Alterations in Source-Sink Patterns by Modifications of Source Strength

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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 “nearier” 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 leaf 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 ratio 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-
ALTERATIONS IN SOURCE-SINK PATTERNS

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 subdicing sinks A' and B'; D, ratemeter; E, potentiometric recorder; F, analytical train for maintaining concentration and specific activity of CO₂ 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.

Table 1 summarizes the data from seven experiments (all plants girdled) on the effect of excising leaf B on TA/R and TAP on the partition ratio TA/R (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, TA/R 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, TA/R declined precipitously during the ensuing 5- to 10-min interval (parameter 7), then revicess and accelerated rapidly, attaining a value usually about 15% higher than its preexcision rate within about 1 h.

Concomitantly TA/R, after a time lag of 8–10 min, also increased rapidly, attaining a value equal to TA/R (actually rather consistently exceeding TA/R by about 10%) within 1.5 h (4.91 versus 4.43 µg carbon min⁻¹, Table I, parameters 1 and 2) or a postexcision partition ratio of 0.91, 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 TA/R in response to imbalances accruing during the adjustment period following excision. The increase in TA/R 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 translocate 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 (TA/Pₐ).
Table I. Effect of Excising Source Leaf B on the Absolute and Relative Translocation

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Before Excision of B</th>
<th>After Excision of B</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Translocation rate from A to A' (TAA)</td>
<td>3.82 µg C min⁻¹</td>
<td>4.34 µg C min⁻¹</td>
</tr>
<tr>
<td>2. Translocation rate from A to B' (TAB)</td>
<td>0.88 µg C min⁻¹</td>
<td>4.91 µg C min⁻¹</td>
</tr>
<tr>
<td>3. Partitioning ratio (TAA:TAB)</td>
<td>5:0:1</td>
<td>0:9:1</td>
</tr>
<tr>
<td>4. Translocation rate from A to total sink (TA)</td>
<td>8.72 µg C min⁻¹</td>
<td>18.1 µg C min⁻¹</td>
</tr>
<tr>
<td>5. Net photosynthetic rate of A (PA)</td>
<td>48.4 µg C min⁻¹</td>
<td>48.7 µg C min⁻¹</td>
</tr>
<tr>
<td>6. TA/PA</td>
<td>0.19:1</td>
<td>0.39:1</td>
</tr>
<tr>
<td>7. Transient inhibition of TAA in response to excision of B (expressed as %)</td>
<td></td>
<td>34 ± 25%</td>
</tr>
<tr>
<td>8. Lag time in response of TAB to excision of B</td>
<td>8.9 ± 1.6 min</td>
<td></td>
</tr>
</tbody>
</table>

*PA constant to within ±6% or better for duration of each experiment.

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'

<table>
<thead>
<tr>
<th>Treatment Periods*</th>
<th>Translocation Rate</th>
<th>Partition Ratio (TAA:TAB)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Girdled</td>
<td>Nongirdled</td>
</tr>
<tr>
<td></td>
<td>TAA</td>
<td>TAB</td>
</tr>
<tr>
<td>1. (PB = PA)</td>
<td>3.9</td>
<td>0.82</td>
</tr>
<tr>
<td>2. (PB &gt; PA)</td>
<td>3.8</td>
<td>0.81</td>
</tr>
<tr>
<td>3. (PB &lt; PA)</td>
<td>4.4</td>
<td>1.29</td>
</tr>
</tbody>
</table>

* Treatment 1: cuvette environments of leaves A and B similar (2,500-3,000 ft-c; CO₂ concentration 340–370 µl/L). Treatment 2: CO₂ concentration of cuvette B increased to 1,300 µl/L. Treatment 3: cuvette B darkened, PB nominally zero. Throughout treatment periods 1, 2, and 3, PA remained constant to within ± 6% for each plant. For actual values of PA and PB, see Table III. Each treatment period was 1.5–3 h in duration, following isotopic equilibrium.

* 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.

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 TAB 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 TAA required to compensate for the putative decrease in TAA 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 lower 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_A/B nor T_B/A 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 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_A/A + T_B/A = T_A/B + T_B/A; (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 characteristically 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_B/A.

These descriptive statements apply specifically to bean and other species with a similar phyllotaxy. Preliminary studies on cottonwood (three-eights to five-sixteenths phyllotaxies) have indicated significantly more complicated relationships.

An analysis of these relationships would be facilitated if measurements of T_B/B and T_B/A could have been made concurrently with the measurements of T_A/A and T_B/A on the same plants. Such measurements, however, would involve major technical difficulties. Tentatively, we have attempted to estimate T_B/B and T_B/A 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 \( \mu g \) carbon translocated \( \text{dm}^{-2} \text{min}^{-1} \) source leaf, and \( x \) = \( \mu g \) carbon fixed \( \text{dm}^{-2} \text{min}^{-1} \). 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

| Parameter | Girdled Plants | | | Nongirdled Plants | | | | | |
|-----------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Period    | Treatment     | Treatment     | Treatment     | Treatment     | Treatment     | Treatment     | Treatment     | Treatment     |
| 1         | 1             | 2             | 3             | 1             | 2             | 3             | 1             | 2             |
| 2         | 39.6          | 39.6          | 39.6          | 55.1          | 55.1          | 55.1          | 34.8          | 86.1          |
| 3         | 34.1          | 69.8          | 0             | 34.8          | 86.1          | 0             | 3.3           | 3.6           |
| 4         | 4.7           | 4.6           | 5.7           | 3.3           | 3.6           | 4.4           | 2.4           | 3.9           |

* Experimentally determined values of T_A/A and T_B/A (from Table II).
* Calculated values of T_B/B and T_B/A (tentative values due to uncertainties in the equation for regression of translocation rate on photosynthetic rate; see text for discussion).
by changing the export ratio of carbon, it appears that T_{AB} = 5.5 - 3.8 or 1.7 \mu g carbon min^{-1}; similarly, since T_{AB}
= 0.8 \mu g carbon min^{-1} (Table II), T_{BB} = 5.5 - 0.8 or 4.7 \mu g 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 with 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 ratio (\mu g carbon exported min^{-1}/

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