

# TRANSLOCATION OF PHOTOSYNTHETICALLY ASSIMILATED CARBON IN TEA PLANTS

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In an earlier study (Sanderson & Sivapalan 1966) it was shown that mature tea leaves were more efficient in carrying out photosynthesis than immature ones and that they also had a greater capacity for carrying out this process. These earlier results suggested that the mature leaves (maintenance foliage) on tea bushes were important suppliers of food material for the developing shoot tips (the flush). The question of whether these mature leaves do in fact supply assimilated carbon to the developing shoot tips has now been put to experimental test. As in the previous study, the radioactive isotope of carbon ( $^{14}\text{C}$ ) was used as a tracer, and the location of the tracer in the plant was determined by autoradiographic techniques.

The results of this investigation may be summarized as follows : Carbon assimilated by mature leaves (that is, the leaf directly below the point of attachment of a developing shoot tip) readily moves into the developing shoot tips, and becomes very generally distributed in the growing tissues after a period of 24 hours. Movement into the shoot tips is very much less in banji than in actively growing shoots. Photosynthetically assimilated carbon does not move out of immature tissues nor does it move into other mature tissues ; old leaves do not appear to become boarders on the plant when they become unproductive. Photosynthetically assimilated carbon being translocated out of mature leaves tends to divide itself between movement upwards into the developing shoot tips and downwards in the direction of the roots ; the greater the amount of foliage between the leaf in question and the developing shoot tip the smaller the amount of assimilated carbon which moves upwards into the developing shoot tips. However, if the intervening mature leaves are removed, which removes the primary source of assimilated carbon to the developing shoot tip, the carbon assimilated by mature leaves far separated spatially from the developing shoot tips is readily redirected upwards into the growing tissues.

The results of this investigation suggest that the maintenance foliage may be important in supplying food material to the flush and roots.

## Introduction

Photosynthesis is the photochemical process by which green plants capture part of the radiant energy of sunlight and use it to reduce the carbon in atmospheric carbon dioxide ( $\text{CO}_2$ ) ; an energy consuming process. This process takes place only in green (chlorophyll containing) parts of plants, especially in the leaves. Photosynthesis is of the utmost importance to plants because it is the process on which they depend for their food supply.

We found in an initial study (Sanderson & Sivapalan 1966) that the ability of tea leaves to assimilate carbon photosynthetically varied markedly with age of the leaf. Specifically, it was found that the photosynthetic efficiency (that is, the amount of carbon which a leaf can assimilate per unit weight of leaf tissue) of tea leaves increases rapidly until the leaves are about one-half full grown and that their photosynthetic capacity (that is, the total amount of carbon which a leaf can assimilate) increases until the leaves are fully grown. The results of this earlier investigation suggested that the mature leaves (the maintenance foliage) on a tea plant served as an important source of carbon compounds for the growing parts of the plant ; both the developing shoot tips (flush) and the roots. However, it remained to be shown whether or not the carbon assimilated by the mature leaves was in fact translocated into the growing regions of intact tea plants for utilization there.

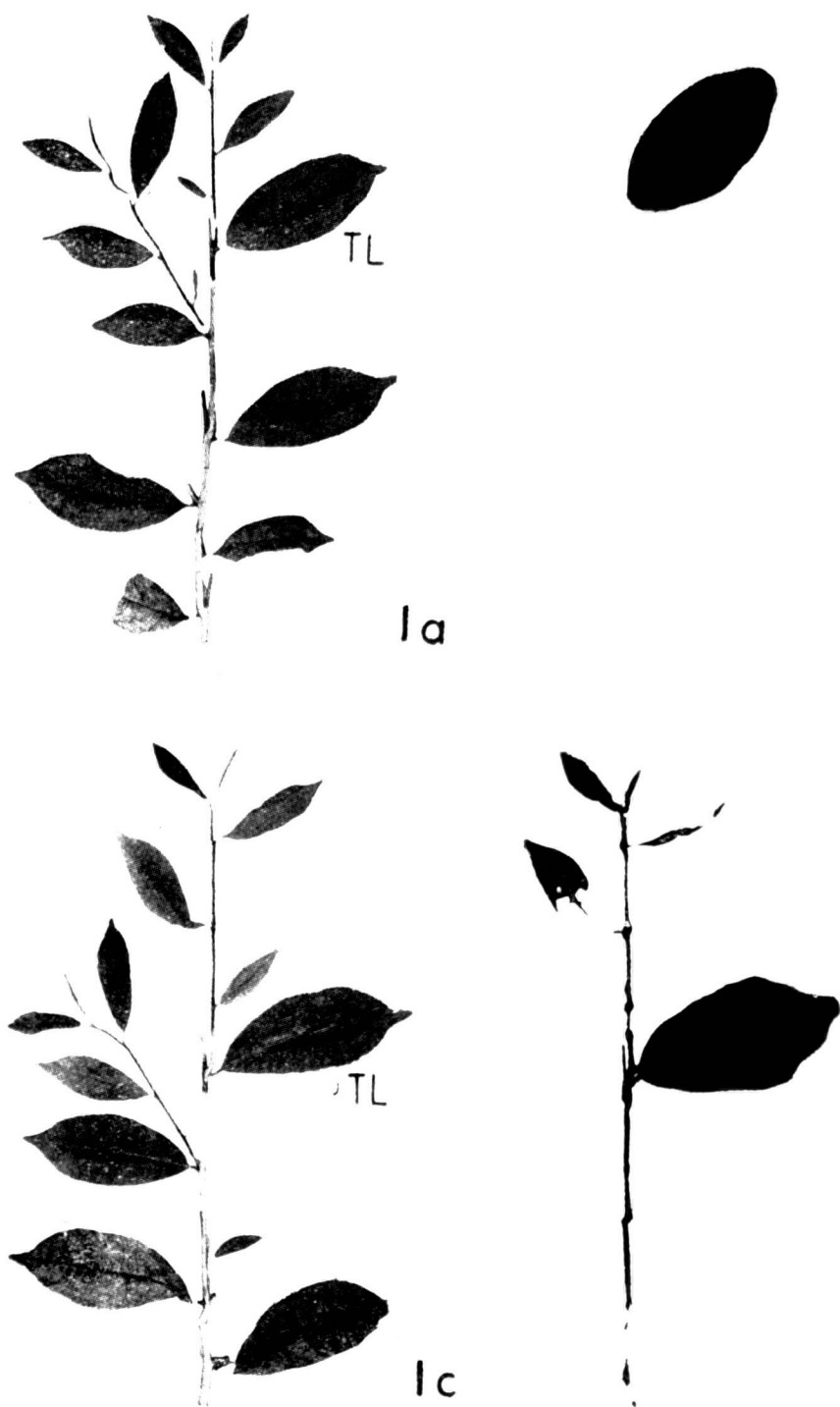
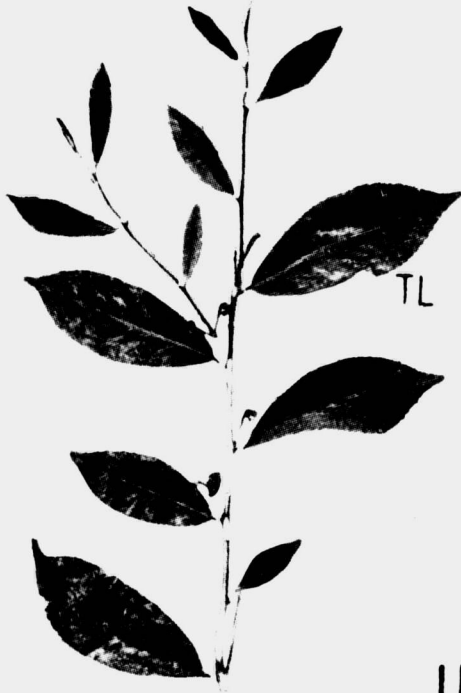


FIGURE 1—Effect of time on the translocation of photosynthetically assimilated carbon out of the treated maintenance leaf (marked TL) — The pressed plant specimen is shown on the left and the autoradiogram is shown on the right — (1a) 20 minutes after exposure to  $^{14}\text{CO}_2$  — (1b) 1 hour after exposure to  $^{14}\text{CO}_2$  — (1c) 4 hours after exposure to  $^{14}\text{CO}_2$  — (1d) 24 hours after exposure to  $^{14}\text{CO}_2$



1b



1d





FIGURE 2—Translocation of photosynthetically assimilated carbon out of a maintenance leaf (marked TL) just below banji shoot tips — This specimen (on the left) was collected 24 hours after exposure to  $^{14}\text{CO}_2$ ; the autoradiogram is on the right



FIGURE 3—Translocation of photosynthetically assimilated carbon out of developing shoot tips (marked TL).—This specimen (on the left) was collected 24 hours after exposure to  $^{14}\text{CO}_2$ ; the autoradiogram is on the right.—Note that no movement of assimilated carbon from the treated tissues has taken place.

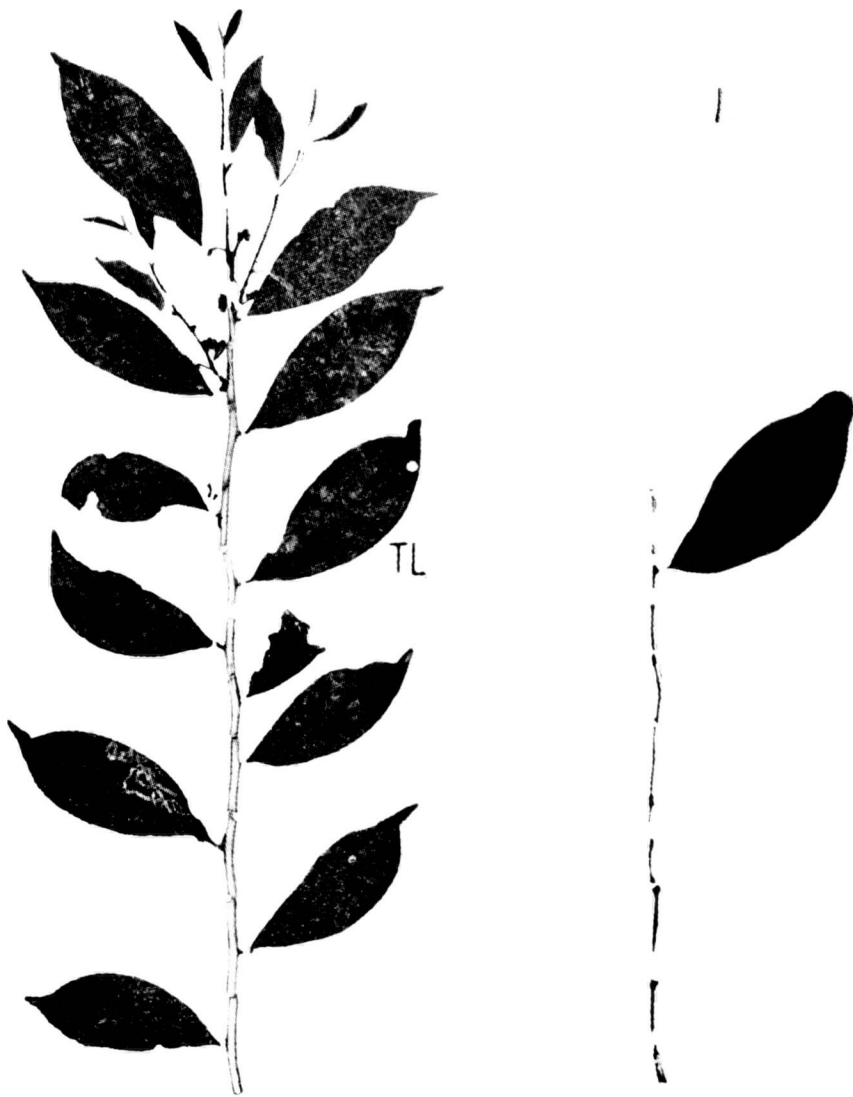


FIGURE 4—*Translocation of photosynthetically assimilated carbon out of a mature leaf (marked TL) removed from the nearest developing shoot tip by 3 other mature leaves — This specimen (on the left) was collected 24 hours after exposure to  $^{14}\text{CO}_2$ ; the autoradiogram is on the right—Note that a small amount of assimilated carbon has moved upwards to the developing shoot tip*

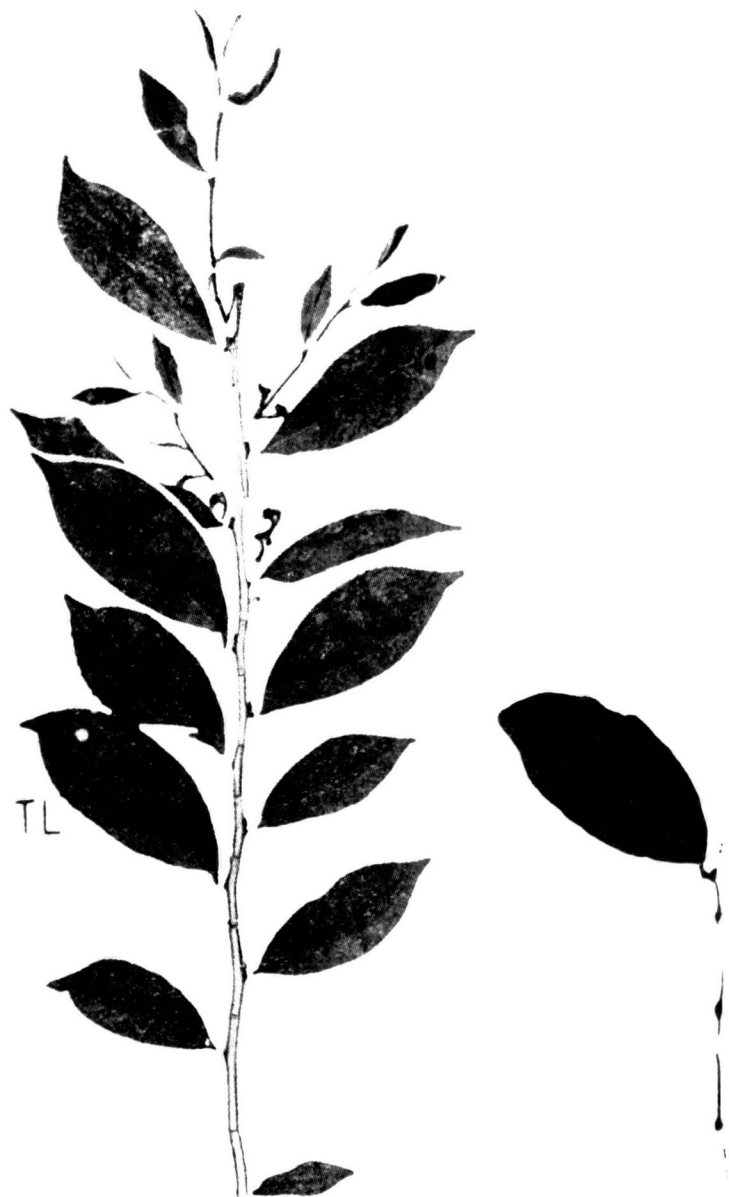


FIGURE 5—*Translocation of photosynthetically assimilated carbon out of a mature leaf (marked TL) removed from the nearest developing shoot tip by 6 other mature leaves — This specimen (on the left) was collected 24 hours after exposure to  $^{14}\text{CO}_2$ ; the autoradiogram is on the right — Note that no assimilated carbon has moved upwards in the shoot; all translocation has been downwards in the direction of the roots*

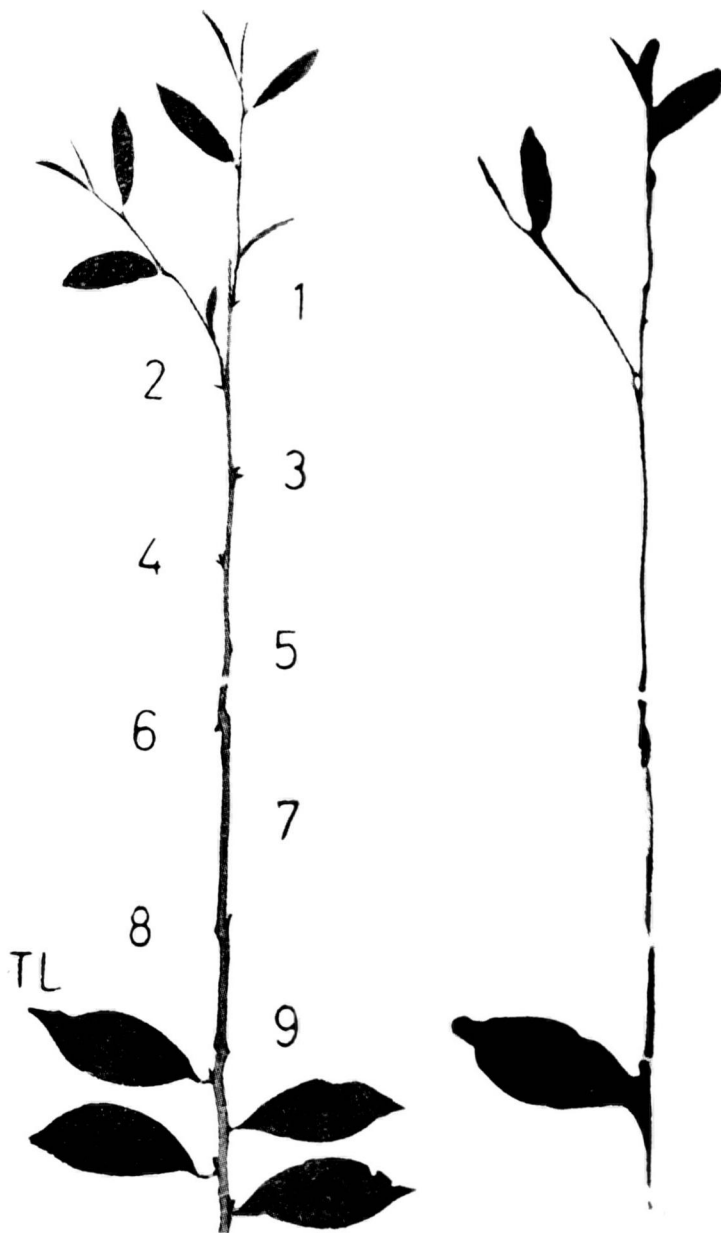


FIGURE 6—*Translocation of photosynthetically assimilated carbon out of a mature leaf (marked TL) which had been removed from the nearest developing shoot tip by 8 other mature leaves which were removed before exposure of the treated leaf (TL) to  $^{14}\text{CO}_2$  — This specimen (on the left) was collected 24 hours after exposure to  $^{14}\text{CO}_2$ ; the autoradiogram is on the right — Note that there is extensive translocation of assimilated carbon upwards into the developing shoot tips under these conditions*



FIGURE 7—*Translocation of photosynthetically assimilated carbon out of a mature leaf (marked TL) when the adjacent leaves (shaded) are kept in the dark — This specimen (on the left) was collected 24 hours after exposure of the treated leaf to  $^{14}\text{CO}_2$ ; the autoradiogram is on the right — Note that assimilated carbon did move out of the treated leaf but that none of it moved into the starving (darkened) mature leaves*

In this paper we report the results of further experiments in our investigation of photosynthesis in tea plants in which we have determined the translocation pattern of photosynthetically assimilated carbon in intact tea plants in the field.

### Materials and Methods

All experiments were carried out in the field on intact tea bushes in a block of clone TRI 777. A perspex treatment chamber was fitted over the leaf to be treated (marked TL in Figures through) and the carbon dioxide ( $\text{CO}_2$ ) labelled with radioactive carbon ( $^{14}\text{C}$ ) was introduced into the treatment chamber by means of a hypodermic syringe. In every treatment 60  $\mu\text{c}$  of  $^{14}\text{CO}_2$  was introduced into the treatment chamber and photosynthesis in the presence of  $^{14}\text{CO}_2$  was allowed to continue for 15 minutes.

After the 15 minutes treatment period, the treatment chamber was removed and the shoot carrying the treated leaf was allowed to remain on the tea bush until the prescribed time for sampling. At the time of sampling, the shoot carrying the treated leaf was cut from the bush and removed to the laboratory for dissection to prevent any further translocation of materials within the shoot ; this operation was completed within five minutes of the time of sampling. After dissection the shoots were pressed and air dried in an oven at  $90^\circ\text{C}$ . The dried specimens were then mounted on sheets of paper (with UHU glue) for autoradiography.

Autoradiography was done by placing the mounted plant specimens next to sheets of Kodak No Screen X-ray film and leaving them pressed together in a light-tight box for four days (see Yamaguchi & Crafts 1958). During this period the radioactivity present in the plant specimens reveals itself by exposing the film. Finally, the location of the radioactivity in the plant specimen is determined by comparing the mounted plant specimen with the developed X-ray film (called the autoradiogram).

### Results and Discussion

In the first set of experiments selected leaves were fed with  $^{14}\text{CO}_2$  and the movement of the photosynthetically assimilated carbon was studied. As shown in Figure 1, photosynthetically assimilated carbon moves steadily out of the treated leaves into the developing shoot tips and it also moves down the stem, presumably to the roots. Within 24 hours after treatment with  $^{14}\text{CO}_2$  the assimilated carbon has become widely distributed in the developing tissues both above and below the point of attachment of the treated leaves (Figure 1d).

If the young shoots are banji, the movement of assimilated carbon from the maintenance leaf into these shoots is very much reduced (compare Figures 1d and 2). If the shoot tip itself is the part of the plant which is fed  $^{14}\text{CO}_2$ , the assimilated carbon does not move from the site of assimilation (Figure 3).

The translocation of carbon which has been photosynthetically assimilated by mature leaves attached to shoots below the point of attachment of developing shoot tips and separated from the developing shoot tips by other mature leaves tends to be divided between movement upwards into the developing shoot tips and downwards in the direction of the roots ; the more mature leaves there are between the treated leaf and the developing shoot tip the less the amount of translocation upwards, until a point is reached when all the translocation is downwards. This is clearly seen by comparing Figure 1d (no mature leaves between the developing shoot tips and the treated leaf), Figure 4 (three mature leaves between the nearest developing shoot tip and the treated leaf), and Figure 5 (six mature leaves between the nearest developing shoot tip and the treated leaf). These results indicate that

photosynthetically assimilated carbon is directed into the immature tissues of the flush from the mature ones but that when the requirements of the developing tissues are adequately supplied by leaves above the leaf in question the assimilated carbon moves downwards. The fact that the leaves far removed from the developing shoot tips are able to supply assimilated carbon to these tissues if needed was demonstrated in an experiment in which nine mature leaves between two developing shoot tips and the leaf to be treated were removed just before treatment with  $^{14}\text{CO}_2$ . As can be seen from Figure 6, under these conditions the assimilated carbon was readily translocated upwards to feed the developing tissues.

It was noticed that in no case did assimilated carbon move into mature leaves (see Figures 1 and 6). Two possible explanations for this observation are :

- 1 — A mechanism exists in the tea plant which prevents food materials (such as photosynthetic assimilates) from being translocated into mature leaves.
- 2 — Food materials can move into mature leaves when they are required, but no movement into these leaves was observed because under the conditions of our experiments all the mature leaves under study were well exposed to sunlight and they were able to assimilate enough carbon by themselves to supply their food requirements.

It is important to attempt to distinguish between these two possibilities because, as was noted earlier (Sanderson & Sivapalan 1966), in the field the older leaves are often heavily shaded by newer foliage above and it may be that under these conditions they become boarders on the more exposed, and therefore productive, foliage of the bush. An experiment was, therefore, designed to determine whether or not photosynthetic assimilates would move into mature leaves when they were kept under conditions in which they could not manufacture their own food (that is when they were prevented from photosynthesizing their own food by keeping them in the dark). In this experiment the mature leaves were placed in the dark by covering them completely with envelopes of black paper. As shown in Figure 7, even after 24 hours no photosynthetically assimilated carbon had moved from the treated leaves into the adjacent starving leaves which had been kept in the dark throughout this period.

The results of these experiments show that the mature leaves on a tea bush are important suppliers of carbon compounds to the developing shoot tips (flush) and to the roots. These results amplify the results of our earlier investigations (Sanderson & Sivapalan 1966) and they add support to the contention that the maintenance foliage of tea bushes is important in supporting the growth of the flush (Barua 1961 ; Sanderson & Sivapalan 1966), and in supplying food materials to the roots.

### **Summary and Conclusions**

An investigation of the pattern of translocation of photosynthetically assimilated carbon in tea clone TRI 777, has been made using radioisotopes combined with autoradiographic techniques. The results of this investigation may be summarized as follows :

- 1 — Carbon assimilated by mature leaves is translocated out of these leaves into the developing shoot tips and down the main stem, presumably direct to the roots. The division of the assimilates being translocated between the developing shoot tips and the roots depends on the number of mature leaves between the leaf in question and the developing shoot

tip : the more leaves between these two the smaller the amount of the assimilates which are translocated upwards into the developing shoot tips.

- 2 — Carbon assimilated by immature tissues does not move out of these tissues.
- 3 — Assimilated carbon does not move into mature leaves : mature leaves do not appear to become boarders on the remainder of the tea bush under the conditions of the experiment.

These results support the contention that the maintenance foliage on tea bushes is important in nurturing the developing shoot tips and roots.

### Acknowledgements

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