Studies on Translocation and Distribution of Photosynthetic Assimilates in Tomato Plants IV. Retranslocation of ^<14>C-assimilates once Translocated into the Roots

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IV. Retranslocation of ^{14}C-assimilates once Translocated into the Roots

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Summary

The retranslocation of the ^{14}C once translocated into the roots was investigated in tomatoes using bilateral plant method. Tomato plants were pinched above the second leaf, and two lateral shoots were developed. Following cooling the basal part of one of the lateral shoots (the tracing shoot) to 1°–0°C, the ^{14}C assimilated by another shoot (the feeder shoot) was mostly translocated to the roots without decreasing the percentage total export, although little of ^{14}C was found in the tracing shoot above the cooled part. When the tracing shoot was released from cooling while the feeder shoot was removed from its base (at zero time), the ^{14}C once translocated into the roots and main stem was retranslocated up to the tracing shoot with a lag time of 6–12 hours. The magnitude of retranslocation reached 10–13 per cent of the total ^{14}C found in the whole plant 3 to 5 days after zero time at night temperatures of about 20°C. At higher temperatures retranslocation proceeded more rapidly, being completed within 5 days after zero time at day/night temperatures of 30°/24°C. At lower temperatures, however, it was delayed markedly, being still in progress 10 days after zero time at 17°/12°C. Moreover, the retranslocates seemed to be principally amino and organic acids which had been transformed from the translocated assimilates in the roots, and for them the then developing leaves were the strongest sinks.

In the previous reports (1, 2), the percentage distribution of the ^{14}C-assimilates exported from a single source leaf to the roots and the lower stem was shown to be higher at lower air- and higher root-temperatures in tomato plants of the 7- to 15-leaf stages. Moreover, it was suggested that the ^{14}C once translocated into the roots would be retranslocated up to the aerial organs and effectively used to keep plant vigour. The time course and the magnitude of such retranslocation, if it exists, are not necessarily easy to investigate in herbaceous plants such as tomatoes. Pristupa and Kursanov (3) applied $^{14}CO_2$ to pumpkin plants and showed that the ^{14}C once translocated into the roots was rapidly transformed into amino and

organic acids, a part of which they assumed to be retranslocated to the aerial organs. In tomatoes, by applying ^{14}C-amino acids to the roots, and in sugar beets and rice plants, by applying ^{14}C-sugars to the roots, Hall and Cocking (4), Fukuju (5), and Fukuju and Sasaki (6) showed respectively that ^{14}C was retranslocated from the roots to the aerial organs principally as amino and organic acids. Moreover, if we calculated using the results of Fukuju (5) and Fukuju and Sasaki (6), the percentage retranslocation in our terminology of about 14 per cent in sugar beets and about 40 per cent in rice plants were obtained respectively 5 and 10 hours after application of ^{14}C-sugars to the roots. The present experiments were conducted to examine the time course and the magnitude of retranslocation in tomato plants using bilateral plant method.

Materials and Methods

Tomato cultivar 'Fukuju No. 2' was used throughout the experiments.

General Procedures of Bilateral Plant Method.

Seedlings were pricked out into 15-cm clay pots filled with potting compost and grown in a glasshouse under natural daylight. The plants were pinched above the second leaf when they reached the 5- to 6-leaf stages. Following pinching several lateral shoots developed, from which two shoots from the first and second nodes were allowed to grow. The plants were used for experimentation when the lateral shoots reached the 8-leaf stage (Fig. 1). From the shoot developing from the second node the basal two leaves and the apical three leaves including the apex were removed, and the remaining shoot with intermediate three leaves (hereafter designated as the feeder shoot) was enclosed in a polyethylene bag and fed with 20 μCi of $^{14}CO_2$ for 30 minutes. Also, from the shoot developing from the first node (hereafter designated as the tracing shoot) the first and the second leaves were removed, and a pair of cooling collars 3 cm long and made of cupper were fitted around the stem between the first and the second nodes, through which was circulated ethanol cooled to 1°–0°C. A layer of rubber clay was laid between the cooling collars and the stem surface to prevent the mechanical injury to the stem surface. The temperature of the stem surface was kept at 1°–0°C, which was continuously checked by inserting a thermister between the clay and the stem surface. $^{14}CO_2$ was applied to the feeder shoot for 30 minutes beginning at 12.30 hr and at least 10 minutes after the stem surface of the tracing shoot was cooled to 1°–0°C. After feeding, the cooling was continued further for 4 hours. Then, simultaneously with stopping the cooling, the feeder shoot was removed from its base (hereafter designated as zero time). The distribution pattern of ^{14}C within the plant and RSS (Relative strength as a sink, refer to the previous paper (1)) of each plant part were determined at zero time and at intervals thereafter.

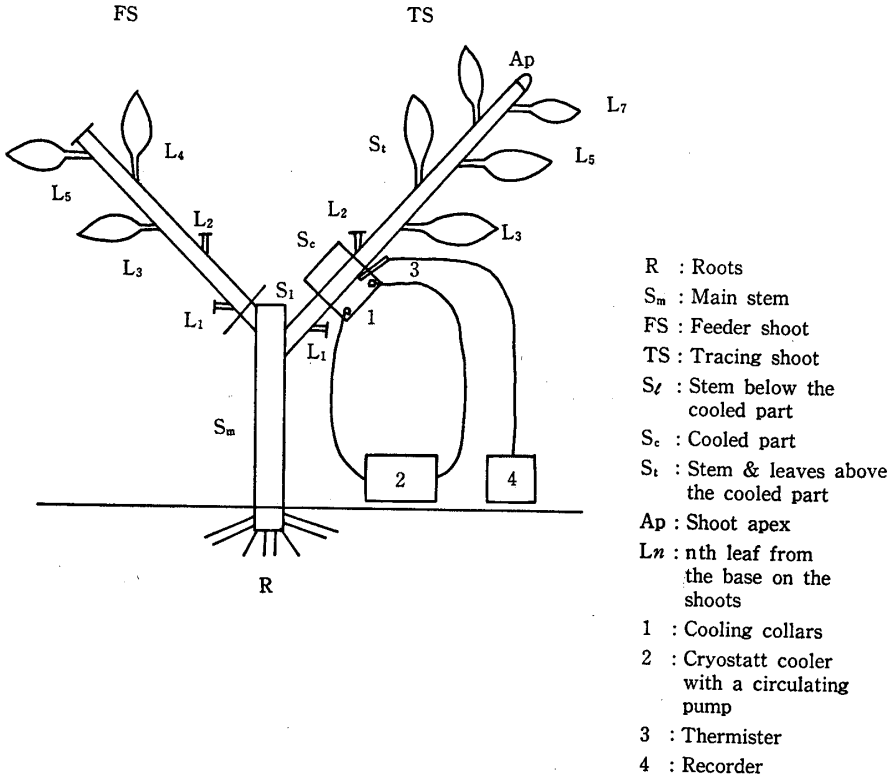

FIG. 1. Bilateral plant used for tracing retranslocation.

Expriments I and II (Time Course of Retranslocation).

The experiments were repeated twice in 1977 (I) and '78 (II). After zero time, the plants which had been treated as mentioned above were transferred to a glass-house at 18°–20°C in the night. Two plants each were harvested after 0, 4 and 12 hours and 3, 5 and 10 days in 1977 and 0 and 6 hours and 1, 3 and 5 days in 1978, respectively. The harvested plants were divided into several component parts as noted in Fig. 2 to 7, which were, then, air-dried, pulverized and determined for ^{14}C radioactivity.

Experiment III (Retranslocation as Affected by Temperature).

At zero time the plants were transferred into day/night temperatures of 17°/12°, 24°/17° and 30°/24°C, and two plants each were harvested after 5 and 10 days, and ^{14}C radioactivity of each component part was determined as in Experiments I and II.

The determination of ^{14}C radioactivity was the same as described previously (1), and the results were expressed as follows.

Percentage total export of ^{14}C from the feeder shoot=(Total ^{14}C in the roots, main stem and tracing shoot/Total ^{14}C in the plant including the feeder shoot)× 100

Percentage distribution of ^{14}C within the plant (or within the tracing shoot)=

(^{14}C in each component part/Total ^{14}C in the roots, main stem and tracing shoot (or Total ^{14}C in the tracing shoot)$\times$100

Percentage retranslocation of ^{14}C=Percentage distribution of ^{14}C to the tracing shoot above the cooled part at a given period after zero time – Percentage distribution of ^{14}C at zero time to the tracing shoot above the cooled part

Results and Discussions

Bilateral Plant Method for Tracing Retranslocation.

The percentage total export of ^{14}C from the feeder shoot to the remaining plant parts 4 hours after feeding was 19–20 (%) whether or not the basal part of the tracing shoot was cooled continuously for the 4-hour period. In the cooled plant, however, 70 per cent of the exported ^{14}C was recovered from the roots and only 3 per cent from the tracing shoot, while in the non-cooled plant 45 and 38 per cent of the exported ^{14}C were distributed to the main stem and roots respectively and as much as 15 per cent was found in the tracing shoot above the cooled part (Fig. 2).

Low temperature, respiration inhibitors such as cyanides and anoxia given regionally to the transport conduit or to an entire sink region were reported to be effective in preventing translocation of photo-assimilates in cucurbits (7, 8), sugar beets (9, 10, 11), sunflower plants (12), saxifraga plants (13), etc.. Moreover,

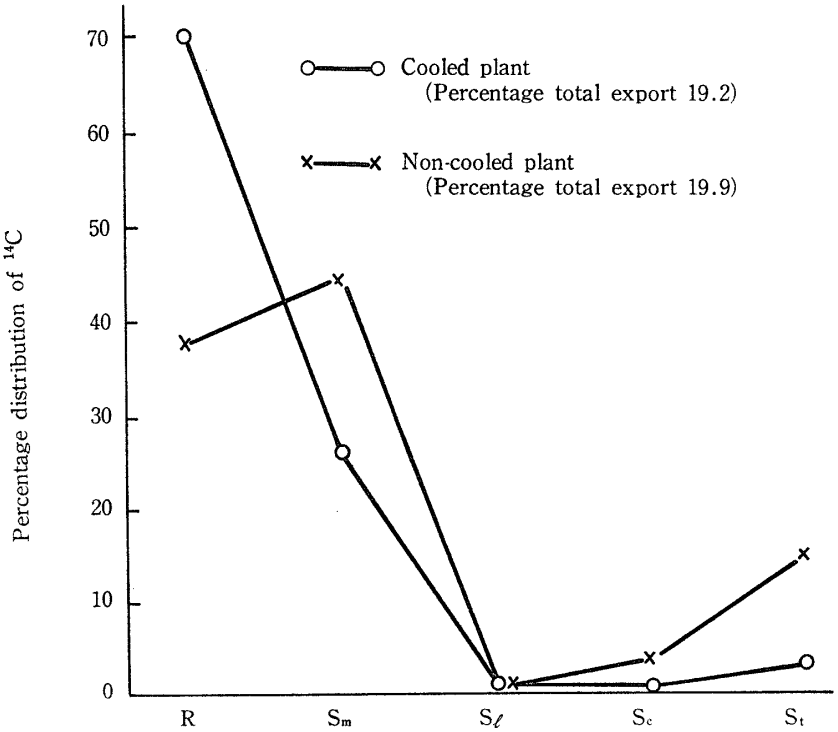

Fig. 2. Effect of cooling on the distribution pattern of ^{14}C exported from the feeder shoot (Exp. I). As to the symbols, refer to Fig. 1.

such effects were recognized to be reversible, at least, in short term experiments. In our bilateral plants, also, the cooling of the basal part of the tracing shoot proved to be effective not only in preventing the upward movement of ^{14}C into the tracing shoot across the cooled part, but also in directing ^{14}C into the roots without decreasing the total export. Thus, bilateral plants proved to be useful models for tracing retranslocation, although the reversibility was not confirmed exactly.

Time Course of Retranslocation.

At zero time, 3.7 and 6.8 per cent of the total ^{14}C exported from the feeder shoot were distributed to the tracing shoot above the cooled part in 1977 and '78 respectively (Fig. 3). Little distribution of ^{14}C across the cooled part seemed to be due to the fact that the inhibition of transport by cooling was not necessarily complete, or a temporary recovery from cooling took place as shown in sugar beets (14). Even so, the value in 1978 seemed somewhat high, the reason of which was unexplainable. The percentage distribution of ^{14}C to the tracing shoot above the cooled part decreased slightly during 6 or 12 hours after zero time. Thereafter, it increased rapidly for about 3 to 5 days, and then the increase slowed down. The reason for the slight decrease of the percentage distribution to the tracing shoot just after zero time was possibly that the inflow of ^{14}C-assimilates into the tracing shoot decreased

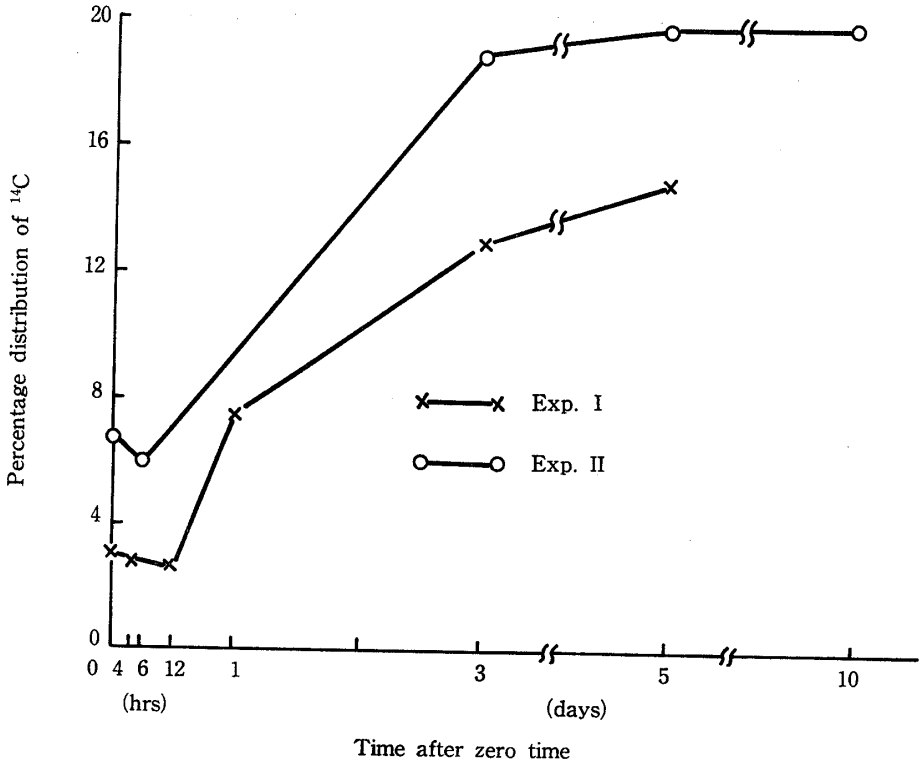

FIG. 3. Distribution of ^{14}C to the tracing shoot above the cooled part in relation to the time after zero time (the time when the feeder shoot was removed from its base while the tracing shoot was released from cooling).

due to the sudden removal of the feeder shoot as a strong source organ as well as the lag time required for the commencement of the normal rate of retranslocation from the roots, and in consequence, the respiratory loss of ^{14}C in the tracing shoot could not be wholly replenished. The percentage retranslocation was obtained as the increase in the percentage distribution of ^{14}C to the tracing shoot above the cooled part during a given period beginning at zero time, though with a reservation that the rate of respiratory loss of ^{14}C was the same in all plant parts. Thus, the percentage values were 10.4 and 12.3 per cent after 3 days and 12.2 and 13.0 per cent after 5 days in Experiments I and II, respectively.

The distribution pattern of ^{14}C within the tracing shoot in Experiment II was shown in Fig. 4. The percentage value in the basal leaves (L 3–6, L–1 was the basal) decreased rapidly from the beginning, that in L7–8 (these leaves were expanding at the feeding time) increased until 3 days after zero time and then decreased, and that in L9 (the apex was included) was still increasing 15 days after zero time. In addition, RSS values were highest in L9 and next highest in L 7–8, both of which had a peak 3 days after zero time. In L 3–6, however, the values were lowest and almost constant throughout the experimental period (Fig. 5). These results seemed to indicate that the retranslocation of ^{14}C once translocated into the roots and main stem proceeded most actively at about 3 days after

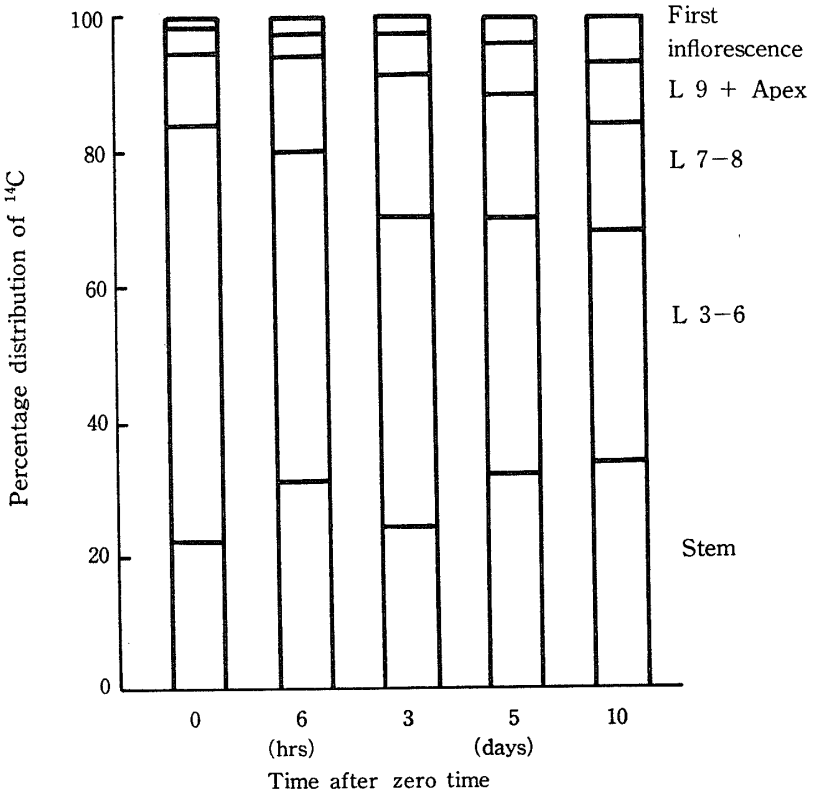

FIG. 4. Distribution pattern of ^{14}C within the tracing shoot above the cooled part varying with the progress of retranslocation.

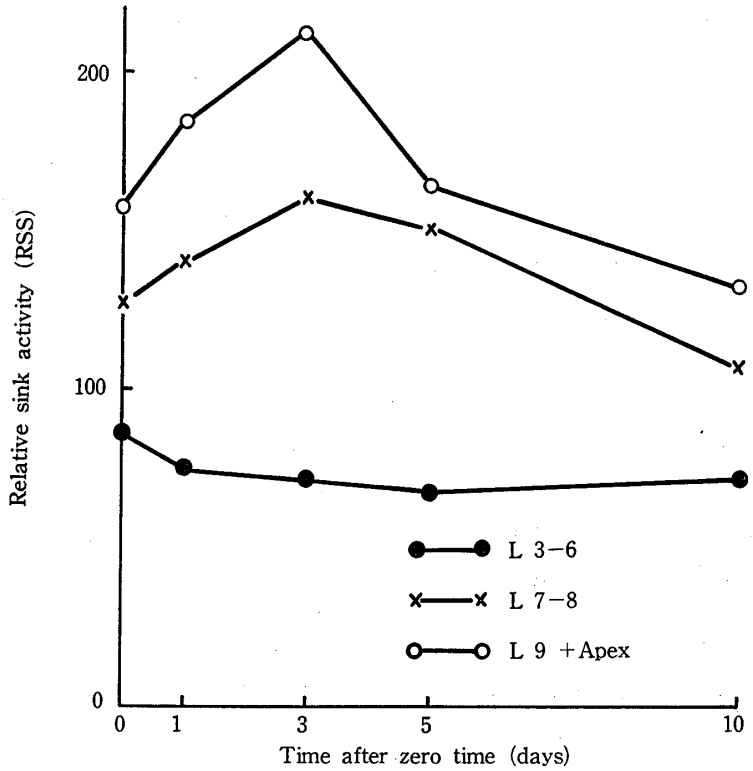

FIG. 5. Sink activity of leaves of the different positions on the tracing shoot varying with progress of retranslocation.

translocated at night temperatures of 18° to 20°C, and also the then developing leaves were the strongest sinks for the retranslocates.

Retranslocation as Affected by Temperature.

In Experiment III, the distribution of ^{14}C at zero time was not measured. The percentage distribution to the tracing shoot above the cooled part 5 and 10 days after zero time was highest at day/night temperatures of 24°/17°C, which was followed by 17°/12°C and 30°/24°C in order but with little difference. Moreover, the increase of the percentage value during from 5 to 10 days after zero time was larger at lower temperatures, being 6.5 per cent at 17°/12°C versus 1.3 per cent at 30°/24°C (Fig. 6).

On the tracing shoot, leaves were divided into three groups of L 3–5 (lower), L 6–8 (middle) and L 9–11 (upper), and the percentage distribution in each group were measured. At 30°/24°C, the percentage distribution to each group of leaves differed little between 5 and 10 days after zero time. This fact appeared to indicate the cessation of retranslocation within 5 days after zero time at high temperatures. At 17°/12°C, the percentage value in the lower leaves was highest 5 days after zero time but it decreased markedly 10 days after zero time, in place of which the percentage value in the middle leaves increased rapidly to surpass the former. The percentage value in the upper leaves increased a little from 5 to 10

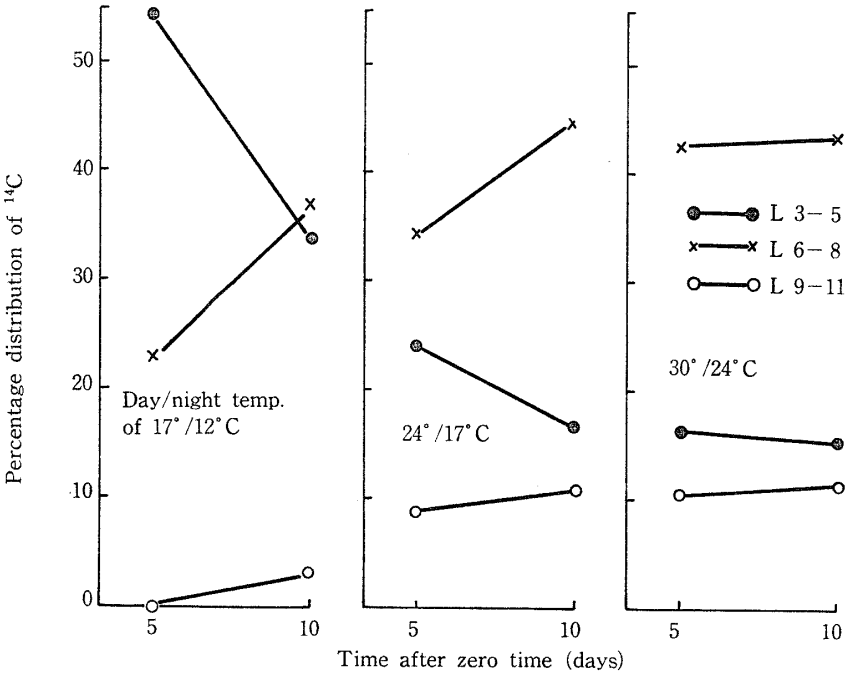

Fig. 6. Distribution pattern of ^{14}C to leaves of different positions on the tracing shoot as affected by temperature.

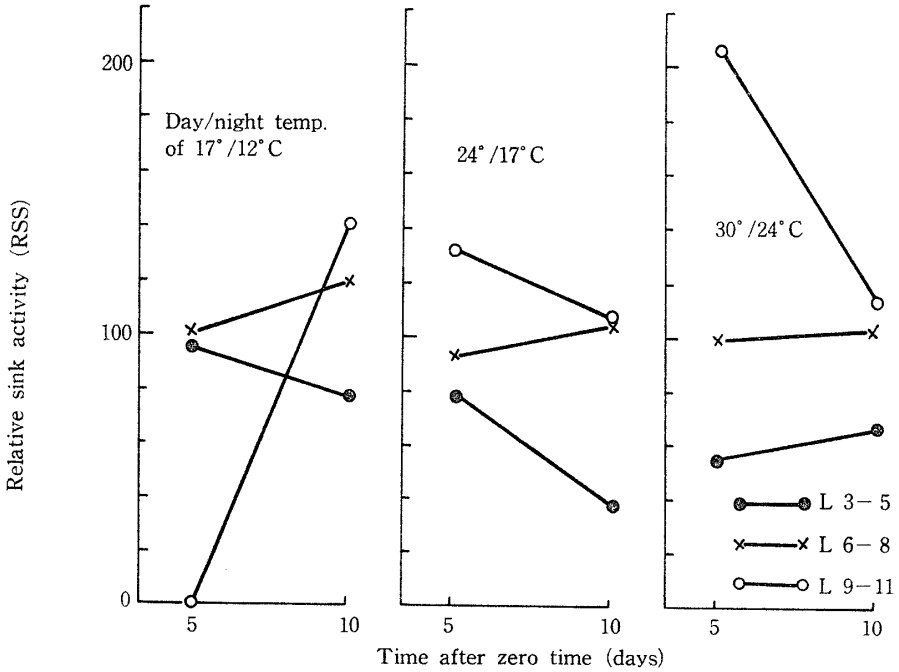

Fig. 7. Sink activity of leaves of different positions on the tracing shoot as affected by temperature.

days after zero time, but it was lower than the value in the lower leaves. At 24°/17°C, the percentage value showed the intermediate trend between those at 30°/24°C and 17°/12°C. As to the RSS values shown in Fig. 7, it was striking that

from 5 to 10 days after zero time, the value of the upper leaves decreased markedly at 30°/24°C, but increased more markedly at 17°/12°C. At 24°/17°C, however, only a slight decrease was found. From these results, it would be probable that the retranslocation ceased within 5 days after zero time at higher temperatures, but at lower temperatures it was still in progress at 10 days after zero time. Moreover, the maximum value of the percentage retranslocation seemed to be obtained at medium temperatures of 24°/17°C.

In herbaceous plants, there are few reports dealing with the retranslocation to the aerial organs of the assimilates once translocated into the roots, especially from a quantitative veiwpoint. In 22-day-old pumpkin plants, 18 to 50 per cent of the ^{14}C-assimilates exported from leaves was reported to enter the root system, of which 60 per cent was transformed into amino and organic acids within 180 minutes, and a part of them was assumed to be remobilized to the aerial organs with the sap (3). In addition, in tomatoes (4), in sugar beets (5) and in rice plants (6), ^{14}C was translocated to the aerial organs as amino or organic acids when it was applied to the roots as ^{14}C-amino acids or ^{14}C-sugars. As to the magnitude of retranslocation, it was reported in sugar beets to be increased by high temperature and light, thus, at 30°C in the light, 11.7 per cent of the ^{14}C initially absorbed to the roots moved to the aerial parts 5 hours after application. This value is equivalent to 14.2 per cent in our terminology of the percentage retranslocation. Similarly, in rice plants, the translocation of the ^{14}C applied to the roots as ^{14}C-sugars was hastened by high air temperature, low root temperature and light. Under such conditions, the percentage retranslocation in our terminology of about 40 per cent was obtained at 10 hours after ^{14}C application. In our experiments, the percentage retranslocation obtained was 10 to 13 per cent at 3 to 5 days after zero time. The discrepancy in the percentage value between Fukuju's and ours can not be well explained, but seemed partly to be due to the difference in the method incorporating ^{14}C into the roots. The pathway and chemical form(s) of retranslocates should be examined hereafter.

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