The Development of Tomato Root System in Relation to the Carbohydrate Status of the Whole Plant

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The decrease in growth rate of the root system or complete cessation of its growth in developed, fruit-bearing tomato plants are known phenomena. It has been suggested that a limited supply of carbohydrates to this organ, due to its relative weakness in competition with the flowers and developing fruitlets is the main cause for these disorders. This theory was tested in the present study with plants grown in an aerohydroponic system up to the appearance of 12–13 trusses per plant, 172 d after transplanting. The changes in the contents of carbohydrates in the various organs during this period were monitored. The concentrations of soluble sugars and starch in the leaves increased with the increase in truss number. The upper stem was found to contain more carbohydrates than the lower stem, while no significant changes in the concentration of these compounds could be detected in the roots throughout the experiment. Nevertheless, 120–130 d after transplanting, the roots of the plants, bearing five to six trusses and two to three inflorescences, ceased growing and remained at the same or a slightly reduced size for another 40–50 d. Calculations show that at the stage of five to six trusses, 38 g total soluble sugars and 35 g starch were stored in the vegetative organs. Therefore, it seems unlikely that carbon deficiency caused by the competition with the reproductive organs (mainly developing fruits), affected the root growth. Instead, it is suggested that some other factor is responsible.

Key words: Lycopersicon esculentum Mill, carbohydrates, root growth rate, sink-source relationship, soluble sugars, starch.

INTRODUCTION

The development of tomato roots is characterized by linear growth during the vegetative phase. Upon flowering, and especially during fruit set and development, the root extension rate has been found to decline (Gasim and Hurd, 1986). Hurd, Gay and Mountfield (1979) observed root growth cessation and some root death 4 weeks after anthesis; they suggested that the fruit grows in competition with the vegetative organs, and that root growth was affected to a greater extent. Leonard and Head (1958) showed that a reduction in total length, caused by rapid death and disappearance of roots, occurred when the plants bore 50–75 fruits per plant. Ho (1988) concluded that the sink strength of the inflorescence increases from the flowering to the fruiting stage, and that during fruiting of the tomato plant the fruits have the highest sink strength and the roots have the lowest. On the other hand, Hocking and Steer (1994) reported that the importance of the root as a strong sink declined as early as the time when the plant reached the nine-leaf stage. Moreover, growing tomato plants of several genotypes under high CO₂ caused a marked increase in starch content of the leaves (Tripp et al., 1991a); but even under these conditions of a CO₂-enriched atmosphere, a reduction in root mass was detected in plants of all genotypes (Tripp et al., 1991b).

Therefore, in the present work changes in root development during vegetative and reproductive phases were monitored and were correlated with changes in carbohydrate contents in the main vegetative organs. Calculations of the total carbon pool show that it exceeded the demand by the developing fruits.

MATERIALS AND METHODS

Plant material

Tomato plants (Lycopersicon esculentum Mill., cv. F121) were grown in an aerohydroponic system in a unheated glasshouse at Bet Dagan (Feigin et al., 1984). The minimum and maximum temperatures throughout the experiment (November 1992 to April 1993) were 10 ± 2 and 21 ± 2 °C, respectively. The aerohydroponic system consisted of two separate polystyrene, 50 × 29 × 20-cm boxes, mounted on a 140 l covered container. Roots were continuously exposed to nutrient solutions which were circulated by a pump and plastic tubes with small holes through which the solution was ejected. The nutrient solution composition has been described previously (Bar-Tal et al., 1994). The plant main stems were supported by vertical threads and the side shoots were removed.

Analysis of carbohydrates

Carbohydrate measurements were performed according to Schaffer et al. (1987). A leaflet was sampled from the first...
leaf above each of the trusses numbered 2, 5, 8 and 11. Each leaf was sampled three times: first at the stage of flowering and beginning of fruit set of the truss next to it; then, concomitantly with the first sampling of the leaf above the next indicated truss, when that was at the same stage of development; and again together with the leaf above to the subsequent indicated truss. All samplings were carried out at noon. Roots (1 g per sample) were sampled concomitantly with the first sampling of each leaf and were patted dry on tissue paper. Samples from four locations along the stem, next to trusses 2, 5, 8 and 11, were taken at the termination of the experiment, 172 d after transplanting. The sampled tissues were extracted five times in 80% EtOH and, after evaporation, reducing sugars and sucrose were measured in the soluble fraction. Reducing sugars were measured using dinitrosalicylic acid, according to Miller (1959). Sucrose was measured using anthrone according to Van Handel (1968) and, after amyloglucosidase treatment, starch was measured with anthrone in the insoluble fraction (Schaffer et al., 1985). Diurnal cycles in soluble sugar and starch contents were detected in discs, 1 cm in diameter, sampled from the leaves indicated in Fig. 5, and at the times indicated. The uppermost truss (number 10) was at the stage of anthesis and early stages of fruit set.

To study the carbohydrate status in the leaves next to the upper trusses and in the stems of the side shoots, plants of two cultivars (522 and 144) were grown in 101 buckets containing volcanic ash (tuff). When the thirteenth inflorescence began to flower, truss number 11 was at the stage of fruit set or fruitlet development. At that stage, in half of the plants, two out of three leaves of the main stem were removed, leaving the leaf above the truss. Two or three side shoots were left on the upper part of the plant, of which one third of the leaves were left. At various dates after the treatments, leaflets of the leaf next to truss number 11 were sampled for analysis of carbohydrates. On the last sampling date, the stems of the side shoots were also sampled for the same purpose.

**Root measurements**

Root volume was determined using a calibrated cylinder into which the entire root system was placed and to which water was added to the height of a mark. The difference between the water quantity required to fill the cylinder up to the mark and the cylinder volume below the mark equalled the root system volume.

**Growth curve**

A Gompertz function was fitted to the root growth data (for details see Bar-Tal et al., 1994).

**RESULTS**

**Root growth**

Three major phases in the root development are shown in Fig. 1. The initial phase, lasting about 40 d, with a relatively small increase in volume, despite a high relative growth rate (RGR), was followed by a second phase of 100 d, with a rapid increase in volume, and a third phase, starting 138 d after transplanting which was characterized by zero growth and even some reduction in the root volume. The relative growth rate was derived from the calculated growth curve.

**Content of carbohydrates**

Data in Fig. 2 show a constant increase in total sugars and starch concentration with increasing truss number at the first sampling of each leaf. This sampling took place at anthesis and the beginning of fruit set in the relevant truss. Lower carbohydrate contents were found in the following two samplings of each leaf, which took place during fruit growth and maturation.

Root samples were taken concomitantly with the first sampling of each leaf to analyse carbohydrate concentrations. Except for a small increase in carbohydrate content from the first sampling to the second, no significant changes in either total sugars or starch content could be detected in the roots throughout the experiment (Fig. 3). The differences in the total sugar content at different points along the stem resembled those of the leaves. Figure 4 shows that the total sugar content was inversely related to the stem age. Thus, younger (upper) parts contained more sugars than older parts of the stem. On the other hand, similar concentrations of starch were detected at different points along the stem.

Significant diurnal changes in total sugars (Fig. 5A) and starch (Fig. 5B) content could be detected mainly in the younger leaves next to the upper trusses. In these leaves, the sugars accumulated towards noon, while starch accumulation took place in the afternoon. During the night, these leaves lost approximately one third of their daytime maximal sugar and starch contents.

Calculations of the amounts of either total sugars or starch in the leaves next to the succeeding trusses along the...
Fig. 2. The concentration of total sugars (□) and starch (■) in tomato leaves positioned next to the indicated trusses along the plant. Each leaf was sampled three times (indicated as 1, 2, and 3), except for the last one (only sampled twice).

Fig. 3. The concentrations of total sugars (□) and starch (■) in the roots of tomato plants. Samples were taken concomitantly with the first samplings of the leaves as indicated in Fig. 2.

Fig. 4. The concentrations of total sugars (□) and starch (■) in tomato stem sections sampled next to the indicated leaves at the termination of the experiment.

Fig. 5. Diurnal changes in total sugars (A) and starch (B) contents in tomato leaves next to trusses no. 2 (●), 4 (○), 6 (□), 8 (●) and 10 (■).

stem showed a constant increase in both (Table 1). The leaf next to truss number 11 contained four times as much total sugar and 13 times as much starch as the leaf next to the
were 11 contents of total sugars and starch in the roots, at that stage, the stem contained about 30 g sugar and 16 g starch. The total starch, respectively, as those next to truss number two. It contained about three and four times as much sugar and starch, respectively, as those next to truss number 11 in the two cultivars examined (Table 3). The decrease in starch content

1. Cultivar
2. Total sugars and starch content (mg g⁻¹ f.wt) in leaves next to truss number 11 (at the stage of fruit set and developing fruitlets), at various dates following the removal of every two out of three leaves along the entire stem (−), and in control plants (+), in two tomato cultivars

<table>
<thead>
<tr>
<th>Leaves</th>
<th>Total sugars</th>
<th>Starch</th>
</tr>
</thead>
<tbody>
<tr>
<td>522</td>
<td>522</td>
<td>522</td>
</tr>
<tr>
<td>144</td>
<td>144</td>
<td>144</td>
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</tbody>
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For the calculation, 50% of the final weight of the stem (1338 g) was estimated at this stage.

Removing two thirds of the leaves, leaving a single leaf per truss, caused a marked decrease in the total sugar and starch content in the leaf next to truss number 11 in the two cultivars examined (Table 3). The decrease in starch content

\[
\text{Starch content (mg g}^{-1}\text{f.wt)} = \text{Total starch content (mg g}^{-1}\text{f.wt)} - \text{Starch content (mg g}^{-1}\text{f.wt)} \times \frac{2}{3}
\]

**Fig. 6.** Total sugars and starch concentrations (mg g⁻¹ f.wt) in the stems of side shoots of two tomato cultivars, 15 d after the removal of two thirds of the leaves of the main stem or side shoot of the whole plant (■). □, Control plants.
could be detected as early as 5 d after treatments, earlier than that of the sugars. The stems of the side shoots of the treated plants, of both cultivars, contained 50% of the total sugars and starch, compared with the side shoots of the control plants (Fig. 6).

**DISCUSSION**

Our results show that after a period of rapid growth, the root systems of tomato plants with five or six fruit trusses and two or three inflorescences cease growing (Fig. 1). This is in agreement with previous observations (Leonard and Head, 1958; Hurd et al., 1979). However, the data presented in the present paper do not agree with previous interpretations that the reduction in growth rate and the die back of part of the root system is solely a result of its relative weakness in competition with the developing fruits.

Data in Fig. 2 show gradual increases, with increasing truss number, in sugars and starch concentration in the leaves. They also show that the upper, younger part of the stem, although associated with the most active trusses, contained more total sugars than the lower parts, and that there was no parallel reduction in the concentrations of starch along the stem (Fig. 4). Moreover, the concentration of carbohydrates in the roots (Fig. 3) did not change throughout the 197 d of the experiment. These results indicate that even in the presence of increasing numbers of flowers, fruitlets and developing fruits on the plant, there was no depletion of the carbohydrate pool. On the contrary, the sugars and starch contents in the leaves increased with increasing truss number, up to number 11 (Table 1), owing to the fact that concentration of carbohydrates increased, while the leaf size remained constant. The calculated reserves of carbohydrates in the vegetative organs at the stage of root-growth decline (Table 2) did not include the leaves above the sixth fruit truss; these leaves support two or three additional inflorescences. Therefore, these calculated reserves can be considered as minimal. Since young tomato leaves become carbon sources early in their development (Hocking and Steer, 1994), the contribution of an additional six to nine leaves, with high carbohydrate content (Fig. 2, Table 1), to the total carbohydrate storage pool, should be taken into account. In addition, the content of only 50% of the final stem weight was calculated and showed net amounts of 38 g of sugars and 33 g of starch. Moreover, it has been suggested (Hocking and Steer, 1994) that much of the carbon in the storage pool in the tomato stem may never be remobilized and used by the plant. The results of the present study, with side shoots (Fig. 6), suggest that the stem may act as a source in case of carbohydrate deficiency. The fact that the stored sugars and starch in the leaves can undergo diurnal fluctuations (Fig. 5), indicates that these compounds are free to be released and translocated to the various sinks according to demand. Data in Table 3, showing the removal of two thirds of the leaves markedly decreased the carbohydrate content in the remaining leaves, support this indication. These results strongly argue against the possibility that the high carbohydrate content in the upper leaves is a reflection of leaf structure rather than low sink demand. Wolf and Rudich (1988) found that fruits of determinate, field grown processing tomatoes accumulate 96–113 mg d. wt d⁻¹. Carbon import rates in fruits of indeterminate, glasshouse tomatoes were measured by Walker and Ho (1977), who observed an import of 5.87–3.11 mg h⁻¹ per fruit, with higher import rates to the smaller fruits. On a per day basis, a smaller fruit was calculated to import 70.4 mg and a large one only 37.3 mg of carbon. Out of five to six trusses per plant only four are at different stages of development. Assuming eight fruits per truss and an average import of 53.9 mg d⁻¹ per fruit, results in a total import of 1.7 g d⁻¹ carbon into the entire trusses of developing fruits. Even with the additional import into the inflorescences, one may consider there to be a very large surplus of carbohydrates in the source pools (Tables 1 and 2). These calculations support the statement of Tanaka and Fujita (1974) that in tomato plants the source exceeds the sink, and they conform with the conclusion of Hocking and Steer (1994) that tomato is sink- rather than source-limited with respect to carbon assimilates. On the basis of the above results and calculations, we would like to suggest that the decrease in root growth rate or the cessation of root growth is not due to assimilate deficiency. Tripp et al. (1991a, b) found that the presence of very high concentrations of starch in the leaves, due to CO₂ enrichment, did not prevent the reduction in root mass; this supports our suggestion.

Flowers, and especially fruits, may dramatically affect the development of the entire plant. In monocarpic species they cause senescence and death. One of the main hypothetical factors involved in these processes is hormonal (Sklenesky and Davis, 1993). We would like to suggest that such a factor, originating in the developing fruits, may be involved in suppressing the root growth of the tomato plant. Furthermore, Huber (1983) found that young plants of various species with relatively low root weights accumulated starch in their leaves. In a separate experiment we found that the leaves of mature plants (bearing up to 11 trusses, with a restricted root system) accumulated starch (data not shown). These findings may indicate that sugars and starch accumulate in the leaves because of a low demand for carbohydrates in the other organs. We therefore suggest that the carbohydrate accumulation in the leaves (Fig. 2) is at least partially a result of the reduction in sink strength of the root system during the reproductive phase of the plant.

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**LITERATURE CITED**


