Artículo por invitación

CARBOHYDRATE DISTRIBUTION IN THE STRAWBERRY PLANT

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The production of assimilates through photosynthesis and their distribution within the plant are important processes which help determine plant growth and development (Forney and Breen, 1985). Plant growth is a result of complex inter-relationships between physiological and morphological processes in the meristems, response to internal and external factors and supply of metabolites and inorganic nutrients (Moorby, 1981). Hence, efforts to improve plant growth and development (yield) must be related to those inter-relationships.

Carbohydrates are essential for strawberry plant growth and development. It has been established (Long, 1935; Greve, 1936; and Bringhurst *et al.*, 1960) that the amount of carbohydrates stored during late summer, autumn or winter (dormancy stage) influenced strawberry plant performance on plant establishment or following dormancy. These responses however may be affected by variety or type (Duner *et al.*, 1985) or by environmental conditions, e.g. photoperiod and temperature (Greve, 1936; Bringhurst *et al.*, 1960; Mass, 1986).

Although the production and distribution of assimilates are affected by several factors, e.g. water, light, temperature (Moorby, 1981), the literature included herein will discuss the pattern of carbohydrte movement in the strawberry plant. Research on carbohydrate movement in the strawberry variety Hapil reported in this thesis only involved qualitative observations on the pattern of distribution, based on detection of ^{14}C-labelled substances by an autoradiographic technique.

Plant organs with a net demand for assimilates (sinks) strongly influenced their production and distribution (Gifford and Evans, 1981). Experimental evidence has shown that fruiting enhances photosynthesis in strawberry (Wolkowa *et al.*, 1974; Choma *et al.*, 1982; Forney and Breen, 1985) as compared to plants that have been deblossomed. Schaffer *et al.* (1985), however, found no differences in the amount of ^{14}C initially fixed by the treated leaf of fruiting and non- fruiting day neutral strawberry plants. Similarly, Lenz and Bünemann (1967) and Schaffer *et al.* (1985) found no differences in total dry weight between fruiting and non-fruiting strawberry plants.

Studies on the distribution of assimilates (dry matter partitioning) in strawberry have been carried out mainly on fruiting plants. The fruit is a strong sink which can accumulate 40 to 50% of total dry weight (Olsen *et al.*, 1985; Forney and Breen, 1985) causing, in most cases, a reduction in growth of other vegetative parts, e.g. roots, leaves, runners, crowns (Jahn and Dana, 1966a; Lenz and Bünemann, 1967; Forney and Breen, 1985). However, in the absence of fruit photosynthates are traslocated to leaves, crowns and roots (Lenz and Bünemann, 1967; Choma *et al.*, 1982).

It has been shown that the intesity of photosynthesis in strawberry varies depending on the stage of fruit development i.e. at an advanced stage of fruit development photosynthesis activity is more intense and thus, the more intense the transport of assimilated substances from leaves to petioles, crowns, roots, fruit pedicels and fruits. Transport of assimilates to the roots diminishes in the middle of fructification (Fabian-Galan, 1968).

Antoszewski and Dzieciol (1973), indicated that fully expanded strawberry leaves exposed to $^{14}CO_2$ exported 40-60% of their labelled assimilates within two days and that the remainder was retained for at least one week. Leaves exposed to $^{14}CO_2$ at weekly intervals exported more labelled assimilates as leaves increased in maturity. With treated young leaves labelled assimilates tended to stay in the treated leaf. Assimilates were mainly translocated to organs which were growing at that time (e.g. fruit).

Schaffer *et al.* (1985) detected, 48 hours after treatment with $^{14}CO_2$, radioactivity in the treated leaf,

untreated leaves, crowns, roots and fruits (if present) of fruiting and deblossomed strawberry plants (60% of total ^{14}C assimilated remained in the treated leaf). In deblossomed plants (^{14}C)-photosynthates moved mainly into the leaves (34%) (crown and roots 4% each) whilst in fruiting plants they moved into untreated leaves (16%), fruits (13%), roots (7%) and crowns (4%). There appears, therefore, to be a direct relationship between the amount of radioactivity detected and the amount of dry matter per fraction.

Results reported by Nishizawa and Hori (1986) indicate that the translocation of ^{14}C-assimilates from unfolding leaves was low though from fully expanded leaves in reached up to 45%. They concluded that the position of the leaf influenced the distribution of assimilates. Of the total ^{14}C-assimilates used for new apical growth, up to 85% was exported from leaves situated at the top of the crown and up to 40% from leaves at the crown base. For root growth, however, up to 75% of ^{14}C- assimilates were exported from leaves at the crown base and up to 29% from leaves at the crown top.

Therefore the objective was to study the carbohydrate relationships between the mother and daughter runner plants growing in solution culture under controlled enviroment conditions.

MATERIAL AND METHODS

Micropropagated strawberry plants, variety Hapil, were treated with $^{14}CO_2$ at 4, 6 and 12 weeks after weaning. The experiment was carried out in a controlled environment room.

$^{14}CO_2$ was supplied by enclosing a fully expanded leaf in a 'Melinex' polyester film (400 -gauge) chamber (Quinlan, 1965). The base of the chamber was clipped to provide a gas-tight seal of closed-cell sponge rubber over the petiole. $^{14}CO_2$ was generated from $NA(^{14}C)CO_3$ by addition of excess of 1N HCl. At the 4 week stage air containing $^{14}CO_2$ was drawn from a gas generator (Priestley, 1980) and injected (3 ml containing 5 μCi) into each assimilation chamber. At the 6 and 12 week stages measured doses of the labelled carbonate (5 μCi) were injected into a vial in each assimilation chamber followed by the addition of HCl (Quinlan, 1965).

$^{14}CO_2$ was applied (injected) between 11:00 and 11:30 hrs. The chambers were kept in place for 4 hrs following treatment and then removed.

In all stages of growth the treatments, which were replicated twice, included.

(a) $^{14}CO_2$ treatment to a leaf on the mother plant.

(b) $^{14}CO_2$ treatment to a leaf on the mother plant, with an emerging stolon.

(c) $^{14}CO_2$ treatment to a leaf on the primary runner of a stolon

Plants were harvested 48 hrs after treatment and held in a refrigerator at 4°C until the plants were dissected and mounted on paper on the same day. Mounted specimens were placed between sheets of blotting paper and left to dry, under slight mechanical pressure, in a freeze dryer at -40°C for a minimum of one week.

Carbohydrate movement was determined by autoradiography. This was achieved by putting the dry mounted specimens, after a 72 hr pressing period, in contact with a Kodak 'X-Omat G' X-Ray film for 14 days. The film was then developed with Kodak LX-24 X-Ray developer and fixed with Kodak FX-40 X-Ray liquid fixer (Yamaguchi and Crafts, 1958; Schaffer *et al.*, 1985).

RESULTS

Results indicate that (^{14}C)-photosynthates are distributed from the treated leaf on the mother plant to all actively growing plant parts e.g. emerging leaves, roots and developing stolons (plates 1, 3, 5) during all growth stages studied (4th, 6th and 12th week growth stages of the June bearing variety Hapil grown in solution under 16 hrs photoperiod, 20/18°C day/night temperatures, 170.9 $mol/m^2/s$ light irradiance). However, when the treated leaf was on the primary runner plant of a stolon at the 4th week growth stage, (^{14}Cl-photosyntrates were found either in the treated runner plant or in the secondary and subsequent runner plants on the same stolon (plate 2). At the 6th and 12th week growth stages (^{14}C)- photosynthates were found in runner plants on the same stolon and in the root system of the mother plant (plates 4 and 6). No evidence of (^{14}C)- photosynthates was found in the crown or leaves of the mother plant. In all cases where the treated leaf was on the runner of a stolon the (^{14}C)-photosynthates were also found in actively growing plant parts (plates 2, 4, 6). Agreement between replicates was good.

DISCUSSION

The results show that the carbohydrate relationship between the mother and daughter runner plant of the strawberry variety Hapil, grown in solution culture under controlled environment conditions, was dependent on the conditions imposed by source-sink inter- relationships (Canny, 1984).

(^{14}C)-photosynthates, at the different growth stages assessed, were exported within 48 hours from

$^{14}CO_2$-treated leaves, on either mother or daughter runner plants, to other actively growing plant parts (e.g. emerging leaves, developing stolons and/or roots). These were the plant organs or sinks with a high demand for assimilates to fulfill requirements imposed by growth (Gifford and Evans, 1981); some (^{14}C)-photosynthates, however, also remained in the treated leaf. Similar results for strawberry plants have been reported by Antoszewski and Dzieciol (1973) and Schafeer *et al.* (1985).

Due to the qualitative characteristic of the method used for measurement of ^{14}C-activity, it was difficult to establish if there were quantitative differences in the amount of (^{14}C)- photosynthates distributed to each growing area. The results, however, are discussed on the assumption that the darker the area on the radiographs the greater the amount of labelled assimilate imported from the treated leaf.

For all treatments and plant growth stages assessed, it was found that greater amounts of labelled assimilates were in sinks closer to the treated leaf (source), confirming the observations of Canny (1984) and Nishizawa and Hori (1986) who also worked with strawberry. An example of this effect is shown in plate 1, here the radiograph shows that a branch crown on the mother plant situated opposite to the treated leaf is less dark than the newly emerging stolon and leaf on the mother plant (plate Ic), implying that greater amounts of (^{14}C)-assimilates have been imported from the treated leaf. When the treated leaf was on the primary runner of a stolon, at the 4th week growth stage, the (^{14}C)-photosynthates are exported to newly growing areas on the runner itself or to subsequent runner plants on the same stolon and to the stolon growing tip. Similar patterns of movement were found at the 6th and 12th week growth stages but, in addition, (^{14}C)- photosynthates were also detected in the roots of the mother plant. This implies that assimilates produced in the primary runner area distributed depending on the position and requirement of the sink. A the 4th week growth stage the runner and the rest of the stolon, which at the time were growing actively, are the dominant sinks on the stolon. However, at the 6th and 12th week growth stages, the stolon on which the treated runner was situated had several runners which were also producing carbohydrates used to support new growth on the stolon. This may have caused (^{14} C)-photosynthates from the treated runner leaf to be distributed to the new and actively growing roots of the mother plant which may have been the closest and most dominant sinks.

This indicates, therefore, that the stolon will depend entirely on photosynthates from the mother plant until the primary runner has developed a particular leaf size or area so as to become carbohydrate self-sufficient and able to export photosynthates to subsequent stolon growth. Canny (1984) suggested that this critical leaf size was approximately half the final leaf area. Later, particularly in situations like those in this experiment where the runners did not root, movement of photosynthates may occur in the opposite direction depending on the source-sink inter-relationship.

The root results for plants treated on the mother plant showed differences between growth stages. More (^{14}C)-photosynthates were, apparently, moved into the roots at the 6th week growth stage as indicated by the darker radiographs; this also occurred with plants with a treated runner. Differences may be associated with greater root growth activity at the 6th week growth stage than at other stages. it is clear, however, that root growth occurred for the duration of the experiment along with shoot growth. This was observed with plants of Hapil grown under the same conditions during the growth and nutrient uptake determination experiments. Additionally, the pattern of (^{14}C)-photosynthates movement into roots could be associated with the participation of assimilates in the processes of energy supply which are necessary for nutrient uptake (Epstein, 1972; Pitman *et al.*, 1976).

The distribution of carbohydrates in the growing system used in this experiment, where the plants only grew vegetatively and the runners did not root, operates according to the source-sink inter-relationships within the plant.

It would be of interest to extend this study to plants grown under the same culture system but which are in flower production and whose runners were allowed to root, and also to plants grown under field conditions. The information obtained would help relate the mineral nutrition of the plant with carbohydrate production.

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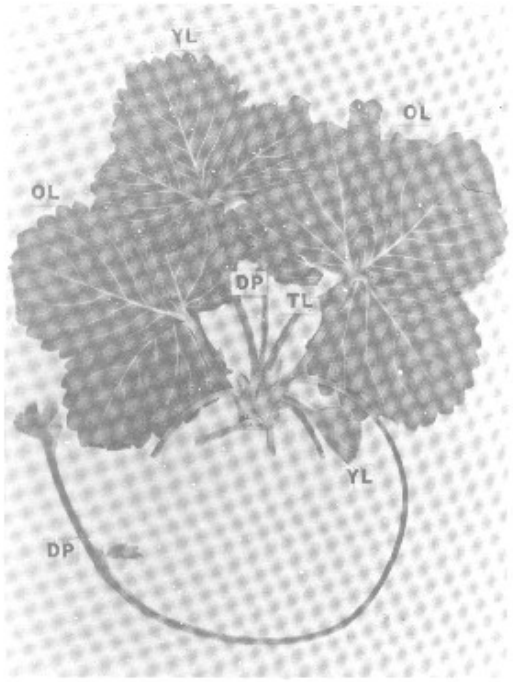

(ai)

(aii)

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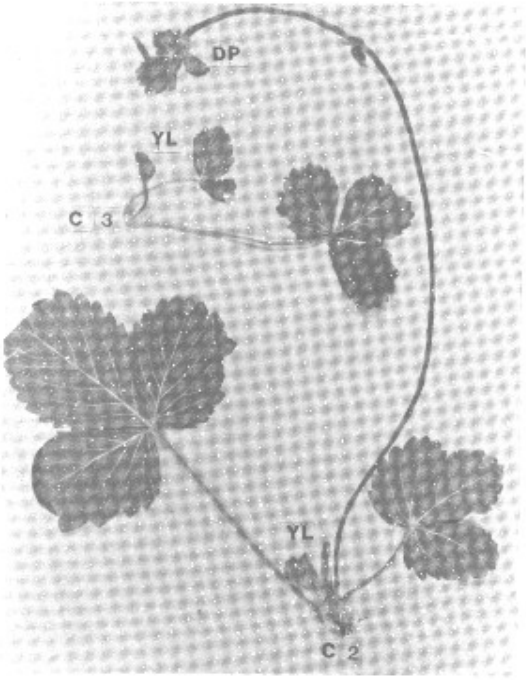
(bii)

Plate 1. (a_i) Strawberry mother plant treated at the 4th week growth stage with $^{14}CO_2$; treated leaf (TL); young leaves (YL) old leaves (OL) and daughter runner plants (DP).
(a_{ii}) Autoradiograph indicates the [^{14}C]-assimilates have been transported into actively growing areas of daughter plants and young leaves.
(b_i) Root system of traeted mother plant.
(bii) Autoradiograph indicates that [14C]-assimilates have moved into the roots.



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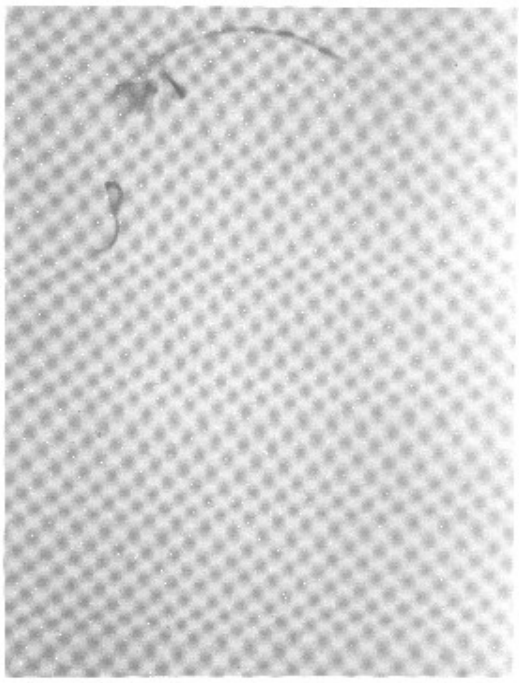
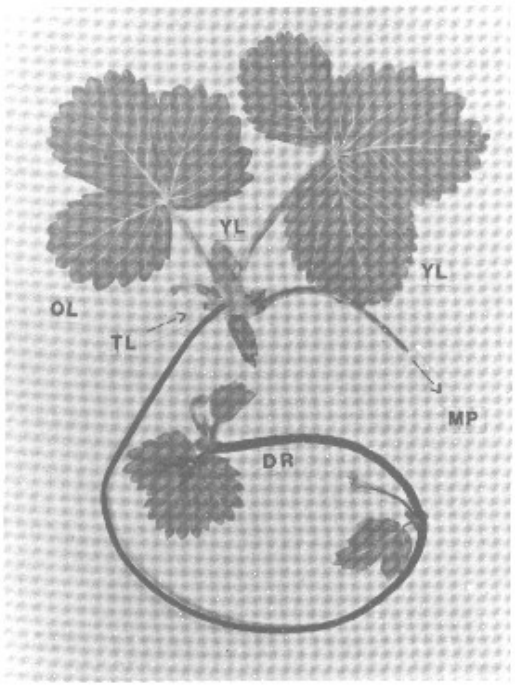


(cii)

(c$_i$) Branch crowns (C2, C3) on treated mother plant (3a).

(c$_{ii}$) Autoradiograph shows [^{14}C]-assimilates in actively growing areas. C2 was sited opposite the treated leaf and received, apparently, less [^{14}C]-assimilates.



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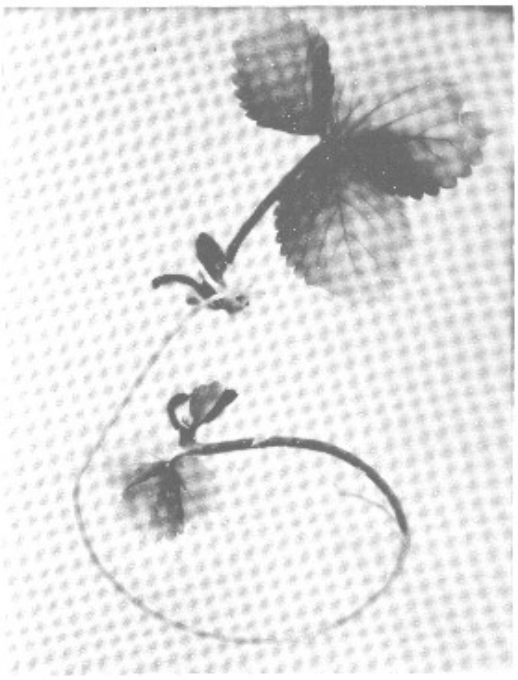
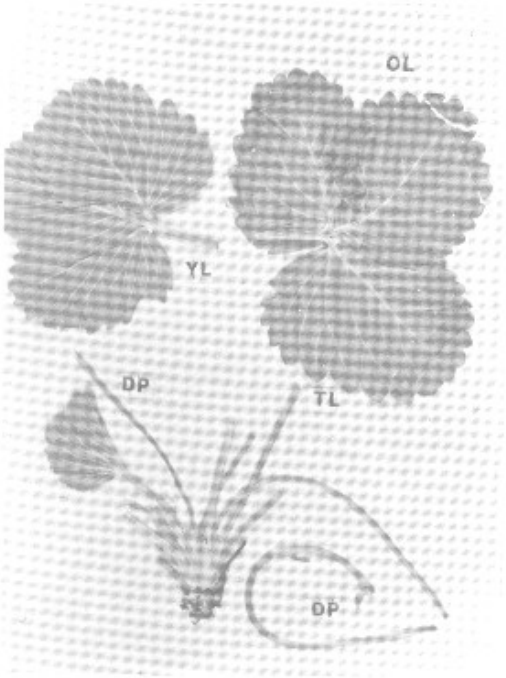


(aii)

Plate 2. Strawberry runner plant treated at the 4th week growth stage with $^{14}CO_2$. (a_i) The position of the treated leaf is indicated by (TL), old leaf (OL), young leaves (YI), subsequent stolon (DR) and position of mother plant (MP). (a_{ii}) The autoradiograph indicates that [^{14}C]-assimilates did not move into old leaves or towards the mother plant.



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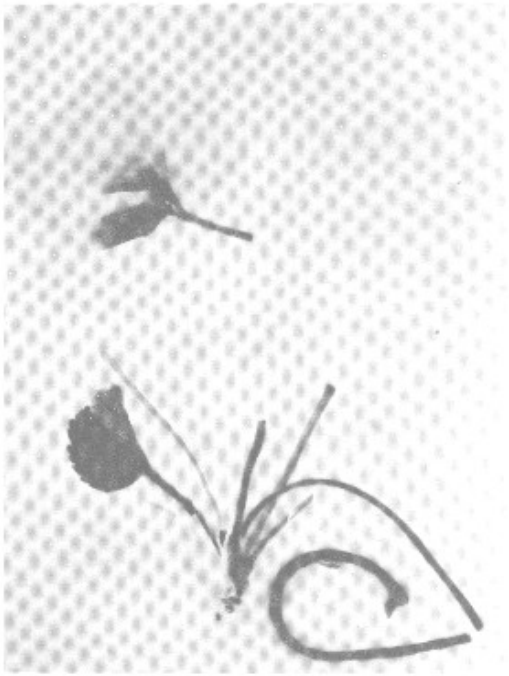

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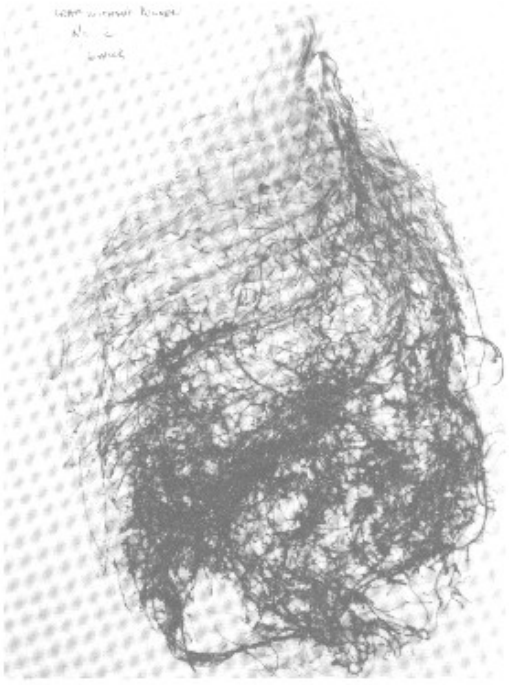


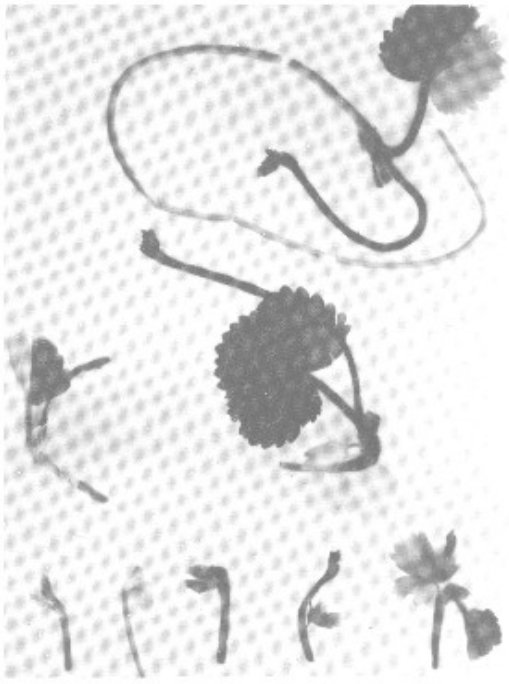
(bii)

Plate 3. (a_i) Strawberry mother plant at the 6th week gowth stage treated with $^{14}C0_2$ (young (YL) and old leaves (OL); daughter plants (DP) and position of treated leaf (TL).

(a_{ii}) The autoradiograph shows [^{14}C]-assimilates in actively growing areas (stolon tip or emerging leaf) some activity can be observed in young leaves but not in old leaves.

(b) More [^{14}C]-assimilates moved into the root system (b_i and b_i).

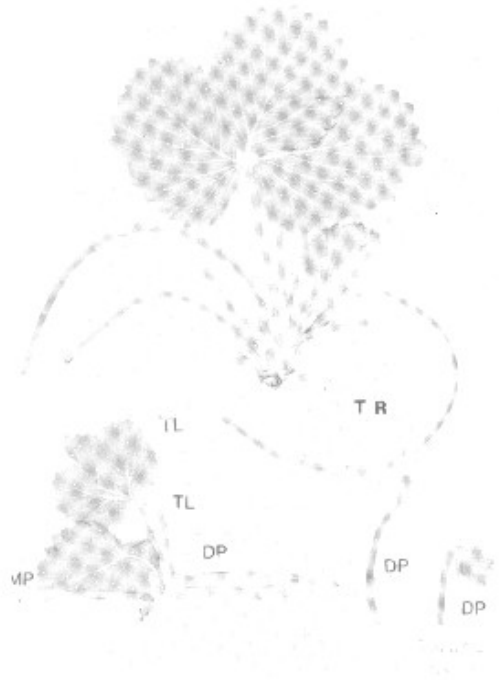
(ci)



(cii)

(c_i) Daughter plants (DP) and stolon tips (RT) from treated plants (5a).

(c_{ii}) The autoradiograph indicates that [^{14}C]-assimilates have moved into all actively growing areas.



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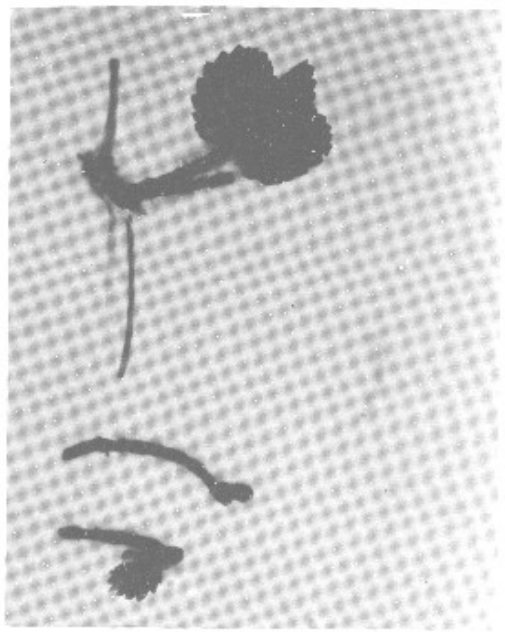

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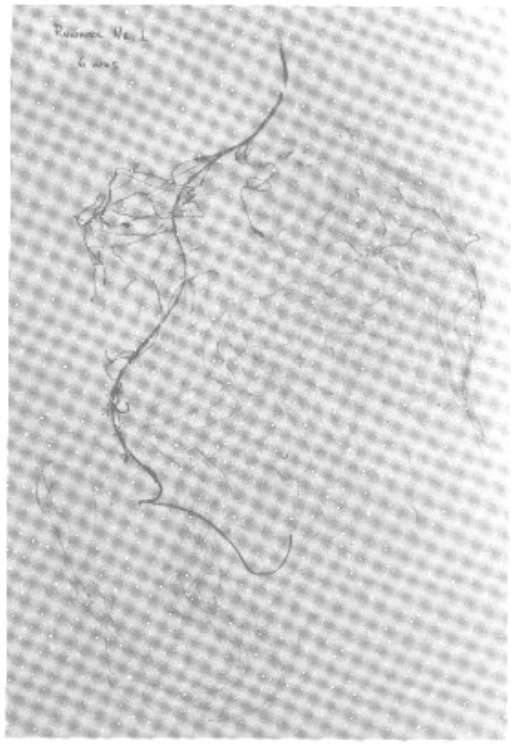
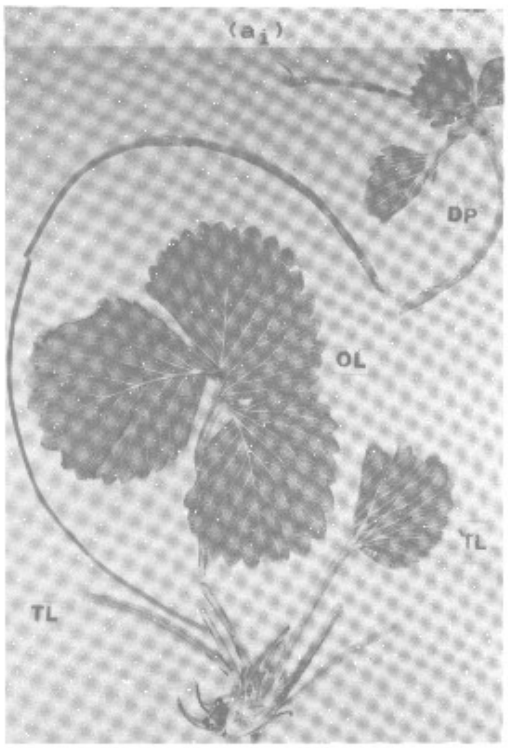


(bii)

Plate 4. Strawberry runner plant ($6a_i$) treated at the 6th week growth stage with [$^{14}CO_2$] (mother plant with a section of the stolon that connected it to the treated runner (TR); treated runner (DP) and direction of the mother plant (MP) (young leaf (YL); treated leaf (TL); tips of subsequent daughter runner plants (DP)). The autoradiograph ($6a_{ii}$) shows that [^{14}C]-assimilates moved into actively growing areas. The assimilates were also transported from the treated runner plant into the root system of the mother plant ($6b_i$ and its autoradiograph, $6b_{ii}$).



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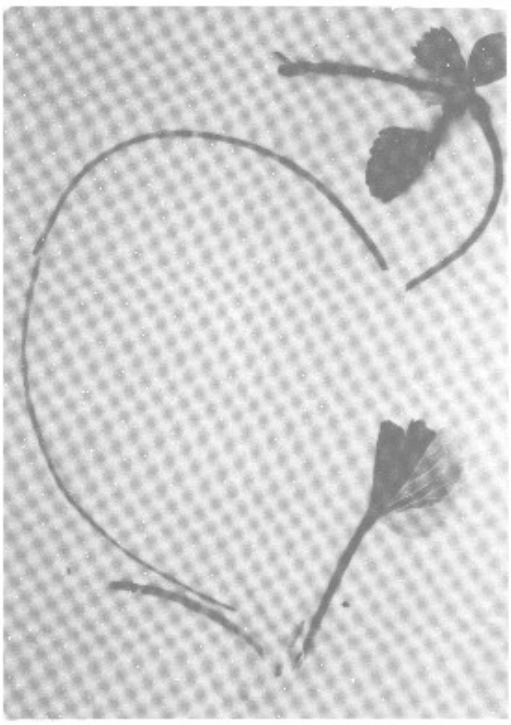

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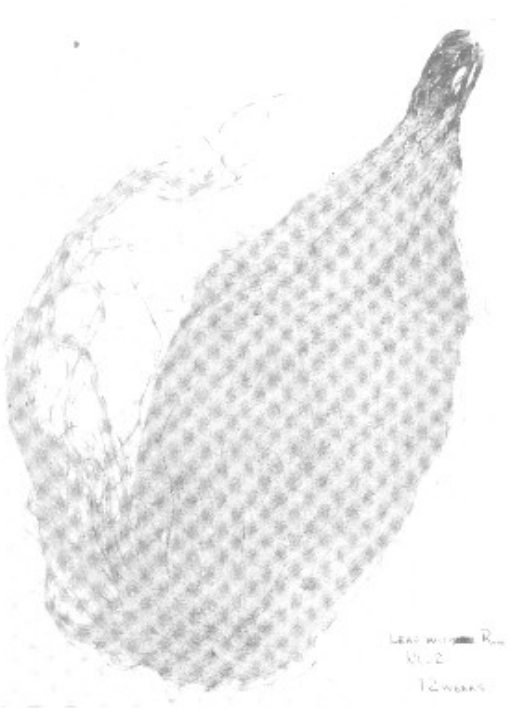

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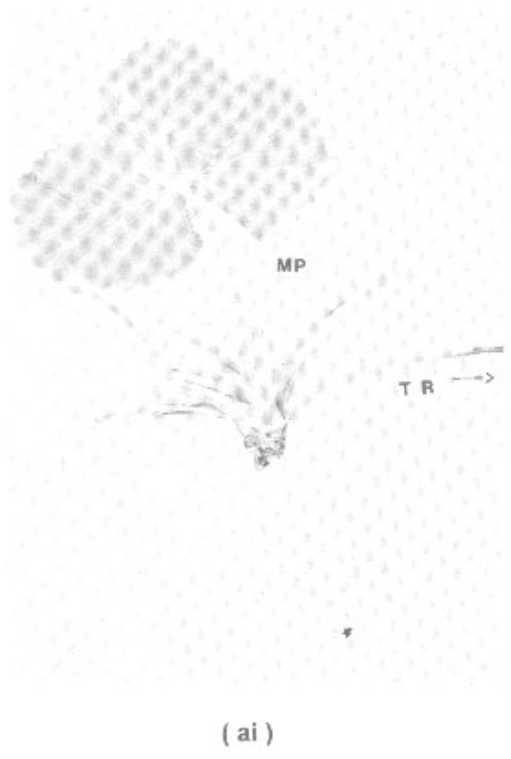
(bii)

Plate 5. Strawberry mother plant (7a$_i$) treated at the 12th week growth stage with [$^{14}C0_2$] (daughter plant (DP) on a developing stolon, treated leaf (TL); young leaf (YL); old leaf (OL). The autoradiograph (7a$_{ii}$) shows that [^{14}C]-assimilates have moved into the actively growing area of young leaves, stolons and daughter plants. [^{14}C]-assimilates also moved into the root system (7b$_i$) of the mother plant (7b$_{ii}$).



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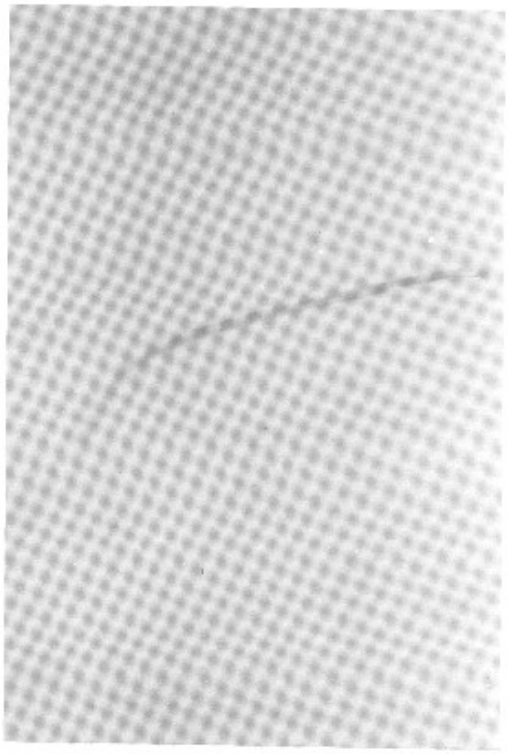

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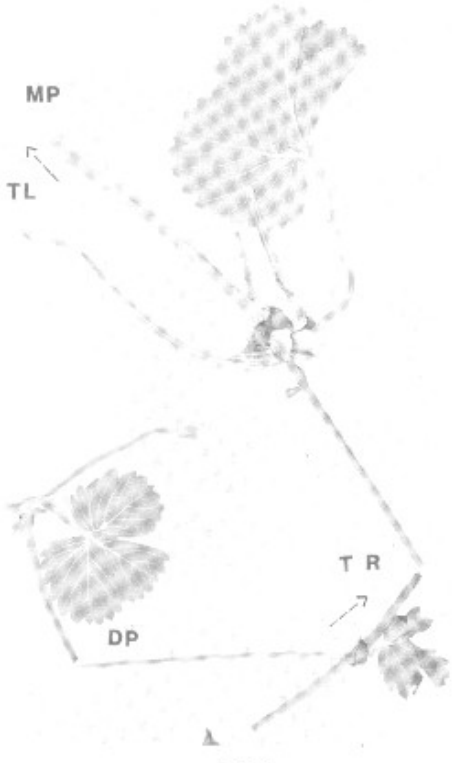

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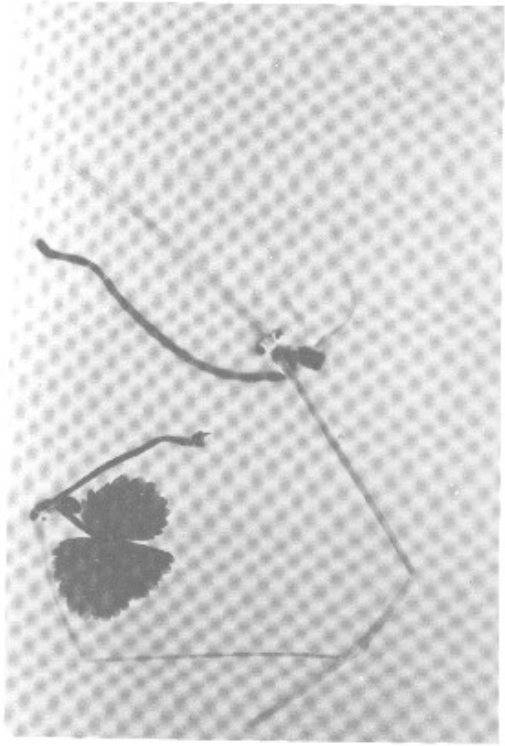
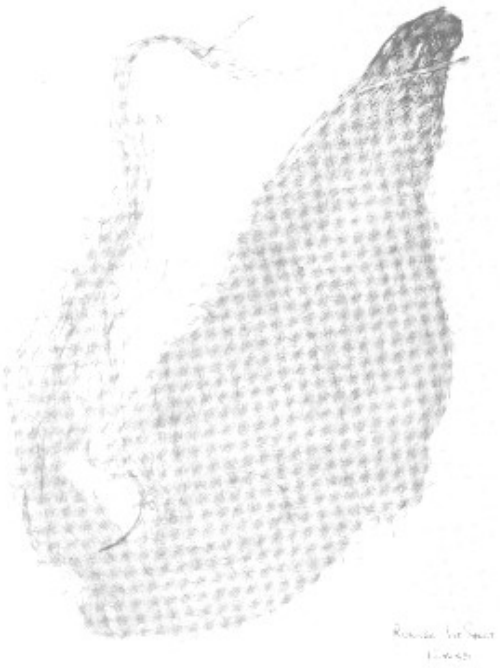
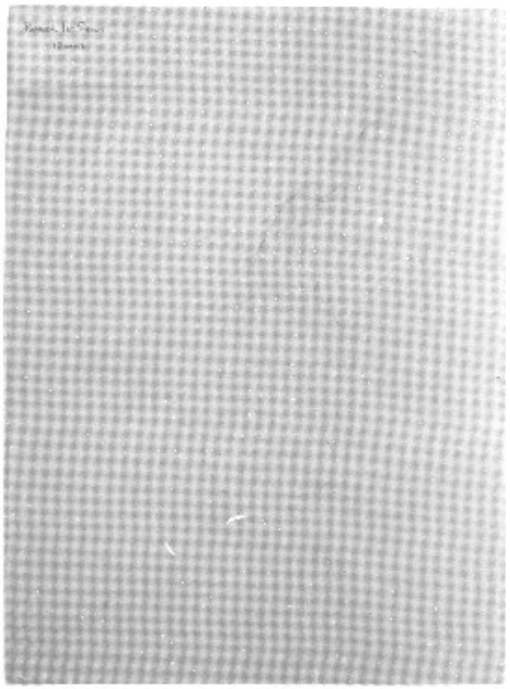


(bii)

Plate 6. Strawberry mother plant (a_i) its root system (e_i) and five subsequent daughter plants (b_i, c_i, d_i) on the same stolon. The first daughter plant was treated at the 12 th week growth stage with [$^{14}CO_2$] (treated leaf= TL, daughter plant= DP, direction of mother plant= MP, direction of treated runner= TR and actively growing runner tip= RT).



(ei)



(eii)