

Effect of Altering the Root-Zone Temperature on Growth, Translocation, Carbon Exchange Rate, and Leaf Starch Accumulation in the Tomato¹

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ABSTRACT

Tomato seedlings (*Lycopersicon esculentum* Mill. cv Vendor) were grown hydroponically with their root systems maintained at a constant temperature for a 2-week period commencing with the appearance of the first true leaf. Based on fresh and dry weight and leaf area, the optimal root-zone temperature for seedling growth was 30°C. The carbon exchange rate of the leaves was also found to increase with rising root-zone temperature up to 30°C. However, a more complex relationship seems to exist between root-zone temperature and the accumulation of ¹⁴C-labeled assimilates in the roots; inasmuch as there is no enhancement in this accumulation at the most growth promoting root-zone temperatures (22-30°C).

The effect of heating the plant root-zone or soil has been studied mainly to ascertain the minimum temperature required to insure satisfactory plant growth. Although root-zone temperature has been shown to affect tomato plant growth, the physiological basis for this response has not been thoroughly investigated. Most studies (4, 11, 13, 17) have elicited increased growth with warmed roots (25-30°C) and a decrease in growth when roots were cooled below ambient with a sharp decrease in growth noted at temperatures below 15.0°C (14, 23).

It has been demonstrated that the metabolic activity of a sink region can be modified by adjusting its temperature (21). Alterations in the source-sink relationship through modifications of their respective strengths have been shown to influence the translocation rates of sucrose from source leaves to sink regions (20) reflecting increased or decreased demand by these sinks. Furthermore, a correlation between sink-controlled translocation rates and photosynthetic rates of leaves which supply those sinks has been demonstrated (18). It is hypothesized that the physiological basis for increased growth of tomato plants at warm root-zone temperatures may be due to the effect of increased sink activity of the roots on increasing the CER² of the leaves.

The objective of this study is to relate the growth response of tomato seedlings to relative translocation and photosynthetic rates of plants grown at various root-zone temperatures. In

addition, leaf starch levels, which have been implicated in controlling photosynthetic rates, will be monitored in an attempt to relate accumulation and depletion of starch to photosynthetic rates.

MATERIALS AND METHODS

All plants were grown in a controlled environment chamber at 22°C with 70% RH and a 12-h photoperiod of 235 $\mu\text{E m}^{-2} \text{s}^{-1}$ PAR provided by a mix of fluorescent and incandescent lights. Tomato seeds (*Lycopersicon esculentum* Mill. cv Vendor) sown in vermiculite were pricked out after 2 weeks and inserted through cylindrical holes drilled in 4-cm-thick styrofoam. The seedlings were secured in place with a ring of soft clay which formed an insulating seal between the plant shoot and plant root. With the cotyledons emerging from above and the roots hanging from below, the styrofoam was fitted tightly into a plastic bin containing 22 L of half-strength Hoagland solution (pH 6.0). The nutrient solution was thermostatically controlled to $\pm 0.5^\circ\text{C}$ of the desired temperature and was kept at maximum level by adding half-strength Hoagland solution. The temperature of the solution had no effect on the temperature of the seedling shoot.

Growth Studies. Growth studies were undertaken to characterize the response of tomato seedlings to a range of root-zone temperatures with the expectation of relating translocation and photosynthesis to growth.

After a 3-d acclimatization period, during which the seedlings' roots were exposed to a nutrient solution temperature of 22°C, the seedlings were subjected to a constant root temperature ranging from 10°C to 38.7°C. After an exposure period of 2 weeks, plants were removed from the treatment conditions and weighed. Leaf areas were determined with a LI-COR 2000 (Lincoln, NE) leaf area meter and plants were oven dried at 70°C for 48 h for dry weight determination.

Translocation Studies. Root-zone temperature commenced at the beginning of the dark period following the 10th d that seedlings had their roots submerged in nutrient solution at 22°C. This gave the seedlings a 12-h pretreatment period. During the following light period, the first true leaf of two plants from each of the root-zone temperature treatments 15.6°C, 22°C, 30°C, and 35°C were exposed to ¹⁴CO₂ for 30 min and were grown at their respective root-zone temperatures for an additional 24 h. ¹⁴CO₂-enriched air was generated by reacting 0.1 ml of 200 $\mu\text{Ci/ml}$ Na¹⁴CO₃ with 3 ml of HClO₄ (1) in a side-arm flask. Through a closed system, the ¹⁴CO₂ was pumped through a Plexiglas leaf assimilation chamber (230 $\mu\text{E m}^{-2} \text{s}^{-1}$) and repeatedly circulated. At the end of a 30-min assimilation period, 3 ml of 20% KOH w/v was injected into the side-arm flask and allowed to reabsorb ¹⁴CO₂ from the circulating air for 10 min. After a 24-h period

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² Abbreviation: CER, carbon exchange rate(s).

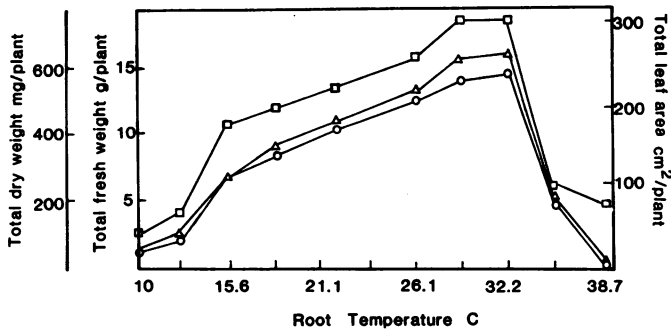


FIG. 1. Total fresh weight (O), dry weight (□), and leaf area (Δ) of tomato seedlings grown at various root temperatures for a 2-week period. Individual points are means from two replications, with a minimum of 10 plants per temperature per replication.

Table I. Specific Leaf Area of the First True Leaf of Tomato Plants Grown at Root Temperatures of 15.6°C and 30°C for a 2-Week Period

Individual numbers are means of six plants. Means from the same day are significantly different for all days using 5% LSD.

Root-Zone Temperature °C	Specific Leaf Area at Following Days after Commencement of Treatment					
	6	8	10	12	14	17
	<i>dm</i> ² / <i>g</i>					
15.6	3.55	3.48	3.39	3.41	3.00	2.76
30	5.12	4.47	4.72	3.82	3.60	3.28

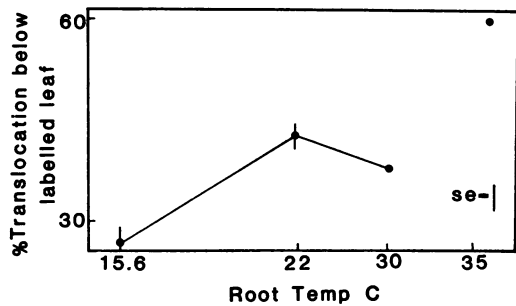


FIG. 2. Per cent ¹⁴C-labeled assimilate translocated and remaining below the first true leaf of tomato 24 h after labeling it with ¹⁴CO₂. Each point is the mean of four plants.

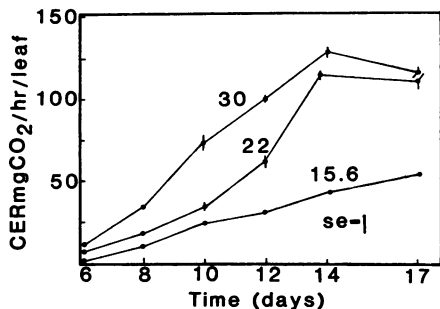


FIG. 3. CER on a whole leaf basis of the first true leaf of tomato when subjected to various root-zone temperatures. Individual points are means of two replications using five plants per temperature per replication per day.

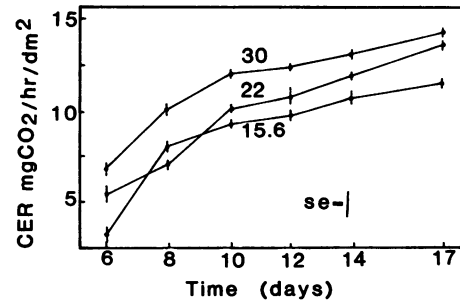


FIG. 4. CER on a leaf area basis of the first true leaf of tomato when subjected to various root-zone temperatures. Individual points are means of two replications using five plants per temperature per replication per day.

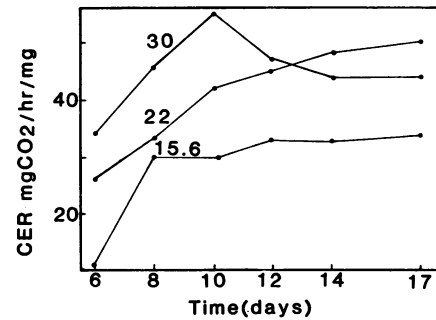


FIG. 5. CER on a dry weight basis of the first true leaf of tomato when subjected to various root-zone temperatures. Individual points are means of two replications using five plants per temperature per replication per day.

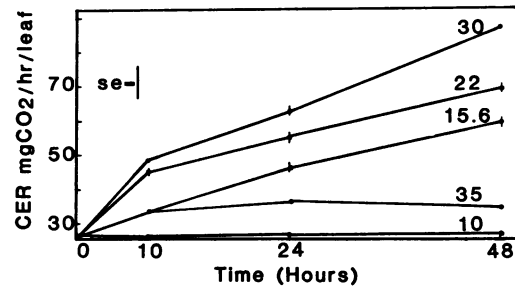


FIG. 6. CER of the first true leaf of tomato when subjected to various root-zone temperatures over a 48-h period. Individual points are means of four plants.

Table II. Starch-Derived Glucose Content of the First True Leaf of Tomato after Being Subjected to Various Root-Zone Temperatures for a Period of 48 Hours

Within an experiment, numbers followed by the same letter are not different at the 5% level using the LSD test.

Root Temperature °C	Starch-Derived Glucose	
	μg/mg dry wt	μg/cm ² leaf area
15.6	123.3a	496.4a
22.0	63.3b	239.1b
30.0	64.3b	222.6b

which allowed for ¹⁴C-labeled assimilate to be translocated throughout the plant, seedlings were sectioned into (a) the labeled leaf, (b) all of the stem and leaf tissue above the labeled leaf, and (c) the stem and cotyledons below the labeled leaf and the root

system.

In evaluating root sink strength, it was felt that ¹⁴C-assimilates, contained in the stem vascular tissue which are moving toward the root system, move under the force provided by the root sink. The stem tissue below the labeled leaf was therefore grouped

with the root tissue in the translocation studies and the net accumulation of imported ^{14}C -labeled compounds after a 24-h period was determined. The three plant parts were immediately frozen, then freeze dried, and extracted with boiling 80% ethanol (1 ml/5 mg dry weight). Aliquots of 0.1 ml of each extract, and the nutrient solution they were growing in, were counted for radioactivity using a liquid scintillation counter.

Carbon Exchange Studies. Carbon exchange was measured using a Beckman 215A IR gas analyzer. The attached leaf whose CER was being measured was inserted into a 2800 cm^3 clear Plexiglas leaf assimilation chamber and the petiole was sealed with clay. The leaf assimilation chamber was equipped with a fan which provided a constant mixing of flowing air and was connected in series with a diaphragm pump to maintain a steady flow rate, a column containing 300 ml of CaSO_4 crystals, used to remove moisture, and an IR gas analyzer in a closed system. The leaf chamber was maintained at $22^\circ\text{C} \pm 1^\circ\text{C}$ with a light intensity of $230 \mu\text{E m}^{-2} \text{s}^{-1}$ reaching the top of the inserted leaf surface. The duration of each carbon exchange measurement did not exceed 3 min so as to avoid depleting the leaf assimilation chamber of moisture.

CER were measured of leaves of plants grown under two conditions: long term and short term exposures to various controlled root-zone temperatures.

In the long term study, the plants were cultured under identical conditions as plants in the growth study. The long term study treatments included plants whose roots were maintained at 15.6°C , 22°C , and 30°C only, because plants whose roots were maintained below 15.6°C or above 30°C did not develop large enough first leaves whose CER could be measured with the leaf assimilation chamber. Photosynthetic measurement of the first true leaf commenced when the slowest growing leaf (15.6°C root-zone temperature) attained the minimum size required for measurement in the assimilation chamber, 6 d after the treatment began, and was measured on alternate days until the leaves began to senesce, 17 d after the treatment began. Leaves of five plants from each of the three treatments were measured on alternate days. Immediately after the net carbon fixation rate per leaf was determined, the leaves were measured for leaf area and dried as described above. The photosynthetic rates were calculated on a whole leaf, leaf area, and mg dry weight basis. The experiment was conducted twice.

The short term investigation was performed to determine how rapidly leaf carbon exchange responds to an alteration in root-zone temperature. For this segment of the experiment plants were cultured in an identical manner as in the growth study except the root-zone temperature treatments did not begin until after the seedlings had been growing in the nutrient solution for 10 d at 22°C . Net carbon exchange was measured at 0, 10, 24, and 48 h after the root-zone warming or cooling began. Two seedlings whose first true leaf had an area of $4.75 \pm 0.25 \text{ cm}^2$ at zero time were used for each root temperature treatment 10°C , 15.6°C , 22°C , 30°C , and 35°C . The experiment was conducted twice.

Starch Determination. Seedlings were grown in nutrient solution maintained at 22.0°C for a 7-d period and then subjected to either a 15.6°C , 22.0°C , or 30°C nutrient solution temperature for exactly 48 h, commencing and ending in the middle of the photoperiod. The first leaves of two seedlings subjected to the same nutrient solution temperature were harvested, combined, (to give approximately 25 mg total dry weight), freeze dried, and then extracted with boiling 80% ethanol three times. The ethanol-insoluble leaf tissue was mixed with 2 ml of H_2O and boiled to remove any remaining ethanol. After cooling, 5 ml of 0.2 M acetate buffer (pH 4.5) and 1.0 ml of 1% amyloglucosidase (20) was added to the leaf tissue, and the suspension was incubated at 55°C for 48 h. Starch-derived glucose was quantified (9)

by monitoring the O_2 consumption when a 0.1-ml aliquot of leaf extract was added to 2.7 ml of 0.2 M acetate buffer at pH 4.5 and 0.2 ml of glucose oxidase (Sigma, 1250 units/ml) using a Clark-type O_2 electrode.

RESULTS AND DISCUSSION

Growth. Tomato plants grown for 2 weeks in a range of root-zone temperatures showed an increase in growth as the root temperatures increased from 10°C to 30°C , with a precipitous decrease in growth above 32.2°C (Fig. 1). This is in agreement with published results (5, 16, 17, 19). A sharp increase in growth was observed when plants were grown with a root-zone temperature of 15.6°C as compared to 12.8°C . Plants grown at cooler root-zone temperatures (18.3°C and below) had thicker darker green leaves with increasing purplish coloration on the underside of their leaves. Their roots were short, thick, and bunched as opposed to plants grown at warmer root-zone temperatures (26.1°C and above) whose roots were long, thin and profusely branched. The differences in leaf morphologies are reflected by the higher specific leaf areas (dm^2/g dry weight) of leaves from plants grown at root-zone temperature of 30°C as opposed to 15.6°C (Table 1). Cooper (3) attributed the effect of root-zone temperature on the growth response of tomato seedlings to the partitioning of dry matter between the root and shoot during the germination period and the few days following true leaf development.

Roots of plants grown at excessively warm root-zone temperatures, above 32.2°C , did not live if they remained in direct contact with the nutrient solution. New adventitious roots were initiated on these plants above the nutrient solution either on the portion of the stem which was in the cylinder of the styrofoam or in the volume below the styrofoam and above the nutrient solution.

It is apparent that an environment which provides for satisfactory root growth would also benefit the shoot growth of the plant. Cool root-zone temperatures are capable of inhibiting and warm temperatures are capable of stimulating plant growth when air temperatures are not limiting to growth (17), because vital, temperature-dependent processes which occur in the root exert control over shoot as well as root activities.

Translocation. Increasing root-zone temperature from 15.6°C up to 35°C increased the percentage of ^{14}C -assimilate detected below the labeled leaf after a 24-h period (Fig. 2). The direction and magnitude of translocation is indicative of the modification in the roots sink strength. In general, it is believed that when the metabolic activity of a sink increases the sucrose gradient from the source(s) to that sink is steepened by direct utilization, chemical transformation or spatial compartmentalization of the incoming sucrose (6). Root-zone warming affected root metabolic activity and consequently root sink strength increased, with the converse being true at a lower root-zone temperature of 15.6°C .

The percentage of ^{14}C detected below the labeled leaf of plants maintained at 30°C root-zone temperature however was low. We hypothesize that these low levels are a result of depletion of the root ^{14}C -assimilate pool through respiration and retranslocation. It has been determined (10) with plants ontogenetically similar to those used in this study, that retranslocation from the roots, of newly arrived assimilate, does not occur until 24 h after its arrival at the root. In this study, it seems that root-zone warming may hasten the appearance of ^{14}C -assimilate in roots and may also accelerate the processes involved in metabolizing and retranslocating that assimilate.

We have shown (James *et al.*, unpublished results) that raising the temperature of tissue culture-grown tomato roots to 30°C increased respiration and K-Mg stimulated ATPase activity. This resulted in increased losses of $^{14}\text{CO}_2$ from roots and indicated an

enhanced metabolic rate. Retranslocation of ^{14}C -assimilates coupled with increased root respiration and possibly rapid incorporation into nonsoluble root components at a root-zone temperature of 30°C contributed to the lower than expected level of ^{14}C -assimilate detected in those roots, although the relative contribution of each has not been determined.

The rapidity of the metabolism of basipetal translocated carbon compounds in the root and the retranslocation process over a range of day/night temperatures has been demonstrated by Hori and Shishido (8) using the bilateral plant method. Although their results neither support nor refute our interpretation of low ^{14}C levels in 30°C root-zone temperature roots, they do demonstrate that the general phenomena of retranslocation occurs in tomato and is effectively manipulated by plant temperature.

While high rates of retranslocation and respiration might account for the low levels of ^{14}C detected in roots of plants maintained at 30°C root-zone temperature, even less ^{14}C would be expected to accumulate in roots of plants grown at 35°C , assuming that the retranslocation and respiration processes are accelerated even further by raising temperature above 30°C , but this did not occur. The fact that death occurred when these roots remained in contact with the 35°C nutrient solution after 1 week indicates that while initially root respiration and retranslocation might have been accelerated by warming to 35°C all metabolic processes soon decline. After 35°C root-zone temperature would have initially stimulated ^{14}C assimilates to accumulate in roots, the inability of these roots to subsequently metabolize these assimilates by retranslocation or respiration could have accounted for the high level of ^{14}C detected there at the end of the 24-h translocation period. Indeed, it is well known that invertase activity which has been related to sink strength increases with increasing temperature well past 35°C which could account for the initial ^{14}C deposition in the roots until root cell integrity was lost due to prolonged periods of exposure to excessive heat (35°C).

It has become obvious from the above discussion that the lack of information on general root metabolism, the retranslocation process and, the timing of root death at 35°C has led to a great deal of ambiguity in interpreting the data resulting from root-zone temperatures of 30°C and 35°C . It is felt that more conclusive interpretation of these data lies in empirically defining these parameters.

Carbon Exchange. Net CO_2 fixation rates of leaves of plants grown in various root-zone temperatures for long periods (17 d) increased with increasing root temperature on a per leaf (Fig. 3), leaf area (Fig. 4), and dry weight (Fig. 5) basis. Net CO_2 fixation per leaf on a short term basis (48 h) increased with increasing root-zone temperature up to 30°C after 10 h and continued for a 48-h period (Fig. 6).

Although CER can be independent of leaf area, the fact that plants grown in higher root zone temperatures up to 30°C had correspondingly greater leaf areas, indicated that root-zone temperatures affected the CER of these plants, in part, by affecting their leaf areas. The higher CER on a leaf area and dry weight basis implies that even though plants grown at 30°C had thinner leaves (Table I), their leaves were more photosynthetically active than plants grown at warmer or cooler root-zone temperatures.

No direct biochemical evidence is presented herein to connect root-zone temperature to a changing CER. It is speculated, however, that the uptake of phosphorus by the root or the rate of translocation of assimilated carbon into the root may be the mechanism through which a changing root-zone environment regulates CER.

In this study, plants grown in low root-zone temperature (15.6°C and lower) environments exhibited purplish coloration on the underside of their leaves symptomatic of phosphorus deficiency. Total leaf phosphorus content was shown to be 0.73% of the leaf dry weight at a root temperature of 21°C and to

increase to 0.92% at 26.5°C , thus correlating with an increase in total plant dry weight as the root temperature was raised (12). Maletta (12) also reported a decrease in total plant dry weight as the root temperature was increased from 26.5°C to 32°C accompanied by a corresponding decrease in the leaf phosphorus content from 0.92% to 0.48%. Wilcox *et al.* (23) by adding phosphorus to tomato plants grown at cooler root-zone temperatures (15.5°C) found that the additional phosphorus partially reduced the stunting effect of low root-zone temperature.

The biochemical basis for phosphate regulation of sucrose and starch synthesis is treated in depth in a review by Giaquinta (7). High intracellular phosphate levels would encourage the synthesis of sucrose which is exported in favor of starch synthesis. High levels of leaf starch and other carbohydrates have been implicated in reducing CER (2). In addition, phosphate has been shown to regulate the Triose-phosphate/phosphate translocator (7), and the photosynthetic carbon reduction cycle by regulating the stromal (ATP)/(ADP) ratio (22) and ultimately carbon fixation.

In addition the response of CER to root-zone temperatures could be due to the high rates of translocation of recently fixed assimilates elicited by increasing sink strength. Root sink strengthening by warming (30°C) could ultimately be responsible for removing large quantities of sucrose from the leaf mesophyll cytoplasm via a phloem sucrose-gradient thereby releasing phosphate from its immediate precursor sucrose-6-P. In a detailed study of the effects of increased sink demand on soybean source leaves (20), it was demonstrated that increased demand for assimilates was followed by increased levels of photosynthesis, sucrose translocation, and intracellular phosphate in the export leaf.

It seems then that root-zone temperature may control leaf phosphorus by absolute uptake and possibly through translocation which regulates phosphorus turnover and availability. Although a phosphorus deficiency is commonly attributed to the sensitivity of uptake rates to low root temperature, phosphate in leaf cells may in addition be bound in inactive pools (*i.e.* sucrose-6-P under low sink demand) hampering physiological function of leaf cells.

Starch. Leaf starch content was approximately twice as high on both a dry weight and leaf area basis of plants grown in a cool root-zone environment (15.6°C) as compared with leaves of plants grown in warmer root-zone environments, 30°C (Table II). This is indicative of a starch buildup concomitant with a decrease in CER. While this seems to be consistent with the starch feedback inhibition (of photosynthesis) theory at low root-zone temperatures, the stimulation of CER at 30°C above the level attained at 22°C seems to be unrelated to starch. Apparently, the additional assimilates accumulated by increased CER at 30°C root-zone temperature were diverted to the translocation pool and the starch pool levels were unaffected by higher levels of photosynthesis.

It is clear from this study that increasing root zone temperatures increased the translocation rate into that sink and the increase correlated well with CER of leaves supplying those roots. Moreover, it may be explained that the increased growth at warmer root-zone temperatures resulted from higher CER in leaves, with CER paralleling growth (compare Fig. 1 to Fig. 6).

Although an alteration in root sink activity apparently was the dominant feature resulting from root-zone temperature modification changes in water absorption, ion uptake, stomatal resistance, root growth factors (15), and other unidentified physiological processes could have collectively contributed to the growth effect of root-zone temperature.

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