Studies on Photosynthesis and Translocation of Photosynthate in Mulberry Tree

IV. On the translocation of $^{14}$C-photosynthetic product in partially defoliated plants

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INTRODUCTION

In a previous paper it was reported that photosynthetic product assimilated by a mulberry leaf was transported to shoot apex, immature leaves, stem, stump and root, but scarcely to mature leaves. And moreover, the age of leaf fed with $^{14}$CO$_2$ had some bearing on the direction of translocation of the photosynthetic product, that is, upper leaves transported relatively larger amount to the shoot apex and immature leaves, but lower leaves mainly to the stump and root. There remained, however, some questions whether the direction of translocation was fixed with the age of the fed leaf or could be altered by any treatment.

The leaves of cultivated mulberry trees are often harvested for silkworm raising and it will be, therefore, of importance to elucidate the effect of defoliation on the movement of photosynthetic product.

In this paper the effect of partial removal of leaves on the pattern of translocation of photosynthetic product will be mentioned removing the leaves between a leaf to be fed with $^{14}$CO$_2$ and sinks of photosynthetic product, i.e., the shoot apex, stump and root in young mulberry plants.

MATERIALS AND METHODS

Materials were 2-year-old mulberry plants of the variety Ichinoe raised from saplings made by semi-soft wood cutting. The saplings were planted in 1/2000a Wagner pots on May 10, 1971 and the stem of the saplings was cut at 5 cm above the shoot base. Developed new shoots on the basal part of the stem were removed remaining only one with care of making growth of each plant equal. The length of shoot and the number of leaves developed were respectively

![Fig. 1 Schematic expression of the defoliation treatment. A: untreated. B: leaves between the leaf to be fed with $^{14}$CO$_2$ and the shoot apex were removed. C: leaves lower than the leaf to be fed were removed. The treatment was carried out 4 days before the administration of $^{14}$CO$_2$. Hatched leaves show the ones to be fed with $^{14}$CO$_2$. Upper leaves to be fed were the 9th from the top of the shoot, middle from the 21th to the 24th from the base and the lower the 9th from the base]

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145 cm and 44 on an average when the treatment to remove leaves was carried out on August 28.

The methods of removal of leaves are shown in fig. 1. Materials were divided into three groups. One third of the materials were left, with all leaves intact (Plot A). In one plot (Plot B) leaves which intervened between the leaf to be fed with $^4$CO$_2$ and the shoot apex were thoroughly removed except for young leaves not yet unfolded. In other plot (Plot C) leaves between the leaf to be fed with $^4$CO$_2$ and the stump were removed.

On September 1, 4 days after the defoliation treatment, 20 $\mu$Ci $^4$CO$_2$ per one plant (specific activity 86 $\mu$Ci/m-mole CO$_2$) was administered to the prearranged leaf in upper, middle or lower part of stem as is shown in fig. 1. The leaf was enclosed with a vinyl bag and $^4$CO$_2$ was circulated over the enclosed leaf as was described in the previous paper for 30 minutes under field conditions. Air temperature was from 27 to 30°C, the light intensity over 20 klx and the initial CO$_2$ concentration was calculated to be 0.33%.

A week after the administration all plants were harvested and dried in a ventilated electric oven of 75°C after dissecting the plant into the fed leaf, other leaves, stem segments each of which had a bud at the top and was designated as coincident with the leaf order, stump, root and shoot apex (including leaves unfolded after the defoliation treatment). The radioactivity in each organ was counted by a liquid scintillation counter. The details of counting were mentioned in the previous paper.

RESULTS

About 5 leaves unfolded in a period from the defoliation treatment to the harvest time, but there was no sign of the development of lateral buds. In this paper the word shoot apex includes leaves unfolded after defoliation.

Effect of removal of leaves on the translocation pattern of $^4$C-photosynthetic product will be mentioned chiefly on A-2, B-2 and C-2 plots. Fig. 2 shows $^4$C-specific activity (radioactivity per unit dry weight) in the individual leaf, stem segment, stump and root of the untreated plant fed with $^4$CO$_2$ from a leaf in the middle part of the stem (Plot A-2). $^4$C-photosynthetic product was transported both upwards to the shoot apex and downwards to the stump and root as was mentioned in the previous paper.

$^4$C-specific activity of each organ in the plant whose leaves between the leaf to be fed and the

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![Diagram](image-url)

Fig. 2 $^4$C-specific activity of each organ of A-2 plot expressed in the logarithmic scale. $^4$CO$_2$ was administered to the 21st leaf number from the base.
Fig. 3 $^{14}C$-specific activity of each organ of B-2 plot expressed in the logarithmic scale. Leaves between the leaf to be fed with $^{14}CO_2$ (the 22nd leaf from the base) and the shoot apex (hatched part) were removed 4 days before the administration with $^{14}CO_2$.

Fig. 4 $^{14}C$-specific activity of each organ of C-2 plot expressed in the logarithmic scale. Leaves lower than the leaf to be fed with $^{14}CO_2$ (the 24th leaf from the base) were thoroughly removed 4 days before administration with $^{14}CO_2$.

Shoot apex had been removed is illustrated in fig. 3. (Plot B-2). While translocation of $^{14}C$-photosynthetic product to the shoot apex was conspicuously increased, translocation to the stump and root was decreased. It is interesting that the $^{14}C$-specific activity in the stem part, where the attached leaves had been removed, increased to some extent and this will await future examination in detail.

Effect of removal of leaves lower than a leaf to be fed with $^{14}CO_2$ in the middle part of the stem is shown in fig. 4. (Plot C-2) $^{14}C$-specific activity in stump was about three times and that in root six times increased, compared with those in the untreated plant. But the activity in the shoot apex was of the same order of that in the untreated plant.

$^{14}C$-specific activity in sink organs of all plots
Table 1 14C-specific activity (dpm/mg D.W.) of shoot apex, stump and root. All symbols in the table were shown in fig. 1

<table>
<thead>
<tr>
<th></th>
<th>A-1</th>
<th>A-2</th>
<th>A-3</th>
<th>B-1</th>
<th>B-2</th>
<th>B-3</th>
<th>C-1</th>
<th>C-2</th>
<th>C-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot apex</td>
<td>1360</td>
<td>37</td>
<td>29</td>
<td>5407</td>
<td>3537</td>
<td>3333</td>
<td>1415</td>
<td>89</td>
<td>47</td>
</tr>
<tr>
<td>Stump</td>
<td>2</td>
<td>93</td>
<td>131</td>
<td>6</td>
<td>1</td>
<td>6</td>
<td>16</td>
<td>287</td>
<td>149</td>
</tr>
<tr>
<td>Root</td>
<td>19</td>
<td>100</td>
<td>342</td>
<td>10</td>
<td>2</td>
<td>7</td>
<td>60</td>
<td>606</td>
<td>535</td>
</tr>
</tbody>
</table>

Table 2 Rate of retention of 14C-photosynthetic product in the fed leaf

<table>
<thead>
<tr>
<th></th>
<th>A-1</th>
<th>A-2</th>
<th>A-3</th>
<th>B-1</th>
<th>B-2</th>
<th>B-3</th>
<th>C-1</th>
<th>C-2</th>
<th>C-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate of retention</td>
<td>66.2%</td>
<td>21.5%</td>
<td>26.9%</td>
<td>53.6%</td>
<td>21.5%</td>
<td>9.3%</td>
<td>23.3%</td>
<td>20.4%</td>
<td>27.9%</td>
</tr>
</tbody>
</table>

is illustrated in table 1. When the comparison was made among treatments as to the corresponding upper and lower fed leaves, the translocation patterns mentioned above was also observed.

The leaf fed with 14CO₂ retained some proportion of 14C-photosynthetic product in itself not transported to other organs. The rate of retention in the fed leaf is shown in table 2. In untreated plants upper leaf retained the largest proportion and middle leaf the smallest as was mentioned in the previous paper⁹. It is worthy to point out that the degree of defoliation had some bearing on the rate of retention, that is, when most leaves were removed as in plots B-3 and C-1, the rate of retention in the fed leaf decreased.

The distribution rate of 14C-photosynthetic product transported from the fed leaf is shown in table 3. By the removal of leaves upper than the fed leaf no less than 40% of 14C-photosynthetic product was distributed to the shoot apex even if the middle or lower leaf was fed with 14CO₂, while distribution rate to stump and root was greatly reduced (Plots B-1~3).

By the removal of leaves lower than the fed leaf (Plots C-1~3) somewhat larger proportion was distributed to stump and root than in the untreated plants.

**DISCUSSION**

The effect of partial defoliation on the translocation of assimilated materials was studied by Quinlan³ in an apple rootstock and it was made clear that removal of leaves below the source leaf caused a reduction of 14C-photosynthetic product in the shoot tip, whereas removal of all unrolled leaves above the source leaf greatly reduced the movement of labelled assimilates to the root system. In tea plants Sanderson and Sivapalan⁶ also investigated the effect of partial defoliation on the movement of 14C-photosynthetic product and demonstrated that the leaves far from the developing shoot tips were able to supply assimilated carbon to shoot tips in an experiment in which mature leaves between developing shoot tips and the leaf to be treated were removed just before the treatment with 14CO₂. Khan and Sagar⁵ reported that defoliation of all leaves except for the test leaf and leaves near the apex had an effect of increasing the amount of radioactivity reaching

Table 3 Distribution rate of 14C-photosynthetic product to each organ

<table>
<thead>
<tr>
<th></th>
<th>A-1</th>
<th>A-2</th>
<th>A-3</th>
<th>B-1</th>
<th>B-2</th>
<th>B-3</th>
<th>C-1</th>
<th>C-2</th>
<th>C-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot apex</td>
<td>52.9%</td>
<td>0.5%</td>
<td>0.4%</td>
<td>47.8%</td>
<td>44.1%</td>
<td>51.6%</td>
<td>38.0%</td>
<td>0.6%</td>
<td>0.4%</td>
</tr>
<tr>
<td>Leaves except fed leaf</td>
<td>3.6%</td>
<td>2.2%</td>
<td>2.4%</td>
<td>3.2%</td>
<td>1.0%</td>
<td>0.4%</td>
<td>0.2%</td>
<td>4.7%</td>
<td>5.9%</td>
</tr>
<tr>
<td>Stem</td>
<td>42.1%</td>
<td>63.9%</td>
<td>30.4%</td>
<td>45.2%</td>
<td>54.9%</td>
<td>47.0%</td>
<td>53.4%</td>
<td>52.1%</td>
<td>31.4%</td>
</tr>
<tr>
<td>Stump</td>
<td>1.0%</td>
<td>16.9%</td>
<td>30.4%</td>
<td>1.2%</td>
<td>0.1%</td>
<td>1.0%</td>
<td>3.0%</td>
<td>25.2%</td>
<td>26.8%</td>
</tr>
<tr>
<td>Root</td>
<td>0.5%</td>
<td>16.5%</td>
<td>36.6%</td>
<td>2.6%</td>
<td>0.0%</td>
<td>0.1%</td>
<td>3.6%</td>
<td>17.5%</td>
<td>35.8%</td>
</tr>
</tbody>
</table>
the fruits and of reducing the activity recovered
in the stem and root in tomato plants.

Translocation patterns reported in the present
paper in partially defoliated mulberry plants
coincide with the results mentioned above.

It is generally accepted that an upper leaf
transports the photosynthetic product mainly
to shoot tip or immature leaves while a lower
leaf mainly to root system and that a middle leaf
shows an intermediate pattern of them\textsuperscript{4,5,8}. The fact that the pattern of translocation is altered
by the partial removal of leaves between the fed
leaf and the sink organs may indicate that the
direction of translocation is not only determined
by the age or position of the fed leaf, but is
also influenced by the gradient of concentration
of photosynthetic product in a plant. In an ex-
nperiment of removal of young leaves upper than
a fed leaf, Hartt et al.\textsuperscript{5} reported a considerable
increase in translocation out of the fed leaf up
into the growing point and down into the stem,
and they attributed the results to the removal
of competing streams from the other leaves in
translocation.

The enhancement of photosynthetic activity in
the remained leaves was reported by Gifford and
Marshall\textsuperscript{9}. Though the photosynthetic activity
was not measured in this experiment, the
authors reported that the photosynthetic activity
of the remained leaves increased when the amount
of photosynthetic organ was decreased by shoot
pruning at at the middle part of the stem\textsuperscript{5}.

It seems that removal of upper leaves had a
greater effect on the pattern of translocation
than the removal of lower leaves. As the upper
leaves have a more important role in the matter
production of mulberry plants\textsuperscript{9}, removal of these
important leaves would have a greater influence
both on the pattern of translocation and on the
rate of retention of photosynthetic product.

**SUMMARY**

The effect of partial removal of leaves on the
pattern of translocation of photosynthetic prod-
uct was studied, by removing the leaves between
a leaf to be fed with $^{14}$CO$_2$ and sink organs of
photosynthetic product 4 days before the ad-
administration of $^{14}$CO$_2$.

The results obtained will be summarized as
follows.

1. When leaves between a leaf to be fed with
$^{14}$CO$_2$ and the shoot apex were removed, trans-
location of $^{14}$C-photosynthetic product to the
shoot apex was conspicuously increased, while
translocation to the stump and root was de-
creased.

2. When leaves lower than a leaf to be fed
with $^{14}$CO$_2$ were removed, translocation of photo-
synthetic product to the stump and root was
slightly increased.

3. $^{14}$C-specific activity in the stem part, whose
attached leaves had been removed, showed higher
value than in stem part whose leaves were left
intact.

4. When most leaves were removed, the rate
of retention of $^{14}$C-photosynthetic product in the
fed leaf decreased to some extent.

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**LITERATURE CITED**

synthesis and assimilate distribution in
* Lolium Multiflorum* Lam. following differential
517—526.

1964. Effects of defoliation, deradication,
and darkening the blade upon translocation
of $^{14}$C in sugarcane. *Plant Physiol.*, 39 :
15—22.


[和文摘要]

桑の光合成および光合成産物の転流・消費に関する研究

第4報 部分的に摘葉処理をした桑における$^{14}$C-光合成産物の転流について

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(農林水産省試験場)

摘の単葉からとりこまれた光合成産物の転流のパターンは同化葉の位置または葉樫によっていちじるしい影響を受け、葉樫の上位葉からは先端部の葉への分配率が比較的高く、下位葉からは株や根への分配率が高くなることが知られている。本報では枝条の上、中または下部の$^{14}$CO$_2$をとりこませるべき葉（以下$^{14}$CO$_2$同化葉という）と枝条先端部、株および根など光合成産物のシナリによるべき器官の間にある葉を摘除し、4日後に$^{14}$CO$_2$を同化させ、その後における$^{14}$C-光合成産物の転流について実験を行なった。

得られた結果の概要は次のとおりである。

1. $^{14}$CO$_2$同化葉と枝条先端部との間の葉を摘除した場合には、枝条先端部への転流が促進され、株や根への転流は減少した。

2. $^{14}$CO$_2$同化葉より下部にある葉を摘除した場合には、株と根への転流がわずかに増加した。

3. 葉を摘除した部分の枝条中の比放射能は摘除していない部分に比べて高くなくなる傾向が認められた。

4. 摘除される葉の量が多い場合には、$^{14}$CO$_2$同化葉に保持されて他の器官に転流しない$^{14}$C-光合成産物の割合が低下した。