these leaves are given in Table II, footnote a, and Table III.

The analytical system used in these studies (shown schematically in Fig. 2) permitted simultaneous measurements of both the net rates of photosynthesis in the source leaves A and B and the net

rates of translocation from A to A' and A to B'. Reference should be made to earlier papers for analytical details (7, 20). For source leaf A, a closed loop system was used to permit steady-state labeling of the assimilates; for source leaf B (which was unlabeled), an open loop system was used.

In a test on the comparative accuracy of the two systems, cuvette A was switched to the open loop and cuvette B to the closed loop without altering the position or external environment of either cuvette. Changes observed in the photosynthetic rates were less than 15% for either leaf compared to its rate in the normal mode. The measured rate, therefore, was reasonably independent of the method used to measure it, hence the actually lower rates observed for leaf B than for leaf A during treatment period 1 (Table III) reflect a generally less favorable cuvette environment for B than for A. Constraints imposed by the placement of equipment accounted in part for this difference.

To assure a constant counting geometry, the leaflet sinks were held in special grids close to the end window of a G-M detector. The space between the leaf and the window, about 3 mm in depth, was force-ventilated to prevent transpiration moisture from condensing on the window and thus significantly altering the counting efficiency. From the data showing the ^{14}C-accumulation rates in the target leaflets in cpm/min, the specific radioactivity in the closed loop in μg^{12}C/μCi^{14}C, and the counting efficiency in μCi ^{14}C/cpm, the translocation rates $T_{AA'}$ and $T_{AB'}$ were calculated in units of μg carbon min^{-1}.

RESULTS AND DISCUSSION

Table I summarizes the data from seven experiments (all plants girdled) on the effect of excising leaf B on $T_{AA'}$ and $T_{AB'}$ and on the partition ratio $T_{AA'}/T_{AB'}$ (series 1 experiments). Figure 3 presents the data from one of the experiments showing the time course of compensated translocation following excision of B.

Prior to excision of B, $T_{AA'}$ and $T_{AB'}$ averaged, respectively, 3.82 and 0.88 μg carbon min^{-1} (Table I, parameters 1 and 2), yielding a pre-excision partition ratio of 5:1 (calculated as the average of the individual ratios, not as the ratio of the averaged rates; in the latter case the ratio would be 3.82/0.88 or 4.3:1). Following excision, $T_{AA'}$ declined precipitously during the ensuing 5- to 10-min interval (parameter 7), then reversed and accelerated rapidly, attaining a value usually about 15% higher than its preexcision rate within about 1 h.

Concomitantly $T_{AB'}$, after a time lag of 8–10 min, also increased rapidly, attaining a value equal to $T_{AA'}$ (actually rather consistently exceeding $T_{AA'}$ by about 10%) within 1.5 h (4.91 versus 4.34 μg carbon min^{-1}, Table I, parameters 1 and 2) or a postexcision partition ratio of 0.9:1, parameter 3). At final equilibrium, we consider it likely that this ratio would be equal to unity. The observed deviations from unity probably reflect temporary compensatory increases in T_{AB}' in response to imbalances accruing during the adjustment period following excision. The increase in $T_{AA'}$ from a preexcision rate averaging 3.82 μg carbon min^{-1} to a postexcision rate averaging 4.34 μg carbon min^{-1}, a gain of 0.52 μg carbon min^{-1}, probably reflects the increased rate required to compensate for the loss of translocate to A' from B following its removal.

A point to be noted here is that the compensated translocation to B' was not at the expense of translocation to A'. Instead, the export rate from A, normalized to the total sink, was increased from 8.72 (preexcision) to 18.1 μg carbon min^{-1} (postexcision), an increase of about 100% (Table I, parameter 4). Within the time course of these experiments, no increase in the net photosynthetic rate of A occurred in response to the doubled export rate from A (Table I, parameter 5). We infer (see below) that the entire increase in translocation resulted from an increase in the "translocation efficiency" of A, that is, from an increase in the ratio of carbon translocated from A relative to net carbon fixed by A (T_A/P_A,

Table I. *Effect of Excising Source Leaf B on the Absolute and Relative Translocation*

Rates from source leaf A to its near and far leaflet sinks A′ and B′. Data are the averages of seven plants. Source leaf A steady-state-labeled with $^{14}CO_2$. Plants were girdled.

Parameters	Before Excision of B	After Excision of B
1. Translocation rate from A to A′ ($T_{AA'}$)	3.82 μg C min^{-1}	4.34 μg C min^{-1}
2. Translocation rate from A to B′ ($T_{AB'}$)	0.88 μg C min^{-1}	4.91 μg C min^{-1}
3. Partitioning ratio ($T_{AA'}$:$T_{AB'}$)	5.0:1	0.9:1
4. Translocation rate from A to total sink (T_A)	8.72 μg C min^{-1}	18.1 μg C min^{-1}
5. Net photosynthetic rate of A (P_A)[a]	48.4 μg C min^{-1}	48.7 μg C min^{-1}
6. T_A/P_A	0.19:1	0.39:1
7. Transient inhibition of $T_{AA'}$ in response to excision of B (expressed as %)		34 ± 25%
8. Lag time in response of $T_{AB'}$ to excision of B		8.9 ± 1.6 min

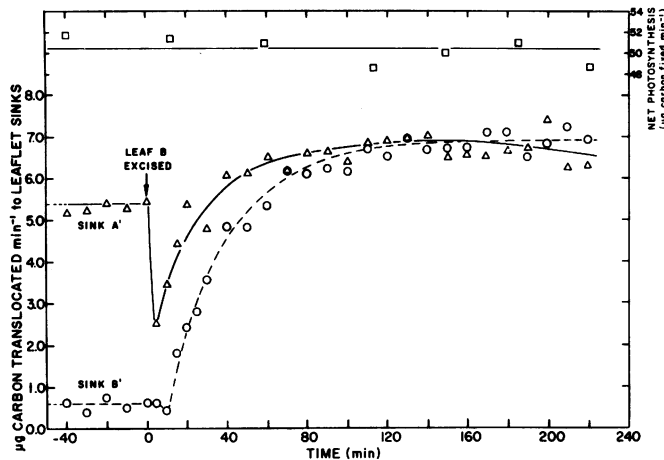[a] P_A constant to within ±6% or better for duration of each experiment.

FIG. 3. Time course of net photosynthetic and translocation rates prior to and following excision of source-leaf B. (□), net photosynthetic rate of source-leaf A; (△), translocation rate from A to A′ (the near leaflet sink for A); (○), translocation rate form A to B′ (the far leaflet sink for A). A preliminary report of some of these data was given by Swanson *et al.* (21).

Table I, parameter 6).

The above data indicate the following: (*a*) that the aggregate translocate from leaves A and B (or the translocate from A alone if B is excised) is partitioned to sinks A′ and B′ in such proportions that each of these sinks receives equal amounts of translocate, yielding an allometric ratio of 1:1; and (*b*) that the total translocate to A′ and B′, in response to a reduction in source size, is maintained more or less constant, with adjustments being made in the T_A/P_a ratio of the remaining source.

Table II summarizes the data from the series II experiments, based on 10 plants (five girdled and five nongirdled). Girdling was without significant effect other than to increase the magnitude of $T_{AA'}$ and $T_{AB'}$ in the girdled plants relative to $T_{AA'}$ and $T_{AB'}$ in the nongirdled plants. The increased acropetal translocation was to be anticipated on the basis that girdling eliminated the roots and the lower stem as major competitive sinks. The partition ratios for the girdled and nongirdled plants during the control period (treatment 1) averaged, respectively, 4.9:1 and 5.5:1, in close agreement with the average control value of 5.0:1 for the series 1 experiments (Table II). Holding P_A constant but increasing P_B (treatment 2) did not significantly change either $T_{AA'}$ or $T_{AB'}$. Hence the partition ratios established during treatment 1 conditions remained unchanged under treatment 2 conditions. Holding P_A constant but decreasing P_B (to below its compensation point—treatment 3) significantly increased $T_{AB'}$ and slightly increased $T_{AA'}$. Hence, the partition ratio was significantly reduced (to average values of 3.4:1 and 2.9:1 for the girdled and nongirdled

Table II. *Effect of Varying the Export Rate from Source Leaf B on the Absolute and Relative Export Rates from Source Leaf A to its Near and Far Leaflet Sinks A′ and B′*

Source leaf A steady-state-labeled with $^{14}CO_2$. Export rate from leaf B varied by varying its photosynthetic rate (P_B), holding photosynthetic rate of leaf A (P_A) constant. See Figure 1 for nomenclature. Data are the averages of five plants in the girdled series and five plants in the nongirdled series; treatment sequence in the order 1, 2, 3 for four plants and 1, 3 for one plant in each series.

Treatment Periods[a]	Translocation Rate				Partition Ratio ($T_{AA'}$:$T_{AB'}$)	
	Girdled		Nongirdled		Girdled[b]	Nongirdled[b]
	$T_{AA'}$	$T_{AB'}$	$T_{AA'}$	$T_{AB'}$		
	μg carbon min^{-1}					
1. ($P_B = P_A$)	3.9	0.82	2.7	0.57	4.9:1a	5.5:1a
2. ($P_B > P_A$)	3.8	0.81	3.1	0.49	4.9:1a	6.3:1a
3. ($P_B \ll P_A$)	4.4	1.29	3.2	1.15	3.4:1b	2.9:1b

[a] Treatment 1: cuvette environments of leaves A and B similar (2,500–3,000 ft-c; CO_2 concentration 340–370 μl/l). Treatment 2: CO_2 concentration of cuvette B increased to 1,300 μl/l. Treatment 3: cuvette B darkened, P_B nominally zero. Throughout treatment periods 1, 2, and 3, P_A remained constant to within ± 6% for each plant. For actual values of P_A and P_B, see Table III. Each treatment period was 1.5–3 h in duration, following isotopic equilibrium.

[b] Mean ratios are the averages of the individual ratios. Means in the same column followed by the same letter are not significantly different at the 1% level.

plants, respectively).

The response to darkening B, therefore, was qualitatively similar to that resulting from excision, but since translocation would be expected to continue from a darkened source leaf at a diminished (or diminishing) rate (15), the compensatory increase required in $T_{AB'}$ would be less than for excision. Consequently, a partition ratio intermediate in value between the control ratio and 1:1 was to be expected, and such was indeed observed. The increase in $T_{AA'}$ required to compensate for the putative decrease in $T_{BA'}$ was too small to be statistically verifiable.

If the decreased ratio is indeed in response to the diminished export rate from leaf B, it follows that this ratio should gradually decline to 1:1 if with continued darkening of B its export rate gradually declines to zero or to a sub-threshold level. We have tested this inference in one preliminary experiment (data not shown). Predarkening of leaf B for 18 h yielded an immediate partition ratio of about 1:1. Thus, sufficiently prolonged darkening of a source leaf appears to be physiologically equivalent to removal.

Although in the girdled plants (characterized by a high source-

to-sink ratio), an increased import rate into the sink leaves was (by inference) fully compensated by a corresponding increase in the export rate from the source leaf (removal of the source leaf in such plants is followed by rapid decay in the rate of entry of labeled translocate into the sink leaves [6]), the relationship in nongirdled plants (characterized by a low source-to-sink ratio) may be considerably more complex. Recent work has shown that in such plants, increased import into the leaf sink is compensated by decreased export to the roots, the total export rate from the source leaf remaining unchanged (Dr. D. R. Geiger, personal correspondence).

Why the partition ratios were unaffected by increasing P_B relative to P_A is unclear. A priori we considered that, associated with the higher photosynthetic rates in B would be higher translocation rates from B, and that associated with these higher rates would be a higher phloem pressure gradient (or an increased cross-sectional area) in the transport pathways from B to both B' and A'. This higher gradient (or increase in pathway area) should tend to restrict translocation from A, particularly from A to B', resulting in an increase in the partition ratio. In point of fact, as noted above, neither $T_{AA'}$ nor $T_{AB'}$ was significantly affected, the partition ratios remaining the same as during the control period. It appears, therefore, that the partition ratios observed under conditions of a balanced source strength are at near an upper limiting value. This relationship should be studied further by imposing higher ratios of P_B relative to P_A (in the present experiments, P_B averaged 1.75 P_A in the girdled series, and 1.55 P_A in the nongirdled, with P_A at or near its light saturation value; Table III).

Similarly puzzling, and perhaps related to these observations, was the finding that reilluminating leaf B, after darkening it for 2-3 h, failed to return the partition ratio to its control value within the usual time limits of these experiments. In a few preliminary experiments, very little if any recovery was exhibited even in 4 h. In general, a decrease in the partition ratio could be affected much more easily than an increase.

Summarizing these data, the following relationships appear evident: (a) although export rates from source leaves A and B may differ, the sum of their pooled translocates allocated to leaflet sinks A' and B' is divided equally between these sinks, such that $T_{AA'} + T_{BA'} = T_{BB'} + T_{AB'}$; (b) to maintain this equality when P_A and P_B are unequal necessitates a disproportionately higher increase in the export rate from the stronger source leaf to its far leaflet sink than to its near leaflet sink; this accounts for the fact that the partition ratio of the stronger source leaf is characteristi-

cally lower than that of the weaker source leaf (this relationship appears independent of the absolute levels of photosynthesis used to achieve the imbalance in source strengths, i.e. higher-than-control versus control, or control versus dark); (c) the partition ratio varies inversely with the degree of imbalance in source strengths, approaching and eventually attaining a lower limiting value of unity for the stronger source leaf as the strength of the other source leaf declines toward zero (or to some threshold level); and (d) increased cross-subsidization (increased transport from B to A' or A to B') does not diminish the main export stream for a source leaf (A to A' or B to B'); i.e. an increase in the photosynthetic rate of B, for example, as in treatment 2 (Table II), though undoubtedly resulting in an increase in translocation to A', did not diminish the main export stream from A to this sink (P_A being held constant). As noted above, this relationship was not anticipated in view of the (putatively) higher phloem pressure gradient, or increased cross-sectional area of the transit pathway, from B to A' associated with the higher $T_{BA'}$. Similar considerations apply to the minor export stream from a source leaf (A to B' or B to A'). These descriptive statements apply specifically to bean and other species with a similar phyllotaxy. Preliminary studies on cotton-wood (three-eights to five-thirteenths phyllotaxies) have indicated significantly more complicated relationships.

An analysis of these relationships would be facilitated if measurements of $T_{BB'}$ and $T_{BA'}$ could have been made concurrently with the measurements of $T_{AA'}$ and $T_{AB'}$ on the same plants. Such measurements, however, would involve major technical difficulties. Tentatively, we have attempted to estimate $T_{BB'}$ and $T_{BA'}$ as follows. Given the net rate of photosynthesis in leaf B for each experimental treatment period (Table III, parameter 2), the (putative) rate of translocation (Table III, parameter 4) was calculated from regression equations determined in a separate series of short-term experiments involving 56 measurements on 18 plants. The regression of translocation rate on photosynthetic rate was found to depend on whether the photosynthetic rate was varied by a series of step increases in light intensity or by a series of step decreases. Step increases yielded the equation $y = 0.17x + 9.8$ ($r = 0.68$), and step decreases, $y = 0.15x + 15$ ($r = 0.55$), where $y = $ total μg carbon translocated $dm^{-2} min^{-1}$ source leaf, and $x = \mu g$ carbon fixed $dm^{-2} min^{-1}$. The value y was then normalized to the actual source leaf area in each experiment and corrected for the proportion of total translocate allocated to A' and B'. Translocation rates from B during treatments 1 and 2 were based on the first equation, and during treatment 3 on the second equation.

Since the sum of the translocate from A and B is divided equally

Table III. *Rates of Net Photosynthesis in Source Leaves A and B and the Translocation Rates from these Leaves in Girdled and Nongirdled Plants*

Data are the averages of five plants in the girdled series and five plants in the nongirdled series.

Parameter	Girdled Plants			Nongirdled Plants		
	Treatment Period 1	Treatment Period 2	Treatment Period 3	Treatment Period 1	Treatment Period 2	Treatment Period 3
	μg carbon min^{-1}					
1. Net photosynthetic rate of leaf A (P_A)	39.6	39.6	39.6	55.1	55.1	55.1
2. Net photosynthetic rate of leaf B (P_B)	34.1	69.8	0	34.8	86.1	0
3. Combined translocation rate: A to A' + A to B' (T_A)[a]	4.7	4.6	5.7	3.3	3.6	4.4
4. Combined translocation rate: B to B' + B to A' (T_B)[b]	4.3	6.3	3.5	2.4	3.9	2.0

[a] Experimentally determined values of $T_{AA'}$ and $T_{AB'}$ (from Table II).

[b] Calculated values of $T_{BB'}$ and $T_{BA'}$ (tentative values due to uncertainties in the equation for regression of translocation rate on photosynthetic rate; see text for discussion).

between A' and B', and the rates $T_{AA'}$ and $T_{AB'}$ are known, the complementary rates $T_{BB'}$ and $T_{BA'}$ can be calculated by difference. For example, for leaf B under treatment 2 conditions (girdled series), the combined translocation rate from A to A' and B' was 4.6 μg carbon min^{-1}, and from B to B' and A', 6.3 μg carbon min^{-1} (Table III). The total translocation rate, therefore, from leaves A and B, divided equally between A' and B', was 5.5 μg carbon min^{-1} to each of the sink leaves. Since $T_{AA'}$ under treatment 2 conditions equaled 3.8 μg carbon min^{-1} (Table II), by difference $T_{BA'}$ = 5.5 − 3.8 or 1.7 μg carbon min^{-1}; similarly, since $T_{AB'}$ equaled 0.8 μg carbon min^{-1} (Table II), $T_{BB'}$ = 5.5 − 0.8 or 4.7 μg carbon min^{-1}, thus yielding a partition ratio of 4.7:1.7 or 2.8:1. This value is of the magnitude expected in view of the fact that B in this treatment was the stronger source. The tentative nature of these calculations, however, must be emphasized in view of the uncertainties in the regression equations and the errors of difference involved in this method.

The general picture that emerges from the above observations is that of a distribution pattern in bean readily adjustable to changing source strengths. Although in the intact plant the translocation pattern is strongly orthostichous, removal of a source leaf or alteration of its source strength rapidly generates compensating export-import patterns, involving significant changes in transport rates to and from other orthostichies. It is possible that "phloem anastomoses", whose prevalence has been demonstrated by Aloni and Sachs (1), play a significant role in facilitating these changes in distribution patterns.

Similar adaptability of distribution patterns has been shown in peas (13), apples (8, 9), sunflower ([18] if source leaves in only one orthostichy were removed), corn (14), tomato (12), and other species. It may be significant that in all these cases young fruits constituted the target sinks. Translocation in vegetative sinks across orthostichous boundaries may be less common. Caldwell (4), e.g. showed that removal of all leaves from one side of the crown stem of the Swedish turnip at an early stage of development resulted in highly imbalanced growth of the turnips, the expansion of the tap root being much less on the defoliated side. Proebsting (unpublished work cited in Auchter [2]) showed that the diameter increase of the shoots soon stopped in the spring on the side of apple trees upon which no leaves were allowed to develop, whereas growth of the shoots on the undefoliated side proceeded normally.

Whether or not these differences reflect differences in the ontogenetic stage of sink strength in relation to the time of experimental treatment is not clear. Loomis (14), e.g. showed that full sized ears of maize were produced by translocation from leaves on sucker branches 2.5–3 m from the ear providing that nearby leaves were left on for a few days until a strong polarizing action of the developing embryos was established. The vegetative sinks in the present experiments were young leaves approaching their peak strength (20). Similar compensatory changes in the export pattern from cotyledons of *Pharbitis nil* in response to differential treatment of the cotyledons have been shown recently by Ogawa and King (17).

Source strength has been defined as equal to the product of source size and source activity (22, 23), and has, therefore, in the present application, the units of carbon fixed per unit of time per leaf. Although by this definition source strength sets an upper limit to the export rate (at least over the longer term), it appears that the export rate is, at least in plants with high source-to-sink ratios, flexibly coupled to the photosynthetic rate, responding rapidly to changes in sink demand. Thus in the limiting situation where half of the source was removed (excision experiments), the translocation rate from the remaining source (leaf A) appears to have rapidly doubled without any increase in its photosynthetic rate; that is, without any increase in its source strength, as defined. As shown in Table I, the T_A/P_A ratio (μg carbon exported min^{-1}/

μg carbon fixed min^{-1}), expressed as a per cent, increased from 18.8 to 38.6% within a period of 1.5 h (Fig. 3) in response to the diminished source area. Although a linear relationship between photosynthesis rate and translocation rate may be taken as the normative situation (5, 10, 19), it is apparent that deviations from linearity can occur readily. Hoddinott (11) has reported a constant translocation rate in *Mimosa pudica*, despite a decline in photosynthesis as a result of pinnule closure. These differences may be related in part to varying degrees of sink- or source-limited translocation rates.

These observations, coupled with the fact that $T_{AB'}$ increased much more strongly in response to removal of B (absolute zero export) than to darkening of B (zero net photosynthesis) suggest that, at least in short-term applications, source strength may be more adequately quantified in units of carbon exported per unit time rather than in units of carbon fixed per unit time.

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