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Incorporation of ^{14}C-assimilates into GA-treated and -untreated Inflorescences Following Assimilation of $^{14}CO_2$ by Individual Leaves in Grape Shoot

Yoshie MOTOMURA

Department of Agronomy, Faculty of Agriculture, Tohoku University, Sendai, Japan

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Summary

Using Delaware and Campbell Early grapevines (*Vitis labrusca L.*), the incorporation of the ^{14}C-assimilates into the inflorescence was investigated 24 hours after the individual leaves were fed with $^{14}CO_2$ at different times. Before and at full bloom, the incorporation was found mostly in leaves just below and above the inflorescence and always on the same side of the shoot as the inflorescence. Moreover, the sink activity of the inflorescence decreased temporarily just before full bloom. After full bloom, however, the inflorescence took up the ^{14}C-assimilates also from the other leaves, inclusive of those on the opposite side of the shoot to the inflorescence, but still in smaller proportions from leaves on the opposite side than from those on the same side as the inflorescence.

The prebloom GA application increased the incorporation before and at full bloom as compared with the control, and it was especially true just before full bloom, while 2 to 3 weeks after full bloom the total export as well as the incoproration from individual leaves decreased somewhat.

It is generally stated, that in grapevines, the inflorescence competes with the shoot apex for photosynthetic assimilates from the onset of its growth to flowering and the early stage of berry development. Moreover, it is probable that the inflorescence takes up the assimilates in varying strength from individual leaves depending on their positions on the shoot and on their maturity (1).

For the production of seedless berries in Delaware, GA is applied to the inflorescence 2 weeks before the expected full bloom, which is followed by a postbloom application 10 days after full bloom. The prebloom GA application not only induces seedlessness but also accelerates the initial growth of the berries, which are brought to full size by the postbloom GA application. Growth regulators such as GA, BA and CCC were reported to effectively induce the movement of photosynthetic assimilates into plant parts treated with them in grapevines (2–6) and other crops (7–13).

Changes with time and leaf positions on the shoot in the distribution pattern of the assimilates from leaves in grapevines were described by Hale and Weaver (1) using autoradiography. In this respect, however, there are almost no quantitative studies. This is especially true in relation to the effect of GA.

In this paper, the time course of the translocation and distribution of the photosynthetic assimilates from individual leaves to the inflorescence was investigated using ^{14}C-label in relation to the leaf position on the shoot and the prebloom application of GA to the inflorescence.

Materials and Methods

Delaware and Campbell Early grapevines (*Vitis labrusca L.*) were used. For each cultivar, shoots of uniform size and vigour were selected, and in each shoot inflorescences were thinned out leaving only one on the third node. The shoots were divided into two groups. In one group, the inflorescence was treated with 100 ppm GA (Aerol OP was added at 100 ppm) by dipping 2 weeks before expected full bloom, while another group was used as control. Postbloom GA application was not carried out.

In both groups, the 10 basal leaves (one per shoot) and inflorescence were separately supplied with $^{14}CO_2$ with different shoots at full bloom and 2 and 1 week(s) before and 1, 2, and 3 weeks after full bloom. The experiment was carried out in triplicate. For $^{14}CO_2$ feeding, each individual leaf or inflorescence was enclosed in a polyethylene bag and supplied with $^{14}CO_2$ for 2-4 hours under natural daylight. $^{14}CO_2$ was generated inside the bag from $Na_2{}^{14}CO_3$ (equivalent to 10 μCi ^{14}C) solution, to which 40 per cent lactic acid was dropped gently. The fed shoots were sampled 24 hours after feeding and divided into 4 parts of the fed leaf, inflorescence, and apical and basal parts (below and above the fed leaf, respectively) of the shoot. They were, then, oven-dried, weighed and pulverized separately. Twenty mg of pulverized material was oxidized by combustion using a Packard tri-carb sample oxidizer type 306, and the ^{14}C activity was counted with a Packard liquid scintillation spectrometer type 3309. The results were expressed by percentage total export, percentage distribution and relative strength as a sink (RSS), which were calculated as follows.

Percentage total export from the fed leaf or inflorescence =(^{14}C recovered in the whole shoot except the fed leaf or inflorescence/Total ^{14}C recovered in the whole shoot including the fed leaf or inflorescence)$\times$100

Percentage distribution to the inflorescence or to the apical part of the shoot= (^{14}C recovered in the inflorescence or in the apical part of the shoot/^{14}C recovered in the whole shoot including the inflorescence except fed leaf)$\times$100

RSS (Relative strength as a sink) of the inflorescence for each individual leaf= (Percentage distribution of ^{14}C to the inflorescence from each individual leaf/

Percentage distribution of dry matter to the inflorescence, the fed leaf being excluded) $\times 100$

Results

1. *Distribution of ^{14}C-assimilates into the inflorescence (Fig. 1).*

In Delaware, the inflorescence took up the ^{14}C-assimilates mostly from the second and fourth leaves (leaves were numbered from the base and are abbreviated as L2, L4, etc. hereafter), which were situated just below and above the inflorescence, respectively and necessarily, on the same side of the shoot as the inflorescence, and the percentage distribution from them reached 40–60 (%) 2 weeks before and at full bloom. One week before full bloom, however, L2 was the exclusive source for the inflorescence, and moreover, the percentage distribution from L2 decreased remarkably to 20–30 (%) instead of the 60 (%) 2 week before.

In Campbell Early, the ^{14}C-assimilates were incorporated into the inflorescence mostly from L2 throughout from 2 weeks before full bloom to full bloom. The percentage distribution from L2, however, decreased to about 20(%) 1 week before full bloom and increased again to about 80 (%) at full bloom as in Delaware.

After full bloom, in both cultivars, ^{14}C-assimilates moved into the inflorescence not only from L2 (and L4 in Delaware) but also from leaves above them inclusive of those on the opposite side to the inflorescence, and the percentage distribution from them increased with time to 70–80 (%), although being smaller from leaves on the opposite side to the inflorescence than from those on the same side as the inflorescence, and thus showing a saw tooth profile.

In the shoots with GA-treated inflorescence, the distribution and its change with time of ^{14}C-assimilates from leaves to the inflorescence differed little from those in the control in both cultivars, except that L2 and L4 continued to be active sources for the inflorescence until full bloom. In fact, there was found no temporary decrease in the percentage distribution from them 1 week before full bloom as observed in the control, and the percentage value was 30–70 (%) before full bloom and 60–80 (%) at full bloom. Moreover, 2 and 3 weeks after full bloom, the incorporation of ^{14}C-assimilates into the GA-treated inflorescence became smaller than that into the untreated one, and it was especially true with leaves opposite the inflorescence.

2. *Sink activity of the inflorescence (Fig. 2).*

RSS value of the inflorescence for the individual leaves varied almost in parallel with the percentage distribution mentioned above in both cultivars. Thus, before and at full bloom, the inflorescence was a strong sink for L2 and L4 in Delaware and for L2 in Campbell Early, although the sink activity decreased temporarily 1 week before full bloom. After full bloom, the 10 basal leaves were all strong sources for the inflorescence displaying a saw tooth profile in the percentage distribution.

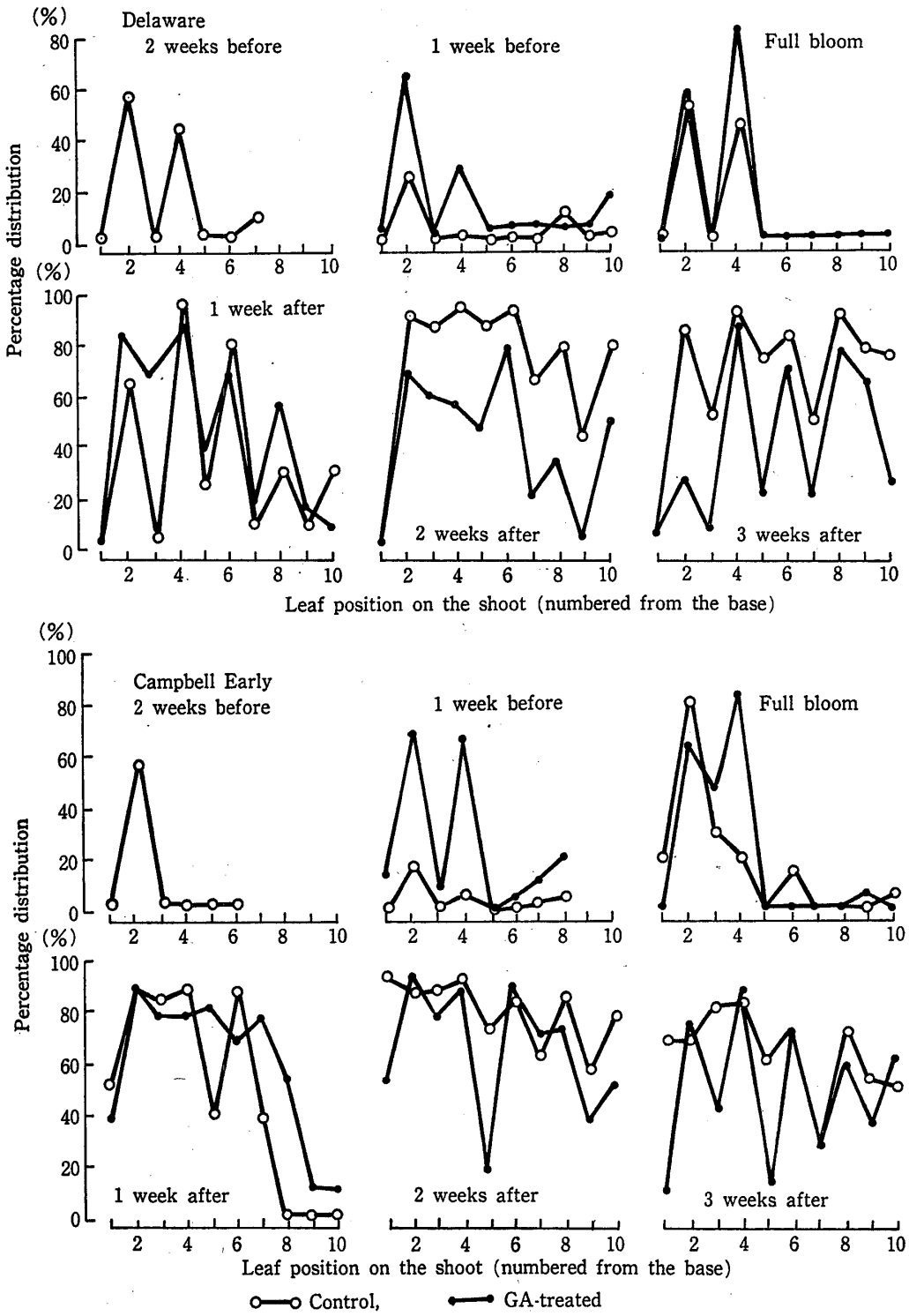

FIG. 1. Distribution of the ^{14}C-assimilates from individual leaves into GA-treated and -untreated inflorescences 24 hours after $^{14}CO_2$ was fed to the individual leaves at different times.

Following GA treatment, the sink activity of the inflorescence increased for L2 in Delaware and L4 in Campbell Early 1 week before and /or at full bloom. After full bloom, however, it decreased somewhat for all of the 10 basal leaves and

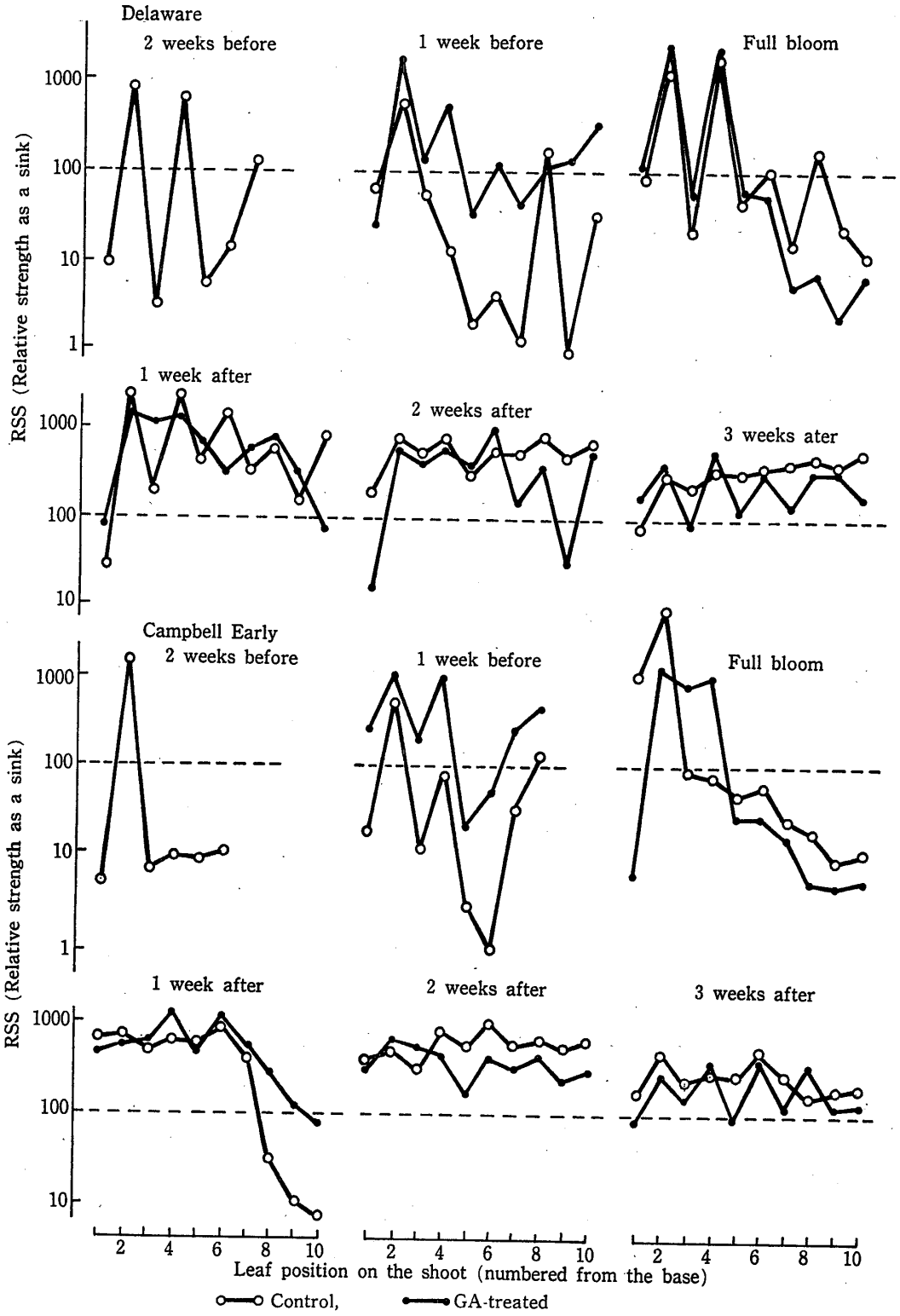

FIG. 2. Sink activity of GA-treated and -untreated inflorescences for individual leaves 24 hours after $^{14}CO_2$ was fed to the individual leaves at different times.

especially for the leaves on the opposite side from the inflorescence as compared with in the control.

3. *Total export of ^{14}C-assimilates from each individual leaves fed with $^{14}CO_2$ (Fig. 3).*

In Delaware, the 6, 7 and 8 basal leaves (+L10) were found to be exporting the ^{14}C-assimilates 2 weeks before, 1 week before and at full bloom, respectively. The percentage total export showed one peak in relation to the leaf position on the shoot and reached 50–70 (%) at its maximum. Thus, the total export from the individual leaf was not affected by leaf position on the shoot until full bloom. At

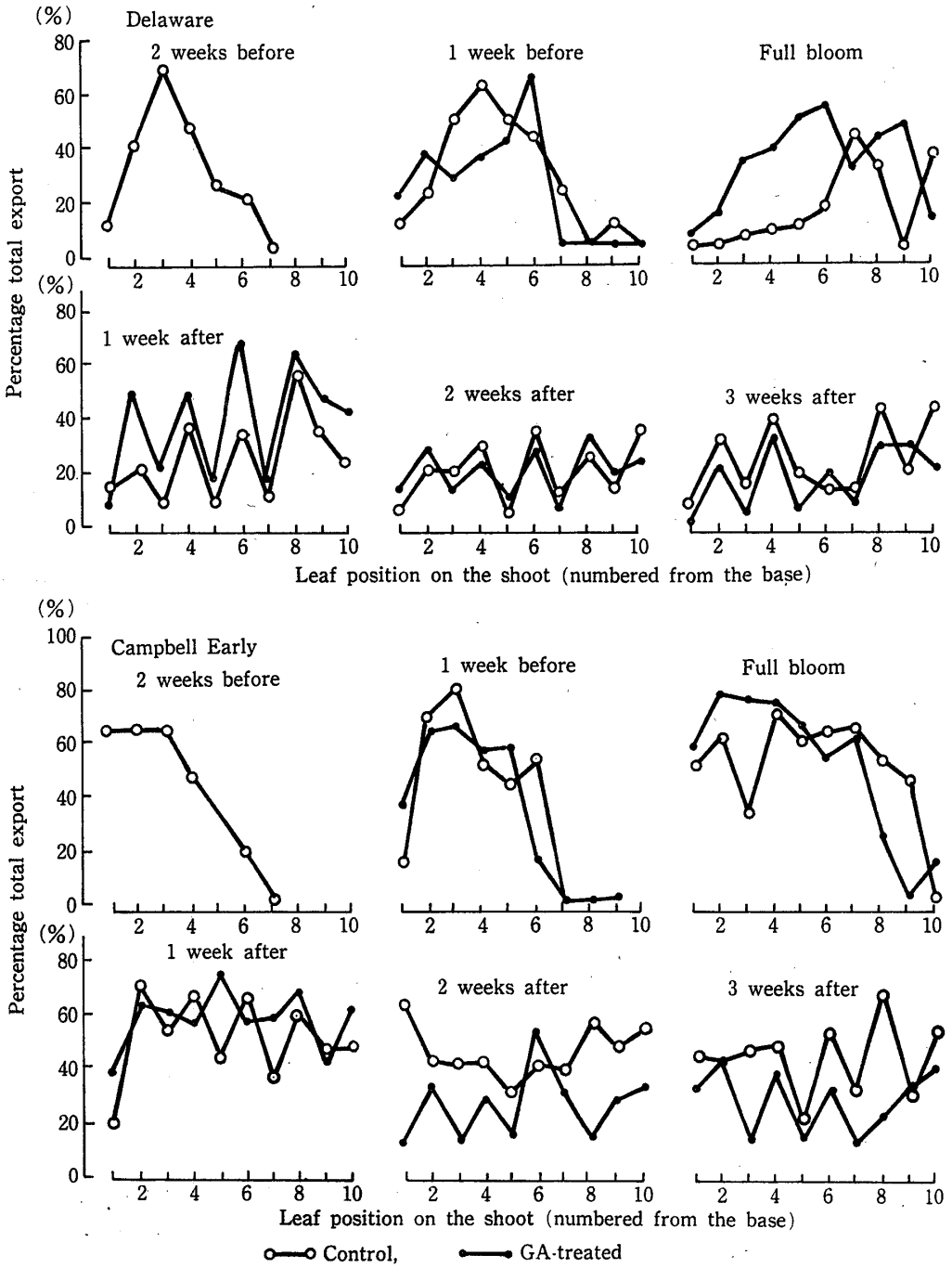

FIG. 3. Total export of the ^{14}C-assimilates from individual leaves and its change with the prebloom GA application 24 hours after $^{14}CO_2$ was fed to the individual leaves at different times.

full bloom, all of the 10 basal leaves were exporting, but 2 to 3 weeks after full bloom, the percentage total export decreased gradually to 25 (%) in an average and at the same time showed clearly a saw tooth profile, being higher and lower from leaves on the same side and opposite side of the inflorescence, respectively. Following GA treatment, the percentage total export increased at and 1 week after full bloom, while it decreased 2 and 3 weeks after full bloom as compared with the control.

The similar tendencies were observed in Campbell Early, except that the decrease in the percentage total export 2 to 3 weeks after full bloom was more marked than in Delaware.

4. *Amounts of ^{14}C-assimilates incorporated into the inflorescence (Fig. 4 and Fig. 5).*

Supposing that the same amount of photosynthates was produced by individual leaves (this supposition was not necessarily reasonable and it was especially true before full bloom, when upper leaves were immature. After full bloom, however, the amount produced might be presumed to be comparable, at least, between neibouring leaves.), the amount of the ^{14}C-assimilates incorporated into the inflorescence from each individual leaves during the 5 weeks from 1 week before to 4 weeks after full bloom was tentatively calculated as follows and expressed in arbitrary units (Fig. 4).

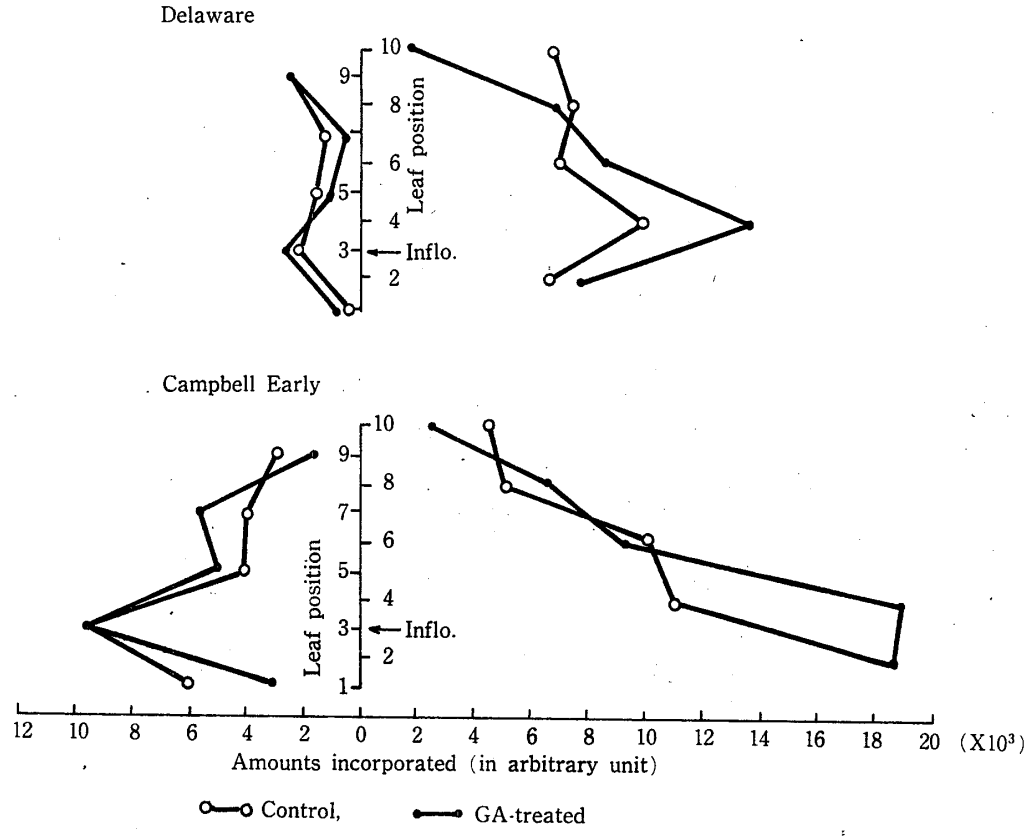

FIG. 4. Estimated amounts of the ^{14}C-assimilates incorporated into GA-treated and -untreated inflorescences from individual leaves during the experimental period.

$\sum_{j=1}^{5}$ Percentage distribution $_{i\cdot j}$ x Percentage total export $_{i\cdot j}$

i: leaf position on the shoot, j: sampling time

In both cultivars, much more ^{14}C-assimilates were incorporated into the inflorescence from the leaves on the same side as the inflorescence than from those on the opposite side of the inflorescence, although, in Campbell Early, incorporation from the opposite leaves could not be neglected. GA treatment increased the incorporation from the 3 basal leaves (L2, L4 and L6) in Delaware and 2 leaves (L2 and L4) in Campbell Early. In addition, incorporation from leaves on the opposite side to the inflorescence was little affected by GA in both cultivars.

The amount of ^{14}C-assimilates incorporated into the inflorescence from the 10 basal leaves at each sampling time was calculated as follows and expressed in arbitrary units (Fig. 5).

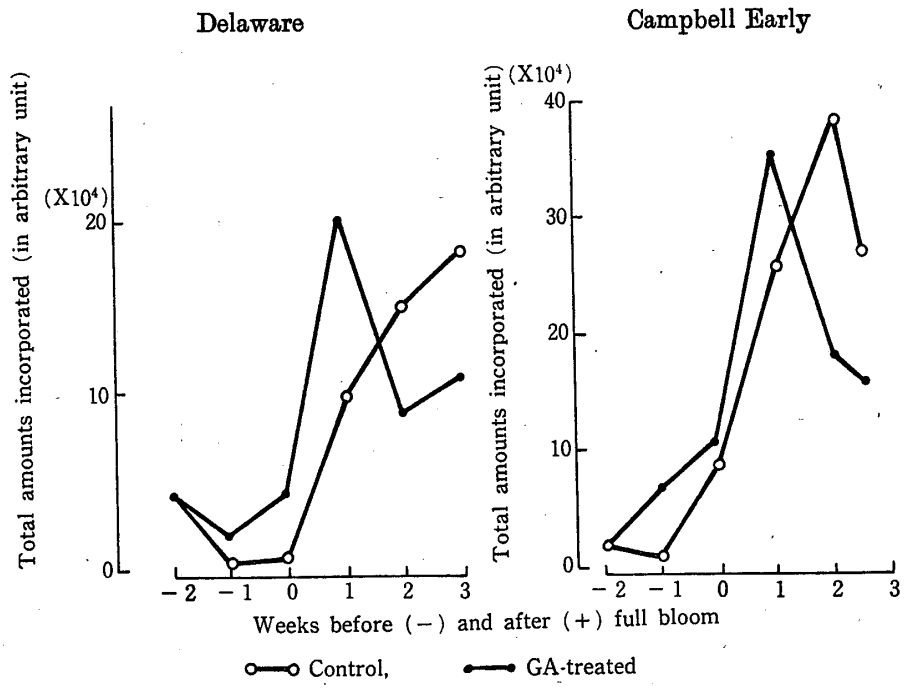

FIG. 5. Time course of the total incorporation of ^{14}C-assimilates into GA-treated and -untreated inflorescences from the ten basal leaves.

$\sum_{i=1}^{10}$ Percentage distribution $_{i\cdot j}$ x Percentage total export $_{i\cdot j}$

In both cultivars, the incorporation was small before full bloom, and decreased a little, 1 week before full bloom. Then, it increased remarkably until 3 and 2 weeks after full bloom in Delaware and Campbell Early, respectively. GA applciation increased the incorporation as compared with the control until it reached a maximum after full bloom. Two and 3 weeks after full bloom, however, it decreased and was smaller than in the control.

5. *Distribution of ^{14}C-assimilates into the apical part of the shoot (Fig. 6).*

Among the basal leaves, those on the same side as the inflorescence (L2 and L4)

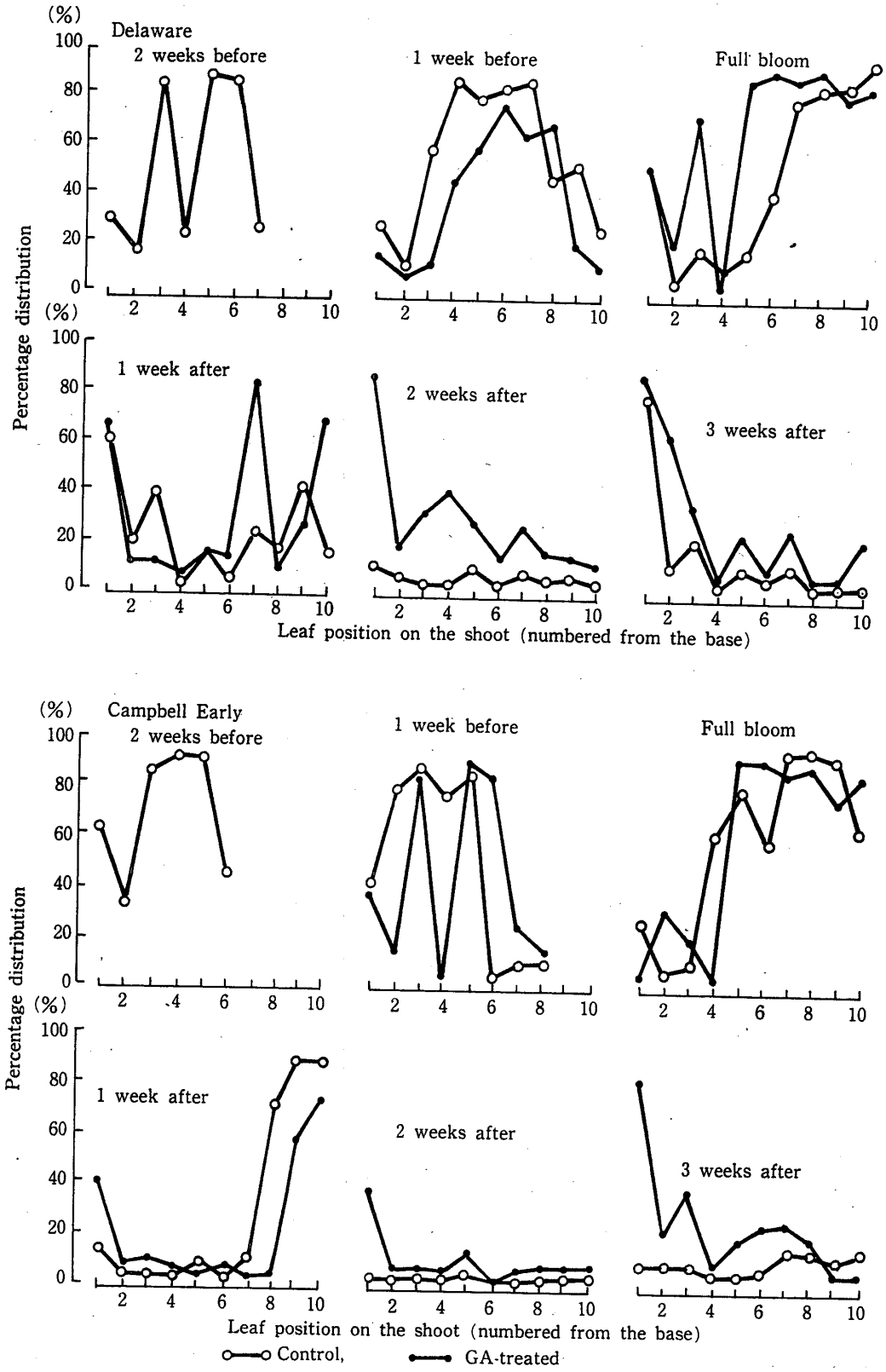

FIG. 6. Distribution of the ^{14}C-assimilates from individual leaves into the apical part of the shoot 24 hours after $^{14}CO_2$ was fed to the individual leaves at different times.

exported little while those on the opposite side to the inflorescence exported much of the ^{14}C-assimilates to the apical part before and at full bloom, although the reverse was true for the export to the inflorescence. At full bloom, a percentage distribution near 100(%) was observed for L7 to L10, from which the inflorescence took up no ^{14}C-assimilates. Moreover, 1 week before full bloom, when the percentage distributions to the inflorescence from L2 and L4 decreased temporarily, those to the apical part increased remarkably. After full bloom, the percentage value to the apical part decreased markedly, but it was striking that in Delaware, L1 continued to be an active source for the apical part, while in Campbell Early, high percentage values were found from L8 to L10 1 week after full bloom.

GA treatment decreased the percentage distribution from the basal leaves to the apical part, as compared with in the control, 1 week before full bloom, while it increased, though only a little, 1 to 3 weeks after full bloom. This was especially true from L1 in Campbell Early.

6. *Export of ^{14}C-assimilates from the inflorescence fed with $^{14}CO_2$.*

When the inflorescence was fed with $^{14}CO_2$ before full bloom, the total activity of ^{14}C found in the whole shoot including the inflorescence was not more than 20–50 (%) of that found when a leaf was fed. Moreover, 24 hours after feeding, ^{14}C activities below 10 (%) in Delaware and 20 (%) in Campbell Early were found in the shoot regardless of GA treatment. These results show that $^{14}CO_2$ is assimilated by the inflorescence *per se*, at least, before full bloom, although in a lower rate than in the leaf, and that a part of the assimilated ^{14}C moves to the shoot out of the inflorescence. This transfer of ^{14}C activity may be due to the phloem translocation, while it may also be possible that the $^{14}CO_2$ respired by the inflorescence was assimilated by the neibouring leaves.

Discussion

It was reported, though the cultivars used were different from those in this paper, that until full bloom, no movement of ^{14}C-assimilates occurred from the fed leaf to the adjacent shoot on the same spur (13, 14) and that at the early stage of berry development, some of ^{14}C-assimilates moved acropetally, but only 1 or 2 internodes below the fed leaf (1). Then, so far as the present experiment was concerned, the export of the ^{14}C-assimilates out of the fed shoot to the parent vine or the adjacent shoots seemed to be negligible.

In Delaware, the 6, 7 and 8 basal leaves were exporting their ^{14}C-assimilates 2 weeks before, 1 week before and at full bloom, respectively. Among them, however, the leaves exporting exclusively to the inflorescence were L2 and L4, which were situated not only just below and above the inflorescence, respectively, but also on the same side of the shoot as the inflorescence, although their neibouring L1, L3 and L5, leaves on the opposite side of the inflorescence, were exporting

mostly to the apical part. Thus, before full bloom, it appeares that the incorporation of the ^{14}C-assimilates from individual leaves into the inflorescence is controlled firstly by the leaf arrangement on the shoot, although the percentage distribution may be modified by the competition between the inflorescence and the shoot apex. When such competition occurred among the 10 basal leaves, L4 rather than L2, the upper leaves rather than the lower ones and the leaves on the opposite side to the inflorescence rather than those on the same side as the inflorescence seemed to be more easily influenced by it.

Such a one-sided translocation in grape shoot has been shown using autoradiography (1), but in the present experiment, it was investigated quantitatively as the percentage distribution to the inflorescence as high as 60 (%) from leaves on the same side as the inflorescence in contrast to that of near 0 (%) from the leaves opposite the inflorescence. On the other hand, the extent of the one-sided translocation from lower leaves to apical, developing ones was suggested to be not so great (14), if any. From the results of this experiment, however, it is impossible to discuss whether it is true or not, because the leaves on both sides of the shoot were included as the apical part.

Although general trend was also similar in Campbell Early, before full bloom, the inflorescence of Campbell Early incorporated the ^{14}C-assimilates mostly from L2 and not from L4, differing from that of Delaware. This difference was recognized repeatedly over 3 seasons, the reason of which seemed to be related to the stronger sink activity of the shoot apex in Campbell Early evidenced by the higher percentage distribution to the apical part.

In both cultivars 1 week before full bloom, it appeared that there was a temporary decrease in the sink activity of the inflorescence, as shown from the lowering in the percentage distribution from L2 and L4, although the time of decrease varied somewhat with seasons. Such a decrease in the sink activity of the inflorescence had been suggested by Hale and Weaver (1) and seemed possibly to be due to the temporary decrease in the growth rate of blossom bud in this stage.

One week after full bloom, the 10 basal leaves were all exporting in both cultivars. Two to three weeks after full bloom, the inflorescence became the exclusive sink for all the 10 basal leaves, although the percentage total export from them decreased to 20 (%) in Delaware and 40 (%) in Campbell Early in average and yet showed a clear saw tooth profile, especially in Delaware, the values being somewhat higher for the leaves on the same side as the inflorescence than those on the opposite side of the inflorescence. It seemed interesting to investigate whether or not such a one-sided pattern of export as well as that of the distribution to the inflorescence could be eliminated when the two adjacent inflorescences opposite to each other were left on the shoot.

The prebloom GA application increased the incorporation of the ^{14}C-assimilates into the inflorescence from L2 and L4 1 week before full bloom and that from L4 at

full bloom, but showed no effect on the incorporation from their adjacent leaves. It was striking that the temporary decrease in the sink activity of the inflorescence just before full bloom was thus prevented by GA application.

After full bloom, the percentage distribution to the GA-treated inflorescence was lower somewhat in Delaware and a little in Campbell Early than that to the control inflorescence. The decrease in the percentage value was larger for the leaves on the opposite side to the inflorescence, and consequently the saw tooth profile became conspicious. In addition, it was interesting that the percentage total export decreased almost in parallel with the percentage distribution to the inflorescence, although the decrease was a little larger in Campbell Early.

However, that may be, the decrease in the incorporation of the ^{14}C-assimilates into the GA-treated inflorescence 2 to 3 weeks after full bloom in Delaware was apparent also in Fig. 5 showing that the amount of total incorporation varied with time, though calculated tentatively. This decrease seemed to be due to the fact that in Delaware, no seeds were formed in the berries of GA-treated inflorescence and in addition the activity of GA applied 2 weeks before full bloom had disappeared before these stages (15–19). Thus, for the further berry development, the postbloom GA application might be required. In the control inflorescence, however, seeds were fully formed, which favoured the further berry development. On the other hand, in Campbell Early, marked thickening and hardening of peduncle and pedicels occured following GA application, and some development of small green berries instead of retained ovaries in Delaware continued until at least these stages. Such growth of the inflorescence as a whole, although not expected to be kept so long, seemed to have resulted in comparatively a small decrease in the incorporation of the ^{14}C-assimilates in spite of there being no seed formation as in Delaware.

The result of feeding to the inflorescence showed that the inflorescence had some photosynthetic ability at least before full bloom, and some of the ^{14}C activity in the inflorescence moved out of it and was found in the shoot. If this movement was due to the translocation via the phloem, it suggests that there may have been simultaneous bidirectional movement. But there seemed to be another possibility that a reversal of movement occurred within the phloem, especially at the time of temporary decrease in the sink activity of the inflorescence.

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