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A FLOW-THROUGH HYDROPONIC SYSTEM FOR THE STUDY OF ROOT RESTRICTION

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ABSTRACT: We have developed a flow-through system (FTS) to study the effects of root restriction stress on plants grown in hydroponic culture. The system was designed to permit the use of varied culture container volumes (from 25 to 1500 cm^3) and dimensions (2.5 to 10 cm. dia. and 5 to 20 cm h.). The modular FTS design is divided into two nutrient delivery systems, one for large-volume containers and the other for small-volume containers. Each plant was grown in a modified Hoagland solution in a separate container. Nutrient solutions were aerated and the pH was automatically controlled at 6.0 ± 0.2. This report describes the FTS and presents growth data for tomato plants (*Lycopersicon esculentum* Mill., cv. 'Better Bush') grown for a 57 day period. Our observations, when compared to the findings of a root restriction study made by Ruff, *et al.* 1987 (J. Amer. Soc. Hort. Sci. 112: 763-769), indicate that similar characteristics result for the same tomato cultivar grown in either pot culture by Ruff, *et al.* 1987 (J. Amer. Soc. Hort. Sci. 112: 763-769), indicate that similar characteristics result for the same tomato cultivar grown in either pot culture (soil) or hydroponics (FTS). The result of this test of the FTS supports the continued use of the system to study various physiological and hormonal parameters in relation to root restriction.

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INTRODUCTION

Root restriction imposes a constraint on plant growth and development through reductions in leaf area, leaf number, plant height, branching, biomass production and other growth parameters (5, 6 , 7, 9, 10, 12, 15, 18, 20, 22, 23, 24). In some cases container shape may play a role in the restriction effect (15).

In most cases, the effects of root restriction do not appear to be due to reductions in nutrient uptake, water stress, or photosynthetic rate (4, 5, 18, 19). In one case, Hanson, *et al.* (15) cite nutrition as a possible limiting factor in relation to restricted root growth in *Quercus*. Studies by Bruinsma (2), Carmi (3), Carmi and Heuer (5), and Carmi and Shalhevet (6) indicate that root restriction causes an hormone imbalance as the result of reduced root activity which interrupts the normal supply of growth substances to the shoots.

Although numerous studies have been conducted on root restriction, relatively few have been conducted in solution culture (3, 4, 5, 6, 9, 10, 18, 20, 23, 24). Use of a soilless culture technique affords the investigator the opportunity of studying the physiology and morphology of intact roots and eliminates the confounding effects of poor aeration and mechanical impedance caused by the substrate. Furthermore, roots of each plant growing in hydroponics are accessible without removing soil, thus minimizing handling at each harvest. In order to conduct a root restriction study with the advantages of a hydroponic system, we developed a flow-through nutrient system (FTS) for growing plants in varied root volumes and container shapes.

To our knowledge, a flow-through hydroponic system, similar to that used for scientific and commercial applications (eg. 8, 17, 25), has not been previously designed for the study of root restriction. The principal design criteria of the FTS were: a) to maintain optimal nutrient and oxygen levels to sustain vigorous growth while imposing a physical limitation to root growth, b) to grow plants in a soil-free environment, c) to provide two separate nutrient recirculating systems so that nutrient depletion and organic substances released to solutions could be monitored separately in large- and small-volume containers, d) to utilize transparent containers that were free of toxic contaminants and would permit non-invasive inspection of the root system and

d) to have a modular design for support racks and culture cylinders to permit the use of varied container diameter and height. The FTS design, as described here, meets the above criteria and permits removal of single plants from their culture vessel for rapid sampling, inspection of roots during culture, and root respiration measurement without marked disruption to the roots.

Ruff, *et al.* (24) demonstrate that greenhouse-grown tomato plants subjected to root restriction in 450 cm^3 volume containers of soil exhibit reduced height, node number, leaf area and plant weight. Roots of these plants were highly branched compared to control plants grown in large pots (13,500 cm^3). If comparable data were obtained by use of a FTS, then they would support use of the FTS for future study of various physiological parameters in relation to root restriction stress.

In this report we describe the design of a FTS and provide preliminary growth data which demonstrate the suitability of the FTS for studying root restriction effects. Comparisons are made here for 'Better Bush' tomatoes grown in both the FTS and in a separate study with plants grown in soil (24). Future studies using the FTS will address morphological, physiological and hormonal changes that accompany the onset of root restriction stress.

MATERIALS and METHODS

Plant Material : Seeds of *Lycopersicon esculentum* Mill. cv 'Better Bush' were surface sterilized with 30% hydrogen peroxide for two to five minutes and germinated in sterile germination bags (Northrup King No. 82700). Each bag contained 50 ml of 0.2 X nutrient solution and 7 seeds were placed in the top fold of the germination paper. Stainless steel racks supporting the germination bags were housed in sterile battery jars that were sealed with plastic wrap (Saran, Dow Chemical) and covered with aluminum foil. Seeds were germinated at room temperature (25 C) under subdued light. Once cotyledonary leaves were visible the battery jars were moved to the growth chamber and placed at the same level as the racks that held the culture cylinders. The aluminum foil and plastic wrap were removed, one and two days later, respectively, and sterile water was added to each bag as needed.

Seedlings were removed from the bags 13 days after sowing and placed into the support base of the culture apparatus described below.

Environmental Conditions: Plants were grown in an Environmental Growth Chamber (EGC) Model M96 (Chagrin Falls, Ohio) walk-in growth chamber under 530 ± 50 μmol m^{-2} s^{-1} of photosynthetically active radiation as measured at the top of the canopy with a LI-COR (Lincoln, Nebraska) Model LI-1000 quantum flux meter. The radiation source consisted of Sylvania 1500 mA cool white fluorescent lamps and General Electric, 52 watt/130 volt, incandescent lamps. The latter supplied ca. 15 % of the total input wattage. The daily light period was 16 h, 30 ± 1 C, with 70 ± 5 % RH followed by dark for 8 h, 25 ± 1C and 70 ± 5 % RH.

Culture System: The flow-through system (FTS) for hydroponic culture was separated into two sections. Each section is identical in construction except that different cylinder sizes were used for plant culture in each system (Fig. 1). For this experiment the culture vessels, hereafter called cylinders, had a diameter and depth of 10 by 20 cm (1500 cm^3) and 2.5 by 5.0 cm (25 cm^3). The cylinders (Fig. 2) were constructed of clear polycarbonate (Excelon) plastic to which a face plate and a bottom plate (0.625 cm black acrylic) were fused with methylene chloride. Polyethylene (PE) hose fittings on each cylinder were secured with silicone sealant (General Electric RTV-108). Larger cylinders were fitted with 90° PE elbows at the solution inlet (as diagramed in Fig. 2), but smaller cylinders had straight connections without elbows. The elbows were used in larger containers to create a circular flow to enhance nutrient mixing as solution flowed from the bottom to the top of the cylinder. Norprene tubing (size 18, Cole-Parmer Scientific) was used for short flexible fittings, drain lines and in peristaltic pumpheads. All remaining tubing was 0.94 cm black PE. All tubing and culture apparatus were washed successively with methanol, 5% Clorox solution and rinsed with distilled water. The washes were made first to remove plasticiser materials and second to reduce the possibility of contamination by pathogens. Plasticisers used in manufacture of plastics are known to be toxic to plant growth (14, 16).

When seedlings were placed into FTS culture they were supported by circular white-mesh-plastic grids inside of black PE plastic base cups. The base cups were fashioned from large (4.0 cm dia.) and small (2.7 cm dia.) end-

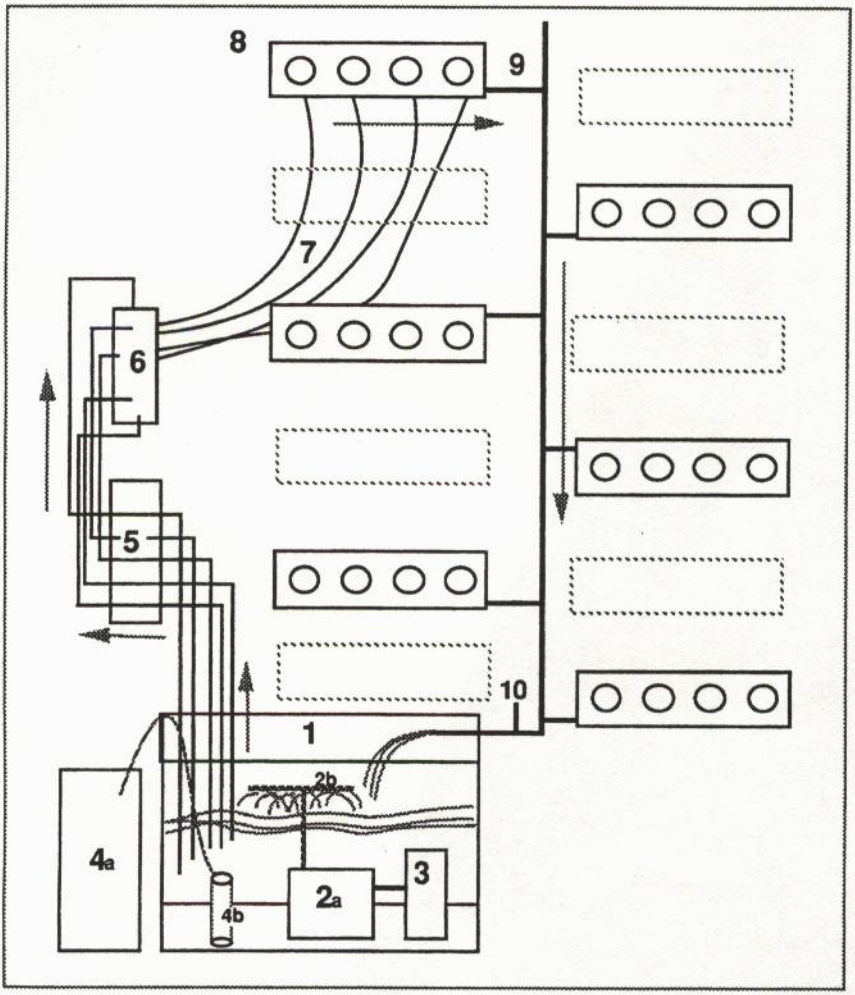

Figure 1. Flow circuit for the flow-through nutrient system (FTS). This top-view diagram of the FTS represents half of the system. A second set of six racks are indicated by dotted rectangles. The second set of racks and the cylinders they hold are serviced by a second flow circuit. Each circuit of the FTS includes: reservoir tank for nutrient solution (1, represented in side-view); submersible pump (2a) with the Aeration'T' (2b); water filter (3); pH controller (4a) with probe for monitoring pH of the nutrient solution (4b); 5-channel peristaltic pump (5); manifold (6, illustrated here with only 4 nutrient delivery lines attached) with solution delivery lines (7) supplying each cylinder in their respective support racks (8); PVC drain lines (9) to return nutrient solution to the main reservoir (1); and a side-arm port (10) on the main drain pipe for the addition of make-up water.

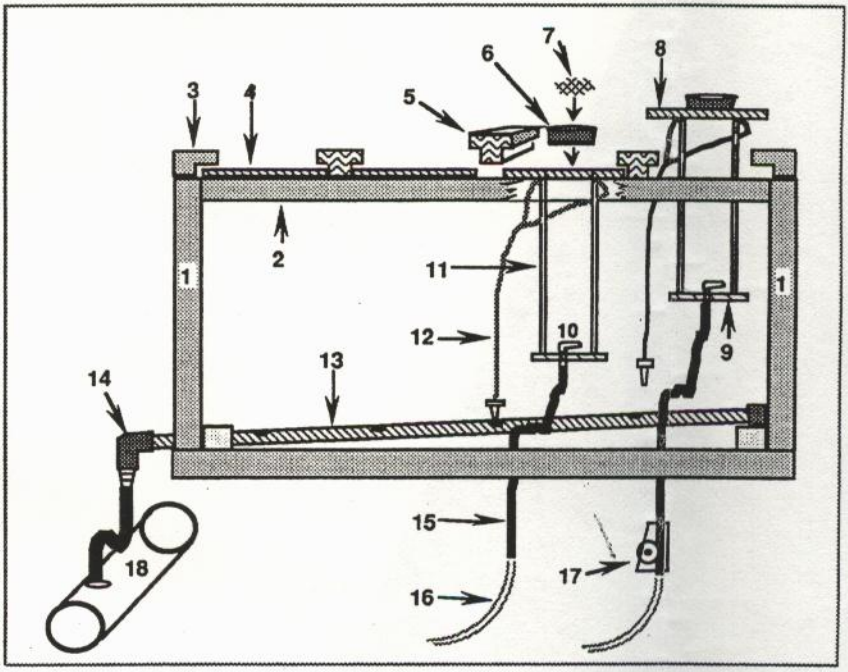

Figure 2. Culture vessels (cylinders) and rack. Each rack supports up to four separate cylinders (11). The cylinder on the right is suspended above the level of the rack's support rail (2). A cut-away view through the rack shows a second cylinder (left) resting on the rail. Each cylinder is held by a face plate (8) that in turn holds a cup-shaped base (6) which supports a plastic grid (7) and polyethylene beads (not shown) that support the roots and stem of the plant. Each vessel has its own nutrient delivery line (16, polyethylene tube) and nutrient outflow lines (12, Norprene tube). Solution flow is adjusted with clamps on each delivery line (17). Nutrient solution returns to the main reservoir by way of rack (13) and main drain (18) pipes. Other features illustrated here include: fixed end cleat (3), dummy cover plate (4), moveable spacers (5), cylinder bottom plate (9), polyethylene elbow (10), PVC elbow (14), flexible Norprene inflow line (15).

cap fittings used on fluorescent light bulbs. The seedlings were supported inside each cup by 3 mm black PE beads (Union Carbide, Danbury,CT). The base cups were fitted into the face plate on the small cylinder or in the case of larger cylinders into an additional support plate that held the cup over an 8 cm opening in the face plate. As the stem of the plant grew in girth, the PE beads were displaced from the cups. If required, mature plants were supported by upright wooden dowels (0.635 cm dia.) that fit firmly into holes positioned at each end of the face plate.

Two 115 liter tanks (Nalgene) served as the main reservoir for the bulk of the 90 l nutrient solution. A modified Hoagland's solution, as described by Hammer, *et al.* (13), was used at full strength for hydroponic culture. Nutrient solutions were drawn from the reservoirs by peristaltic pumps (Masterflex Five Channel Drives, Cole-Parmer Scientific) and pumped to a central manifold (Fig. 1). Manifolds were constructed of 5 cm diameter PVC pipe, PVC end caps and barbed PE tube fittings. Separate PE tubes connected the manifold to the bottom of each culture cylinder. Excess nutrient solution was drained at the top of the cylinder by one or two tubes leading to a 1.25 cm PVC rack drain (Fig. 2). The rack drains emptied into one of two main 2.5 cm PVC drain lines (Fig. 1) which returned the nutrient solutions to their respective reservoirs.

Racks were constructed of pine, painted black inside and white outside (Fig. 2). The bottom and two ends of each rack were made of solid pine board. Each side was open such that the cylinders and fittings were accessible during plant culture. Each rack had four positions for placement of the cylinders. For this experiment only three cylinders were positioned in each of 12 racks. Blank positions were covered with opaque plastic plates. The cylinders were covered on the outside by a single layer of black plastic. Black and white plastic covers, attached by velcro fasteners, were mounted over each of the open sides of the culture racks (Fig. 2). Flow rates for nutrient solutions entering each cylinder were controlled by adjusting the speed of the peristaltic pump and by adjustment of Keck Ramp Clamps mounted on each delivery line. Flow rates were monitored several times weekly during the experiment. As plants were harvested, empty cylinders were drained, the open tops of each empty cylinder were covered with a PVC plastic plate and the nutrient lines were closed.

The pH of recirculating solution was adjusted automatically at pH 6.0 ± 0.2 with a pH controller (Type 45A, Chemtrix, Hillsboro, OR) with 0.2 N KOH or 0.2 N HCl (Fig. 1). Each pH controller regulated a pair of solenoid valves (ASCO No. 8260A14) to dispense acid or base solutions that entered the system at the main PVC drain line just before the return flow spilled into the reservoir. Reservoir solution was further mixed and aerated by the continuous action of a submersible pump (Model LC-2CP-MD, March Manufacturing, INC., see Fig. 1). A portion of the pump's flow was diverted to a water filter (Sears, Roebuck and Co.), which held a 5 μm filter element, such that the nutrient solution was under continuous filtration.

During a preliminary experiment we observed that root-restricted plants developed dense root masses and caused plants to rise from the cylinder due to the pressure from the inflowing nutrient solution. For subsequent experiments, we fabricated retainer plates of white plexiglass and retainer clips of aluminum stock to hold the plants in place. The retainer plate secured the base cup to the face plate and the retainer clips clamped the plate securely to the cylinder's face plate. Furthermore, to prevent roots from growing into the solution inlet of the small cylinders, a circle of 0.45 μm Versapor filter (Gelman) was placed over a piece of plastic grid that covered the bottom of the cylinder. The placement of the grid and filter assisted in dispersing the solution flow to the cylinder side walls in all directions from the inlet line.

Pump and Flow Rates: Flow rates were calculated for each cylinder by collecting the outflow, for a 5 minute interval. Adjustments were made, two or three times each week, to equilibrate the flow rate if it deviated from 12 ml min^{-1} or 60 ml min^{-1}, for small-volume and large-volume cylinders, respectively. Flow rates varied somewhat, from day to day, depending on the mass and morphology of roots within a given cylinder. Based on a calculation, equal to five times the half time for each container, one can estimate the time required for a complete turnover of the nutrient solution in the small- and large-volume cylinders. Therefore, turnover times equal 5.2 and 62.5 min, for empty 25 cm^3 and 1500 cm^3 volume cylinders, respectively. As roots filled the cylinders these turnover times were reduced. The choice of flow rates for this experiment was in part determined by the capacity of the peristaltic pumps and the ability to adjust and maintain relatively constant flows within a set of cylinders.

Nutrient Depletion: Nutrient solutions were initially made to 90 l for each of the two FTS reservoirs. Distilled water was added daily to make up for solution volume lost through transpiration. Samples were taken from each reservoir several times each week to monitor nutrient levels by ion chromatography (Dionex). Nutrient solutions were changed every two weeks or more frequently when N or P levels declined.

Experimental Design: The 12 racks, holding their respective cylinders, were arranged into two rows with six racks per row (Fig. 1). Racks sitting side-by-side or opposite one another did not hold the same cylinder size (ie. large-volume cylinders placed as shown in Fig. 1 with small-volume cylinders in racks represented by dotted rectangles) . At each harvest three pairs of plants were removed, from 'mirror-image' positions, from racks directly opposite one another in each row. Each pair of plants, removed in this manner, included one grown in a large cylinder and one grown in a small cylinder. The racks were divided into three blocks of four racks, such that replicate samples were removed from each end and the middle quadrant of the growth chamber at each harvest. In this manner harvests included pairs of plants that experienced similar environmental conditions. Samples were removed from each block of racks on a random basis.

Plant Growth Data: Seedlings placed in the FTS 13 days after germination were designated day 0 plants. Growth measurements were taken for harvests of plant material on day 11, 18, 25, 32, 39, and 46. For each harvest, fresh weights of roots and shoots were determined, followed by determination of leaf areas using an electronic leaf area meter (LI-COR Model LI-3000). Plants were separated into leaves, stems and roots and dried for at least 2 days in a forced-draft oven at 65 C prior to weighing.

Statistical Analysis: Means and standard errors of the means for experimental treatments were calculated for three replicate samples for each treatment harvested at 6 different times during the course of the 8 week culture period. Significant differences in growth between treatments, as indicated in the text, were determined by the Student's t-test.

RESULTS and DISCUSSION

One of the main advantage of using a FTS to study the effects of root restriction is the ability to harvest whole root systems without the necessity of washing soil from the roots. The confounding effect of soil impeding root growth is removed since only roots are contained within the cylinder. Optimum control of oxygen, pH and nutrient delivery was provided by constant solution flow into each container, as opposed to periodic application of fertilizer solution in soil-grown plants. Several investigators have employed screen or mesh on the bottoms of the containers in their experimental systems (4, 5, 7, 12, 22) . The disadvantage of this approach is that it may create a diffusion barrier as the roots cover this surface. In the FTS diffusion is only impeded by the presence of the roots and not by other barriers. Furthermore, many studies on root restriction have been done under greenhouse or field conditions which are subjected to large variations in light, temperature and relative humidity. Under growth chamber conditions one can study the effects of root restriction under defined light, temperature and relative humidity which effectively place a constant transpirational load on each plant. Differences in plant growth between large-volume and small-volume cylinders are thus likely to be free of many confounding factors experienced in field or greenhouse experiments.

Direct comparisons between plants grown in the growth chamber in the FTS and those grown in soil in the greenhouse (24) should be viewed with caution since container volumes were different and since growth conditions in the greenhouse were not identical in the two environments. Despite these differences, both culture systems produced similar results when the same cultivar of tomato was used.

Overall Growth: Both root and shoot growth were reduced by root restriction treatment (Fig. 3). Significant differences ($p \leq 0.05$) in shoot and root growth in large and small-volume containers were apparent as early as 25 days (Figs. 5, 6 and 7). However, in contrast to 'Better Bush' plants subjected to root restriction in soil, there were no apparent inhibitory effects of root restriction on lateral bud growth in the FTS.

Shoot Elongation: Root restriction had no consistent effect on shoot elongation (Fig. 4). During the initial 6 to 24 days, plants in small cylinders were taller than those in large cylinders. During days 18 to 26 there was no difference in shoot

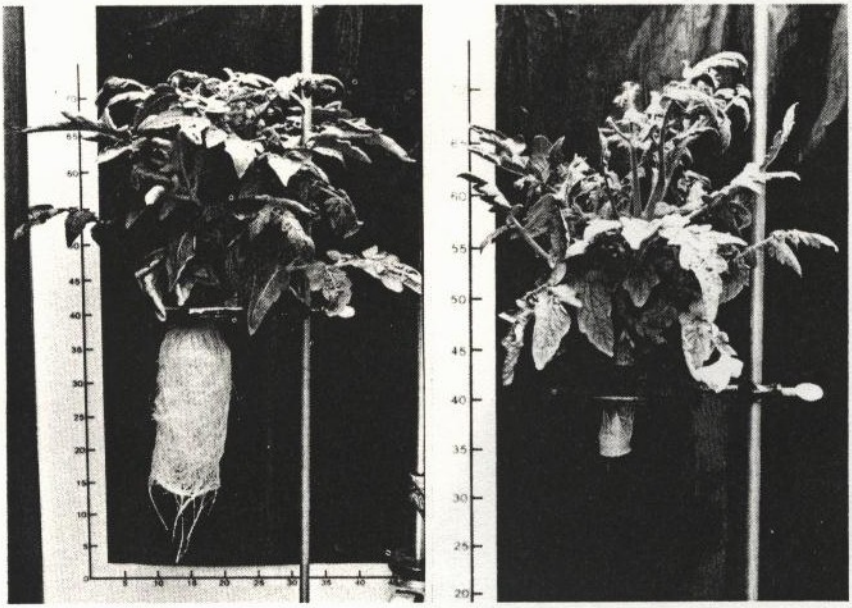

Figure 3. Comparative shoot and root growth of 'Better Bush' tomato plants grown for 35 days in 1500 cm^3 (left, control) or in 25 cm^3 volume (right, root restricted) containers in a specially designed flow-through system. Scale in centimeters.

elongation between the two plant groups. However, from days 28 to 34, the rate of shoot elongation in small cylinders began to decline. This may have been caused by the higher flow rates of the nutrient solution in the small cylinders. Comparative shoot (height) growth in root-restricted plants in soil culture and FTS culture was inhibited 40% and 20%, respectively, six weeks after germination .

Leaf Enlargement: Root restriction significantly ($p \leq 0.05$) reduced leaf enlargement, by more than two fold, by day 25. By day 46 there was over a four-fold difference in total leaf area between large- and small-cylinders (Fig. 5). Leaves of root-restricted plants showed little additional increase in area after day 32. After eight weeks of treatment, plants grown in small-cylinders in

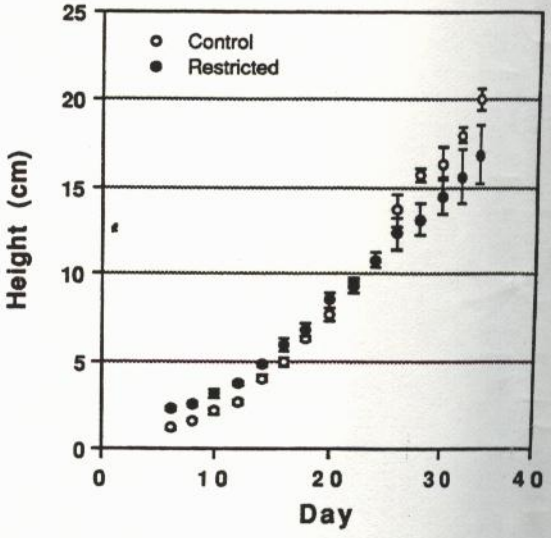

Figure 4. Influence of root restriction on shoot elongation (height) of 'Better Bush' tomato plants. Measurements for controls (n=3) and root restricted (n=3) plants from day 6 to day 34. Vertical bars indicate ± one standard error.

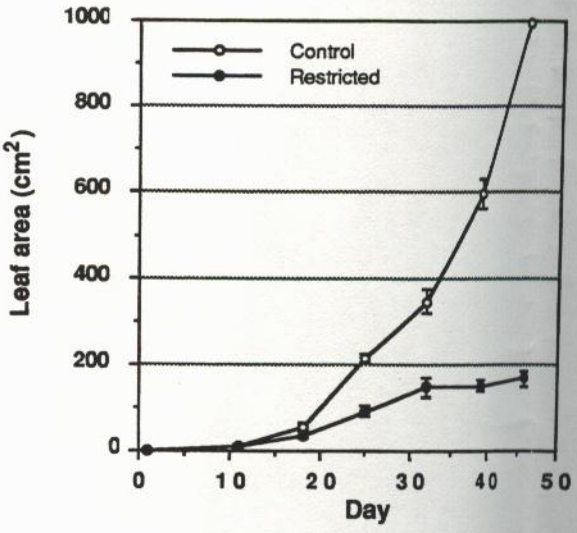

Figure 5. Influence of root restriction on total leaf area of 'Better Bush' tomato plants. Vertical bars indicate ± one standard error.

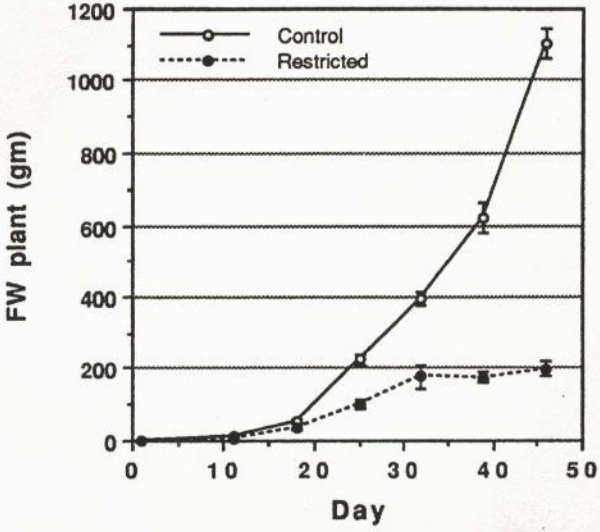

Figure 6. Influence of root restriction on fresh weight of 'Better Bush' tomato plants. Average plant fresh weight measurements for controls (n=3) and root restricted (n=3) plants. Vertical bars indicate ± one standard error.

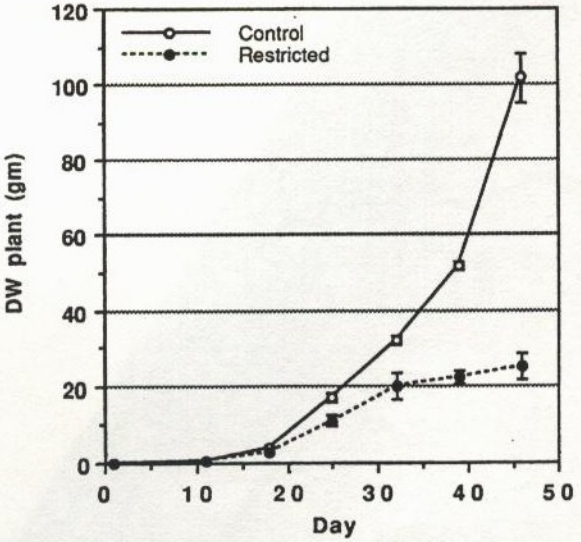

Figure 7. Influence of root restriction on dry weight of 'Better Bush' tomato plants. Average plant weight measurements for controls (n=3) and root restricted (n=3) plants. Vertical bars indicate ± one standard error.

the FTS in the growth chamber and in soil in the greenhouse (24) had 16.7 % and 21.2 %, respectively, of the leaf area as plants grown in large containers.

Biomass Production : The effects of root restriction on biomass production were not observed until day 25. After 32 days, there was little or no further increase in growth in small-volume containers (Figs. 6 and 7). At 25 to 46 days there was a 2.0 to 5.5-fold difference in total fresh weight of the plant (Fig. 6) and a 1 to 5-fold difference in total dry weight of the plant (Fig. 7). By 8 weeks of treatment, plants grown in small cylinders in the FTS in the growth chamber and in soil in the greenhouse (24) had 24.6 and 36.1% of the total dry weight, respectively, as those in large cylinders.

Growth Analysis: Calculations, made here and by Ruff *et al.* (24), for the mean relative growth rate (MRGR) and net assimilation rate (NAR) revealed interesting differences in the culture systems (Table 1). In each case, the MRGR and NAR values dropped during the course of the experiment. The NAR for greenhouse control plants was initially 18.0 (week 2 to 4) and decreased to 2.3 (week 6 to 8), while NAR values for comparable plants in the FTS started at 13.5 and dropped to only 8.9 (Table 1). The larger NAR values for the FTS controls were likely due to a combination of improved environmental conditions, optimal nutrition, and better control of other culture conditions. The MRGR values for root restricted plants in the FTS were one order of magnitude lower than those for greenhouse plants and NAR values at the end of each experiment were 2.7 and 3.0, for the FTS and greenhouse plants, respectively. Because of differences in container volume between the FTS and greenhouse experiment,
it is likely that lower MRGR values for the FTS grown plants resulted from using a much smaller container volume which in turn greatly limited root biomass accumulation.

The appearance and effect of root restriction treatment may appear to be relative to container size and time. For example, the plants grown in the FTS large cylinders did not show any sign of growth inhibition over the course of the experiment. In this regard these plants serve as controls. Had the same volume been filled with soil, these same plants in a growth chamber or in a greenhouse may have developed the characteristic symptoms of root restriction within the same time. Furthermore, the small cylinders supported growth of tomato plants, without loss of any plant during the experiment. The

Table 1: Influence of root restriction on mean relative growth rate (MRGR)† and comparative net assimilation rate (NAR)†† of 'Better Bush' tomato plants grown in a flow-through hydroponic system for 46 days. Measurements were based on 7-day intervals from the first to the last weekly harvest for the small-volume (25 cm^3) and large-volume (1500 cm^3) containers.

Day	MRGR 1500 cm^3	MRGR 25 cm^3	NAR 1500 cm^3	NAR 25 cm^3
11-18	0.116	0.099	13.505	13.834
18-25	0.096	0.068	13.990	18.402
25-32	0.034	0.034	7.513	11.119
32-39	0.039	0.001	5.996	1.972
39-46	0.037	0.008	8.977	2.713

† $MRGR = (\ln[\text{Dry Weight } (g)_2] - \ln[\text{Dry Weight } (g)_1])/(\text{Time}_2 - \text{Time}_1)$

†† $NAR = ((\text{Dry Weight}_2 - \text{Dry Weight}_1)/(\text{Time}_2 - \text{Time}_1)) * (1/((\text{Leaf Area}_2 + \text{Leaf Area}_1)/2))$

smaller volume was chosen to compress the time required to induce a root restriction stress. These plants exhibited severe growth inhibition but were maintained during the experimental period because of the constant supply of water and nutrients provided by the FTS.

Various designs were considered during the development of the FTS. Various concerns were addressed in order to avoid producing artifactual data. One consideration was the minimal rate of delivery that would be required to provide nutrients in excess of ion uptake. Second, when root volume approached that of the cylinder the localized point of entry was the sole source of nutrients with the compacted roots serving to impede diffusion. Furthermore, roots at the top of the cylinder may have received less nutrients and thus may have had lower metabolic activity. Schumacher and Smucker (25), using a flow-through system designed for measuring root respiration in vessels of

approximately 175 ml volume, noted that flow rates greater than 6 ml per minute were desirable for measurement of root respiration independent of flow rate. In the FTS, the half-time of solution residence in the small cylinders decreases dramatically as the roots grow. The velocity of solution movement in the cylinder increases as the root mass increases. As the roots become confined they build a back pressure to the solution flow as they grow over or into the inlet opening that delivers solution to the cylinder. Rather than roots becoming compacted and constricted by a soil matrix, in this case, the roots themselves impede their own progress. During harvests on days 39 and 46 we observed that many roots in small cylinders were translucent and had turned light brown in color possibly indicating that they had become waterlogged. It is likely that roots in this condition would lose organic materials into the flowing nutrient solution. This breakdown in the root system might be accompanied by the generation of ethylene (1). Measurements are needed to test this hypothesis. Furthermore, the loss of older roots was also accompanied by the initiation of newly formed roots from the base of the shoot.

Finally, concerns about microbial and pathogenic growth in the FTS seem minor in that root growth was always healthy and vigorous. Various measures including use of fungicides and UV radiation treatment are possible techniques to combat pathogens in the FTS (11, 21, 26, 27). However, UV treatment should be reviewed with caution since iron chelates are known to be destroyed by UV treatments and thus require special measures to ensure proper iron nutrition (26).

Root restriction may result in an imbalance of growth substances that are normally transported from the roots to the shoots. Our observation of tomato root systems grown in small cylinders (25 cm^3) in the FTS indicate that roots were lost with the onset of root restriction. New roots were initiated, but an apparent delay between the loss of older roots and the generation of new roots may in part explain the imbalance in root hormones or root synthesized metabolites that are required by the shoots. Based on the results presented here the FTS appears to provide a useful method of studying the effects of root restriction stress under controlled conditions. Subsequent papers, will characterize the physiological and morphological responses of tomato plants to root restriction using the FTS.

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