To increase fruit yields in tomato cultivation, it is essential to increase photosynthetic production, and also to enable rapid and highly efficient translocation and accumulation of photosynthates into fruit to be harvested. In the cultivation under structures such as glasshouses or plastic greenhouses, it is possible to control artificially environmental conditions inside the structures to a certain extent, independently of outdoor conditions, because the crops are completely enclosed under covering materials. Therefore, it is possible to increase crop productivity by providing the crops with a favorable environment to photosynthesis and translocation of photosynthates.

The translocation of photosynthates is intrinsically determined by the interrelation between source and sink, and also largely influenced by environmental factors such as temperature and light. The present study was carried out to examine effects of these internal and external factors on translocation and distribution of photosynthates in tomato plants by the use of the $^{14}$C tracer technique, with the purpose of finding out the direction of environmental control.

**Source-sink relationship**

As given in Fig. 1, it was made clear that leaves growing on a plant were not equally
functioning, but their role as the source was different with different leaf positions. Fig. 1 shows the distribution pattern of $^{14}$C-photosynthates produced in each leaf of different position fed with $^{14}$CO$_2$ at the fruit development stage of the first truss of a tomato plant with 3 trusses. It was found that trusses and roots acted as major sinks, and the leaves which mainly supplied photosynthates to each of them are of different positions (Table 1).

<table>
<thead>
<tr>
<th>Sink</th>
<th>$^{14}$CO$_2$-fed leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$L_5$</td>
</tr>
<tr>
<td>3rd truss</td>
<td>0.3 %</td>
</tr>
<tr>
<td>2nd truss</td>
<td>1.7</td>
</tr>
<tr>
<td>1st truss</td>
<td>20.4</td>
</tr>
<tr>
<td>Roots</td>
<td>53.2</td>
</tr>
</tbody>
</table>

* The total amount of $^{14}$C translocated from each $^{14}$CO$_2$-fed leaf is taken as 100.

Namely, the main supplier of photosynthates to each of the major sinks was several leaves adjacent to it. Each of the sinks and several adjacent leaves constitute a group, which Tanaka et al. proposed to name a source-sink unit. The photosynthates produced in the unit are mostly translocated into the truss or roots, the core of the unit. Thus, it was made clear that a tomato plant consists of a series of such units as given in Fig. 2.

However, the sphere of influence of a given source-sink unit in a plant is not constant throughout the growth period, but it varies depending on the competition between the strength of the sink and that of other neighboring sinks. The sink-strength of a fruit changes according to the fruit development as shown in Fig. 3. Therefore, when there are several trusses differing in the fruit developmental stage, they differ in the sink-strength, and accordingly in the sphere of influence. For example, at the pre-flowering stage, the sink-strength of trusses is low, and the sphere of influence is limited. As the fruit develops, the sink-strength increases, and the sphere of influence expands. This provides a basis for understanding the spatial distribution of photosynthates in the plant.

Due to the competition among different sinks in a plant, a dominant sink attracts photosynthates from leaves of other units locating in a wider portion of a plant. The extent of the portion is termed "the sphere of influence" in this paper.

Fig. 2. Schematic expression of structure of source-sink units in a tomato plant

Fig. 3. Change in sink-ability of tomato fruit during fruit development and ripening
The single truss plants with 2 fruits were exposed to $^{14}$CO$_2$ at successive stages and harvested 24 hr after $^{14}$CO$_2$-feeding.
stage of the first truss, the source-sink unit including roots is predominant. At the stage of vigorous fruit development of the first truss, the source-sink unit including the first truss comes to expand its influence to the greatest sphere. At this stage, the sink-strength is in the order of the first > second > third truss, and hence the sphere of influence of the corresponding units shows the same order. When the first truss comes to nearly the harvesting stage, the source-sink unit including the second truss exerts the widest influence in place of the former. In this way, the unit exerting the widest sphere of influence in a tomato plant ascends from the unit centering roots at the stage before flowering to the upper truss according to the plant growth.

On the other hand, such a structure composed of source-sink units is greatly influenced by various factors such as the number of bearing fruit, defoliation and low solar radiation which affect competitive interrelations among sinks. As a result, imbalance of photosynthetic distribution occurs, which affects seriously the later growth in some cases. For example, under low solar radiation, production of photosynthates is reduced, but produced ones are mostly translocated into developing fruit, so that it happens that the source-sink unit centering a lower truss with developing fruit absorbs photosynthates at the sacrifice of upper trusses and roots, i.e., the sphere of influence of the former is larger than the latter. It induces lowering of root activity and severe flower abscission or fruit drop.

Thus, it was made clear that the extent of sphere and the duration of influence of the most dominant source-sink unit of a plant greatly alter the photosynthetic distribution to other sinks, and, as a result, the balance between source and sink in the succeeding growth stage is determined, i.e., plant growth is affected.

**Effect of temperature on photosynthetic translocation**

Effect of environmental factors on translocation and distribution of photosynthates will be described taking temperature as an example. To examine effects of night temperature, it is necessary to know how much of the photosynthates produced during a day is translocated during the night and how much of them is influenced by night temperature. Therefore, after \(^1\text{C}O_2\) was fed at different time of a day, translocation of \(^1\text{C}\)-photosynthates was examined during the daytime (9–18 o'clock, 25°C, 30 klux) and night time (18–9 o'clock, 13°C). As shown in Fig. 4, the most of photosynthates produced in the forenoon were translocated already by the evening, and photosynthates translocated in the night were mainly those produced in the afternoon. Two-thirds of the photosynthates produced during a whole day was translocated in the day time, while one-third in the night. However, this result was obtained on an assumption that the photosynthesis was carried out at a constant rate during the daytime. As the photosynthetic rate generally shows a diurnal change with a peak soon after noon, the above proportion regarding daytime and night time translocation must be regarded approximate.

![Fig. 4. Translocation during the daytime, the following night, and a whole day (24 hr) of \(^1\text{C}\)-photosynthates produced by \(^1\text{C}O_2\)-feeding at different time in a day.](image)

Temperature gives great effects on translocation of photosynthates. As shown in Fig. 5, the speed of translocation at a petiole increased with increasing temperature from ca. 11 cm/hr at 3°C to the peak (83 cm/hr) at 33°C, and it turned to decrease beyond
This result suggests the possibility of regulating the translocation (particularly, the speed of translocation) by controlling the temperature (night temperature) in structures.

Then, effects of night temperature were examined. Plants fed with $^{14}$CO$_2$ in the evening were placed in the darkness at 8, 13, and 18°C (Fig. 6). Translocation from leaves to each sink, fruit and roots, was faster at higher temperature and slower at lower temperature. At 8°C a considerably large portion of $^{14}$C-photosynthates still remained in leaves after 16 hr of darkness, which coincided with the following morning. It indicates that translocation of photosynthates produced in daytime was not finished in the night. Under such a condition, photosynthates remaining in leaves give an adverse effect on photosynthesis in the following day.

As mentioned above, it is considered that relatively high temperature (particularly night temperature higher than 13°C) is desirable for translocation of photosynthates, but high temperature causes a problem of increased respiratory consumption of photosynthates. Accordingly, both translocation and respiration have to be taken into account in setting up night temperature for crop management under structures. In view of this, the alternate night temperature treatment, that is a combination of relatively high temperature in early half of night time (ca. 5 hr from sun-set) to promote translocation, and relatively low temperature in later half to suppress respiration is desirable.

Furthermore, the distribution of photosynthates is also greatly influenced by temperature. Fig. 7 shows distribution ratios of $^{14}$C-photosynthates in plants fed with $^{14}$CO$_2$ after different periods of low night temperature (8°C) treatment. The longer the period of low night temperature treatment, the less the distribution to fruit, but the more was the distribution to roots. In general, the translocation to roots is increased when tomato plants are kept at low temperature. This fact
Fig. 7. Distribution of $^{14}$C-photosynthates in single truss tomato plants placed at low night temperature ($8^\circ$C) for 1, 3 or 5 days and then fed with $^{14}$CO$_2$

The plants were harvested 24 hr after $^{14}$CO$_2$-feeding.

Distribution of $^{14}$C is expressed in % of the total $^{14}$C assimilated.

offers an important advice for night temperature management. When tomato plants are grown under low light intensity, photosynthetic distribution to roots is reduced. It is one of the causes of losing plant vigor. In such a case, low night temperature treatment is able to increase the distribution to roots.

Thus, it was made clear that the translocation and distribution of photosynthates in tomato plants are markedly influenced by temperature, and that the temperature management (particularly night temperature) under structures is able to control the translocation and distribution.

References


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