Re-interpretation of an Experiment on the Role of Assimilate Transport Resistance in Partitioning in Tomato

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The importance of transport resistance (distance between source and sink) on assimilate partitioning in tomato is questioned. Slack and Calvert (Journal of Horticultural Science 52: 309–315, 1977) concluded that, in tomato, excising of fruit trusses showed a direct influence of distance from source on assimilate partitioning. A dry matter distribution model for tomato, based on the hypothesis that distribution is regulated by the sink strengths of the plant organs and that no influence of transport resistance on partitioning exists, has been described and validated by Heuvelink (Annals of Botany 77: 71–80, 1996). Using this model, it is shown that the results of Slack and Calvert (1977) can be explained more simply on the basis of the succession of trusses with growth shifted with respect to time. Therefore, their results do not prove that transport resistance plays a role in assimilate partitioning.

Key words: Allocation, distance, dry matter distribution, model, assimilate pool, partitioning, simulation, transport resistance, tomato.

INTRODUCTION

Assimilate partitioning into different parts of a plant is of great importance in crop production. It is generally agreed that the distribution of assimilates among sinks is primarily regulated by the sinks themselves (Gifford and Evans, 1981; Farrar, 1988; Ho, 1988), whereas the transport resistance along the pathway from source to sink is of minor importance (Farrar, 1992). The latter point, meaning equal access to an apparent common assimilate pool for all sinks, was shown in double-shoot tomato plants (Heuvelink, 1995). However, a significant influence of distance between source and sink on partitioning in tomato was claimed by Slack and Calvert (1977). They observed that when one of the first nine trusses of a tomato plant was removed at anthesis, growth of the remaining trusses was increased compared with plants where no trusses were removed. Increased truss growth was negatively related to the distance of a truss to the position of the removed truss, suggesting that transport resistance played a significant role in partitioning (Slack and Calvert, 1977). However, a more straightforward explanation of their results would be that trusses closest to the one excised get the highest yield increase, as lower trusses have a shorter growth period left to profit from removing a truss and higher trusses miss a larger part of the period when removal of the truss plays a role.

In the present work, the dry matter distribution model presented by Heuvelink (1996) is used to test whether the results of Slack and Calvert (1977) could be explained quantitatively, ignoring transport resistance. Daily plant dry weight increase was not measured by Slack and Calvert (1977) and therefore in the simulation it is taken from an experiment with about the same sowing date and growth period as their experiment. Sensitivity of model predictions to model input (daily dry weight increase and temperature) is tested. In accordance with the observations of Slack and Calvert (1977), it is assumed that removing one out of ten trusses does not influence number of set fruits on the remaining trusses.

MODEL DESCRIPTION

A complete model description is given by Heuvelink (1996). Here only the most important features of the model are summarized. In the model, dry matter partitioning is primarily regulated by the sinks. Time step of the model is 1 d. Average 24 h temperature is input to the model. The elements described in the model are the individual fruit trusses and vegetative units (three leaves and stem internodes in between two trusses). The term ‘sink strength’ is used to describe the competitive ability of an organ to attract assimilates (Wolswinkel, 1985).

Sink strength of an organ is quantified by its potential growth rate (growth rate under non-limiting assimilate supply). Sink strengths of trusses and vegetative units follow an optimum curve based on their developmental stage. Developmental stage of a sink organ results from its integrated development rate, which is primarily determined by temperature. The initiation rate of new organs is determined by temperature only.

Potential fruit weight is known to increase with truss number on the plant (De Koning, 1994). This effect may be important for the present use of the model, however, it is not simulated. Therefore, a relationship describing the
increase in organ sink strength with position on the plant, taken from De Koning (1994), was added to the model:

\[ a_i = 9.2 \left( 1 - 0.878 e^{-0.1451 \cdot 0.0465 \cdot \text{RAD}} \right) \]  

(1)

where \( a_i \) is the asymptotic maximum of the Richards growth function \([a \text{" in eqn (5) from Heuvelink (1996)}], i \) is the truss number and \( \text{RAD} \) is the average daily radiation integral received by the crop over a period of three weeks after flowering of the first truss (MJ m\(^{-2}\) d\(^{-1}\)). Hence, also daily global radiation was input to the model. According to eqn (1), sink strengths of trusses and vegetative units are dependent on their position on the plant, lower trusses and units following a reduced curve (Fig. 1). The increase of the potential growth curve with position on the plant depends on irradiance. Maximum potential growth curve is reached at a lower position on the plant under high irradiance compared with low irradiance. The influence of the assumption that organ sink strength increases with position on the plant was tested by comparing simulation results with results using the original model of Heuvelink (1996).

MATERIALS AND METHODS

Slack and Calvert (1977) removed one of the first nine trusses of a plant as soon as possible after its appearance at the growing point. No trusses were removed from control plants, and all plants were ‘stopped’ by pinching out the growing point, leaving two leaves above truss 10.

Treatments of Slack and Calvert's (1977) experiment were simulated, using the total daily growth rate [calculated as described by Heuvelink (1996)], 24 h average temperature and daily global radiation of expt 3 (six fruits per truss; ‘unstopped’ plants) from Heuvelink (1996) as input to the model. Experiment 3 was used as this crop had about the same sowing date (Nov.) and growing period as the experiment of Slack and Calvert (1977). In the simulations sink strength of vegetative units higher than the 11th unit and sink strength of trusses above truss 10 were set to zero, as plants were ‘stopped’ two leaves above truss 10.

To test the sensitivity of model predictions to model input, simulations were also conducted, assuming a constant daily plant growth rate of 3.5 g [average value measured in expt 3 (six fruits per truss) from Heuvelink (1996)] or 5.0 g, and assuming constant temperatures of 17, 20 or 23 °C. In these simulations seven fruits per truss were assumed.

Relative weight (relative yield) of a truss was calculated as final truss dry weight in a treatment (e.g. excision of truss 4) divided by final truss weight in the control plants (no trusses excised).

RESULTS

In agreement with the measurements of Slack and Calvert (1977), the distribution model predicted weight increase in some of the remaining trusses when one truss was removed at anthesis (Fig. 2). The largest increases occurred on the trusses adjacent to the excised truss, with smaller increases on the more distant ones. This was also true for the individual treatments (Table 1), just as observed by Slack and Calvert (1977).

Although both simulated values of relative truss weight with or without positional effect were within the range of the data reported by Slack and Calvert (1977), a small difference between the simulated values was observed (Fig. 2). Taking into account a positional effect resulted in more profit for higher positioned trusses and less profit for lower positioned trusses compared with predictions without assuming a positional effect.
In the simulation, no positional effect on sink strength was assumed and daily plant growth rate and temperature were assumed to be 3.5 g and 20 °C, respectively.

<table>
<thead>
<tr>
<th>Truss removed</th>
<th>Truss harvested</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.05 ± 0.01</td>
</tr>
<tr>
<td>2</td>
<td>1.04 ± 0.01</td>
</tr>
<tr>
<td>3</td>
<td>1.03 ± 0.01</td>
</tr>
<tr>
<td>4</td>
<td>1.02 ± 0.01</td>
</tr>
<tr>
<td>5</td>
<td>1.01 ± 0.01</td>
</tr>
<tr>
<td>6</td>
<td>1.00 ± 0.01</td>
</tr>
<tr>
<td>7</td>
<td>0.99 ± 0.01</td>
</tr>
<tr>
<td>8</td>
<td>0.98 ± 0.01</td>
</tr>
<tr>
<td>9</td>
<td>0.97 ± 0.01</td>
</tr>
</tbody>
</table>

Fig. 3. Relative truss weight over controls for trusses above (positive numbers) and below (negative numbers) an excised truss (0) on tomato plants. Measurements [●], reprinted, with permission, from Slack and Calvert, *Journal of Horticultural Science* 52: 312 (1977) and simulation [lines; 17 °C (— — —) or 23 °C (— — —) and a daily plant growth rate of 3.5 g (— — —) or 5 g (— — —); no positional effect on organ sink strength was assumed]. Vertical bars indicate standard error of mean.

Whether or not position on the plant influenced simulated organ sink strength (Fig. 2), the conclusion drawn before was valid for all three simulations, although relative truss weights were slightly different depending on model input. Temperature and daily plant growth rate hardly affected the predicted influence of truss position on relative dry weight increase (Fig. 3).

DISCUSSION

In trusses closest to the excised truss a higher yield increase was observed than in trusses further away form the excised truss (Table 1, Figs. 2 and 3). Slack and Calvert (1977) explained this by assuming that the remaining trusses would absorb larger amounts of assimilates unused by the excised truss the smaller their distance from the providing leaves. However, this ‘distance effect’ was also observed in the present simulations, whereas distance to the providing leaves was not taken into account in the model. Therefore it is more likely that the trusses closest to the one excised get the highest yield increase as lower trusses have a shorter growth period left to profit from the removal of a truss and higher trusses miss a larger part of the period when removal of the truss plays a role (Fig. 1). One fruit growth period (about 60 d at 20 °C; De Koning, 1994) after expected anthesis date of the excised truss, its removal does not play a role any more. From that moment onwards, partitioning will not be different for a plant having lost a truss by removal at anthesis compared with a plant having lost a truss as it was harvested ripe. Note that trusses closest to the excised truss exhibit greatest sink strength in the period where excision has the largest influence on total sink strength, i.e. the period where the greatest sink strength of the excised truss would have occurred (Fig. 1).

The small difference in simulated relative truss weights, using the model with or without positional effect (Fig. 2), could be explained by the occurrence of assimilate storage when a positional effect was assumed. This storage resulted from too low a total plant sink strength in the young crop, compared with the assumed growth rate (3.5 g d⁻¹). When assimilates are stored, organ growth occurs at its potential rate and removal of a truss has no influence on growth rate of the other organs as long as the assimilate storage pool is not empty. This explanation was supported by simulation results assuming a low growth rate of only 0.5 g d⁻¹. In that case no assimilate storage was simulated and relative truss yields were not different for the simulation with or without assuming a positional effect on organ sink strength (results not shown).

The general observation that sinks are supplied by the nearest sources (e.g. Tanaka and Fujita, 1974; Shishido and Hori, 1977) is often (e.g. Evans, 1975) explained by a significant resistance to movement in the phloem. However, the present simulations show that such a distribution pattern may be observed, even when assuming that distance...
between source and sink plays no role in assimilate partitioning.

It is concluded that the results of Slack and Calvert (1977) can be explained more simply than they did, on the basis of the succession of trusses with growth shifted with respect to time (Fig. 1). Slack and Calvert’s (1977) experiment does not contradict the assumption of a common assimilate pool, equally accessible to all sinks on a tomato plant. This assumption was further supported by double-shoot and truss removal treatments (Heuvelink, 1995). Hydraulic resistance of the phloem is expected to be negligible in most cases, as several authors concluded that fully differentiated phloem networks have considerable spare transport capacity (Milthorpe and Moorby, 1969; Passioura and Ashford, 1974; Wardlaw, 1990).

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LITERATURE CITED


