BASIS OF SHOOT RESPONSE TO ROOT TEMPERATURE IN TOMATO[1, 2]

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Shoot growth of young tomato plants increases as root temperature increases over the range 10° to 25° C (29, 38). When roots are subjected to a temperature of 10° C, the growth rate of shoots approaches zero, even though the shoots are exposed to normal greenhouse temperatures. Rapid shoot growth due to increased root temperature is accompanied by increased concentrations of potassium and phosphorus in the shoot. Concentrations of calcium and magnesium reach maxima at approximately 20° C. Similar variations in mineral concentrations are found in a few other species (35), but are by no means exemplary for plants in general (2, 23, 33, 39).

In the case of the tomato, it might be proposed that reduced rates of mineral transport are responsible for slow shoot growth at cool root temperatures. On the other hand, slow growth might be due to the depressing effect of cool root temperature on the water absorption of plants. The rate of nitrate reduction has also been considered as a possible factor.

This paper reports experiments designed to explore the basic nature of this phenomenon. The evidence is at variance with the above proposals. A possible endogenous mechanism will be outlined in the general discussion.

METHODS

SAND CULTURE: Seeds of the Improved Pearson variety of tomato (*Lycopersicon esculentum* Mill.) were planted in 8-liter glazed crocks containing pure quartz sand and grown in the greenhouse until they had true leaves about three centimeters long. During this period they were watered daily with nutrient solution no. 2 of Hoagland and Arnon (19). A chelated iron compound (sodium ferric diethylenetriamine pentaacetate) was substituted for iron tartrate and used at the concentration of 5 ppm metallic iron. This solution shall be referred to as Hoagland's solution, and dilutions or concentrations thereof as 0.2, 0.4, and 2.0 Hoagland's solution.

Air temperature in the greenhouse fluctuated from a constant night temperature of 18° C to a daily maximum of 35° C. Noon light intensity was about 5,000 ft-c. Daylengths varied from 11.5 to 13 hours. Cloudy days were not encountered. At the start of the treatments, the crocks were placed in water baths which were gradually brought to the desired temperatures. Gravity drainage was provided for the crocks.

SOLUTION CULTURE: Seeds were germinated between sheets of blotting paper tilted to allow seedlings to grow upright. Upon sprouting, the plants were transferred to individual compartments of a single tank. This procedure provided a common nutrient medium, yet prevented root intertwining, and produced uniform plants for experimental use.

When the sixth leaf of such a plant was about three centimeters long, the plant was transferred to treatment conditions. In treatment, each plant constituted an experimental plot. The root medium for each was an aerated solution in an individual glass jar from which light was excluded. These jars in turn were immersed in thermostatically controlled water baths. The plant shoots protruded through corked openings in the water bath covers. By this technique the micro-climate around the shoot was kept independent of the root medium temperature. Treatments were replicated from 6 to 12 times.

The aerial portions of the plants were enclosed under a single plastic-covered frame, through which a constant air movement was maintained. The plastic material permitted a light intensity of approximately 3,500 ft-c at noon. In experiments involving humidity as a variable, this frame was divided by a glass partition, providing two chambers for humidity treatments which transected root temperature treatments. The relative humidity at night approximated 70 % for all plants. Each morning, during experiments which involved humidity, a differential of 15 % in relative humidity was rapidly established between the two chambers, and maintained until sunset. The relatively dry air of the greenhouse was blown unaltered into one chamber. Into the other was blown air which was drawn through moistened filter pads. Air movement was extremely gentle in all cases. By careful adjustment of the ventilation, the difference in humidity could be maintained while providing a natural cycling of illumination and air temperature which was uniform for all plants. Relative humidities were measured with an aspirator-type psychrometer. In experiment IV, relative humidities reached daily minima of about 40 % and 55 %, respectively, for the low and high humidity groups. In experiment VI, the corresponding minima were 35 % and 50 %.

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CHEMICAL ANALYSES: Shoots and roots used for analysis were dried at 71° C in a forced-draft oven. The dried tissue was ground to pass a 40-mesh screen of a Wiley mill. Total phosphorus was determined by the method of Fiske and Subbarow (15), and cations by flame photometry (6). Nitrate and soluble phosphorus were determined from a 2% acetic acid extract of dried material as outlined by Johnson and Ulrich (22). Nitrate, calculated on a nitrogen basis, is referred to as nitrate-nitrogen (NO_3 as N). In experiments III and V, potassium was determined from the acetic acid extract. Analysis of the residue showed potassium to be completely displaced by this method. In experiment IV (table II & III), the phosphorus fraction designated as insoluble phosphorus refers to the difference between total phosphorus and the acetic acid-soluble fraction.

All analyses, performed in duplicate, are reported on the dry weight basis. Unless otherwise qualified, all treatment differences cited in the text are significant at the 95% or 99% level.

EXPERIMENTAL RESULTS

EXPERIMENT I. *Interaction of nutrition & root temperature*: In an earlier sand culture experiment (29), warm-rooted tomato plants responded more to an increased level of phosphorus than did cool-rooted plants. At all root temperatures, increased phosphorus in the root medium induced higher levels of phosphorus in the shoots. Thus, the phosphorus level in the shoots of cool-rooted plants did not appear to be the factor limiting their growth. It was decided to modify this experiment by varying the nutrient solution as a whole. Plants were grown in sand at three levels of nutrition, 0.2, 0.4, and 1.0 Hoagland's solution, and at two root temperatures, 18° and 24° C.

Plants were thinned uniformly to three per crock, and treatments were replicated four times. The experimental period was 7 days. Tissue was analyzed for phosphorus and potassium.

The interaction mentioned above was observed to reoccur. Plants growing at a root temperature of 18° C did not respond to increased nutrient levels. At 24° C they did. Plants growing in 1.0 Hoagland's solution were 30% greater in dry weight than those in 0.4 Hoagland's solution, and 60% greater than those in 0.2 Hoagland's solution. At a root temperature of 18° C, increased nutrient concentrations raised the shoot concentrations of phosphorus from 0.22% to 0.33%, and of potassium from 2.65% to 4.45%. At 24° C, intensified nutrition increased the concentration of phosphorus from 0.43% to 0.47%, and of potassium from 4.25% to 6.10%.

At the lower root temperature, the growth of the shoot was independent of its nutrient status, at least with respect to phosphorus and potassium.

EXPERIMENT II: *Xylem exudate*: Should root temperature-induced variations in shoot mineral concentrations be due to altered rates of mineral transport, and if the mineral content of the xylem exudate reflects the transport pattern of the intact plant, then the mineral composition of the exudate and of the intact shoot should vary similarly in response to root temperature. The rate of exudation in the tomato, as affected by root temperature, has been studied by Kramer (24), but he did not report on ion concentrations in the exudate. We studied this effect by collecting the 12 hour day or night exudate of decapitated plants growing in sand, watered with Hoagland's solution, at root temperatures of 15°, 21°, and 27° C. The plants were about 20 cm high when topped. The volume of exudate varied as reported by Kramer (24). The exudate was analyzed directly for potassium, phosphorus, and nitrate.

Phosphorus concentration varied from 33 ppm at 15° to 52 ppm at 27° C. Conversely, the concentration of potassium declined from 534 ppm at 15° to 457 ppm at 27°. Nitrate-nitrogen did not vary significantly and averaged 270 ppm.

Because of the divergent nature of these variations, they cannot be attributed to variation in volume flow of exudate. Under like conditions, the concentrations of these elements in the intact shoot invariably increase in response to an increase in root temperature. Just as classical studies have shown poor correlation between salt uptake and water uptake (25), so these data indicate that patterns of salt accumulation in the shoot do not always bear a close relation to salt concentration in the xylem exudate. In addition, note that the concentrations of phosphorus, potassium, and nitrate in tomato exudate are only one to two times that of Hoagland's solution, whereas their concentrations in the intact fresh shoot are from 10 to 40 times their concentrations in Hoagland's solution. The importance of the shoot cells in the concentration phenomenon is treated more fully in the Discussion.

EXPERIMENT III. *24-Hour response*: In the young tomato plant, response of the shoots to a decreased root temperature is discernible within 24 hours. The response is evidenced by a darkening of leaf color and accumulation of purple pigmentation in the stem. If differences in mineral composition are detectable within 24 hours, they should parallel differences found in longer term experiments, provided that an unqualified change in basic rate of transport is responsible.

To determine the 24-hour response, young plants were placed in aerated Hoagland solution held at 13° or 25° C, having developed in Hoagland's solution first at 13°, then at 25° root temperature, in their pre-treatment. Experimental procedures were as previously described. Potassium, nitrate, and phosphorus determinations were made on acetic acid extracts of each individual plant, of which there were 24.

No differences in concentrations of potassium or soluble phosphorus in the shoot, due to treatment, were detectable in 24 hours. Nitrate nitrogen, however, varied from 880 ppm at 13° to 1,060 ppm at

25° C. Average increase in plant weight was 90 mg at 13° and 560 mg at 25° C.

DISCUSSION OF EXPERIMENTS I, II, III: The evidence of the three experiments just described indicates that rate of nutrient supply is not the factor which limits shoot growth at cool root temperatures. The results of experiment I show independence of shoot growth from its nutrient status at the low root temperature. Experiment II discloses the fact that the pattern of mineral accumulation displays considerable independence from the composition of the xylem exudate. The results of experiment III suggest that the reduced amounts of phosphorus and potassium in shoots of cool-rooted plants do not necessarily represent an immediately reduced transport of these ions to the shoot.

The data do not support the idea that a slow rate of nitrate reduction at low root temperature might be a chief factor in the depression of shoot growth. An increase in tissue nitrate would be expected to result from an inhibition of nitrate reduction (12). However, in response to low root temperature, the nitrate content of shoots and roots decreases in both long and short-term trials, and nitrate concentration in the exudate does not vary.

EXPERIMENT IV. *Interaction of humidity and root temperature*: Previous to experiment IV, we used two widely differing methods of determining the importance of water stress in the over-all response of tomato plants to a cool root temperature.

The gradual decrease in the moisture content of plant tissues which occurs during the day is well known (25). Our measurements, using root temperatures of 18° and 24° C, failed to detect a greater diurnal moisture loss from the tissues of plants growing in the cooler root media. These measurements were made under many varied conditions of pretreatment and nutrient media. A 12-hour nocturnal period of adjustment to root temperature was allowed before measurements were started.

Eaton (11) demonstrated that a tomato plant having a portion of its root system in a nutrient solution will remove water amply from a distilled water supply via the remaining portion of its root system. Working on this basis, we grew plants with part of the root system in a warm or cool nutrient solution and the other part in warm distilled water. Several types of control treatments were provided. Results showed that the growth of plants in cool root media was not enhanced by provision of an auxiliary warm water supply.

In experiment IV, the approach to this problem was to superimpose humidity treatments (15 % R.H. differential) on plants growing at two root temperatures (15° & 25° C) in solution culture. The reasons for using a narrow humidity differential are discussed later. Under these conditions it was expected that shoot growth would be enhanced by higher humidity if water stress was a limiting factor. In addition, the use of 1.0 and 2.0 Hoagland's solution was introduced since such a variation is known to affect water absorption, and to expand our body of data on the interaction of root temperature and nutrient concentration. The treatment period was 7 days.

The effects of root temperature, humidity, and root medium concentration on shoot and root growth are shown in table I. Considering, first, only plants growing in 1.0 Hoagland's solution, the standard treatment, it is evident that higher humidity signifi-

TABLE I

EFFECTS OF ROOT TEMPERATURE, RELATIVE HUMIDITY, & NUTRIENT CONCENTRATION ON SHOOT & ROOT GROWTH*

NUTRIENT CONC	ROOT TEMP	PER SHOOT				PER ROOT				SHOOT-ROOT RATIO***	
		FR WT		DRY WT		FR WT		DRY WT			
		REL HUM., %		REL HUM., %		REL HUM., %		REL HUM., %			
STANDARD	° C	40	55	40	55	40	55	40	55	40	55
		grams								g/g	
1.0	15	5.1	5.7	0.40	0.44	1.6	1.4	0.10	0.10	4.1	4.6
	25	8.1	10.1	0.56	0.70	1.9	2.2	0.09	0.10	6.5	6.9
2.0	15	4.4	5.3	0.35	0.43	1.3	1.5	0.08	0.10	4.6	4.4
	25	7.3	7.3	0.53	0.51	1.7	1.7	0.10	0.10	5.6	5.5
Significant levels of mean difference, %											
Root temperature		99		99		99		N.S.		99	
Nutrient conc.		99		99		95		N.S.		97.5	
Relative humidity		97.5		97.5		N.S.		N.S.		N.S.	
Interaction**		95(H×T×C)		95(H×T×C)		N.S.		N.S.		99(T×C)	

* Experiment IV.

** All possible interactions are nonsignificant except those which are shown.

*** Dry weight basis.

T, root temperature; C, nutrient concentration; H, relative humidity.

TABLE II

EFFECTS OF ROOT TEMPERATURE, RELATIVE HUMIDITY, & NUTRIENT CONCENTRATION ON MINERAL COMPOSITION OF SHOOT*

NUTRIENT CONC STANDARD	ROOT TEMP °C	K REL. HUM., % 40	K REL. HUM., % 55	SOL. P*** REL. HUM., % 40	SOL. P*** REL. HUM., % 55	INSOL. P*** REL. HUM., % 40	INSOL. P*** REL. HUM., % 55	Ca REL. HUM., % 40	Ca REL. HUM., % 55	NO_3 AS N REL. HUM., % 40	NO_3 AS N REL. HUM., % 55
		g/100 g *Dry weight*									
1.0	15	4.8	4.8	0.31	0.33	0.25	0.24	3.2	3.2	0.79	0.95
	25	6.1	5.7	0.54	0.55	0.25	0.25	3.2	3.2	1.04	1.16
2.0	15	5.0	5.0	0.37	0.36	0.23	0.25	3.3	3.1	0.88	0.90
	25	5.7	5.6	0.52	0.54	0.26	0.25	3.3	3.1	1.19	1.17
Significant levels of mean difference, %											
Root temperature		99		99		N.S.		N.S.		99	
Nutrient conc.		N.S.		92		N.S.		N.S.		N.S.	
Relative humidity		N.S.		92		N.S.		N.S.		97.5	
Interaction**		95(T×C)		99(T×C)		N.S.		N.S.		97.5(H×C)	

* Experiment IV.

** All possible interactions are nonsignificant except those which are shown.

*** Acetic acid soluble or insoluble phosphorus.

cantly promoted shoot growth in warm-rooted plants, but did not do so in cool-rooted plants. A separate statistical analysis of this data (1.0 Hoagland's solution) showed differences due to root temperature or humidity to be highly significant as was the interaction of root temperature and humidity. Root growth exhibited a positive response to root temperature if measured by fresh weight, but not by dry weight. The shoot-root ratios indicate that the warmer root temperature stimulated shoot growth more than root growth.

The more concentrated nutrient solution consistently depressed shoot and root growth, and at the warm root temperature depressed shoot growth more than root growth (see shoot-root ratios). The depressing effect of concentration was not additive to that of cool root temperature. The 2.0 Hoagland's solution induced the greatest growth depression when the root temperature was warm and the humidity relatively high (i.e., when growth was normally the fastest). This suggests that cool root temperature

TABLE III

EFFECTS OF ROOT TEMPERATURE, RELATIVE HUMIDITY, & NUTRIENT CONCENTRATION ON MINERAL COMPOSITION OF ROOT*

NUTRIENT CONC STANDARD	ROOT TEMP °C	K REL. HUM., % 40	K REL. HUM., % 55	SOL. P*** REL. HUM., % 40	SOL. P*** REL. HUM., % 55	INSOL. P*** REL. HUM., % 40	INSOL. P*** REL. HUM., % 55	Ca REL. HUM., % 40	Ca REL. HUM., % 55	NO_3 AS N REL. HUM., % 40	NO_3 AS N REL. HUM., % 55
		g/100g *Dry weight*									
1.0	15	7.0	6.6	0.63	0.55	0.64	0.64	0.75	0.63	1.18	1.08
	25	7.5	7.8	0.81	0.74	0.62	0.57	0.96	0.67	1.38	1.36
2.0	15	6.8	7.7	0.80	0.70	0.74	0.65	0.82	0.75	1.27	1.24
	25	7.4	7.9	0.84	0.85	0.54	0.52	0.96	0.91	1.53	1.50
Significant levels of mean difference, %											
Root temperature		99		99		99		99		99	
Nutrient conc.		N.S.		99		N.S.		97.5		99	
Relative humidity		97.5		99		N.S.		99		N.S.	
Interaction**		99(H×T)		95(H×T)		94(T×C)		92(H×C)		N.S.	
		95(T×C)		99(T×C)							
		97.5(H×T×C)		92(H×T×C)							

* Experiment IV.

** All possible interactions are nonsignificant except those which are shown.

*** Acetic acid soluble and insoluble phosphorus.

and nutrient concentration were not active through the same mechanism.

It will be noticed (table II) that an increase in humidity did not greatly affect the concentrations of mineral elements in the shoot. Doubling the standard concentration of Hoagland's solution had the same general lack of effect, depending on levels of root temperature and humidity. Environmental effects on mineral accumulation in the roots were complex (table III).

Nightingale and Mitchell (34) found that tomato plants grew more vigorously in response to increased humidity. Freeland (16) found the opposite to be the case. In our preliminary experiments, shoot growth was significantly reduced by a very high humidity (90 %) when maximum daily light intensity was about 1,500 ft-c. Clearly, the effect of humidity on shoot growth depends on several qualifying circumstances. The conditions of experiment IV are considered valid for the primary purpose of the investigation. The range in intensities of the variables was narrow and closely approximated greenhouse conditions. An abnormal situation was not created. The humidity levels employed appear to be in the limiting region where a small variation would be expected to evoke a tangible response in a dependent variable. From the results of our experiments it may be concluded that water stress is not the factor responsible for the shoot growth depression occurring at cool root temperatures.

EXPERIMENTS V & VI: With the indication that rates of mineral and water absorption are causally unimportant in the relationship of shoot growth to root temperature, the possibility of an endogenous mechanism remained to be explored. By growing plants in dilute salt solutions and distilled water, it was speculated that the situation might occur in which no net movement of salts to the shoot would take place in response to root temperature treatment. Should this occur, the response or lack of response of shoot growth to root temperature would have particular significance.

Furthermore, it was possible in experiments I and IV that an actual limiting role exerted by water or ion transport was masked because both were limiting or nearly so in plants growing in cool root media. If such were the case, the limiting role would be interchanged in experiments testing each separately, and the limiting nature of neither would be disclosed. To test this possibility, plants growing in distilled water were exposed to two different levels of humidity. With one factor thus definitely limited, the apparency of shoot response to variation in the other could be ascertained.

TABLE IV

COMPOSITION OF SOLUTIONS IN EXPERIMENT V

SOLUTION	MOLARITY	K	P	N
		ppm (*approx*)		
KCl	0.0001	4	...	...
KH_2PO_4	0.0001	4	3	...
NaH_2PO_4	0.0001	...	3	...
0.01 Hoagland (macro only)		2.3	0.3	2
1.0 Hoagland (for reference)		234	32	200

EXPERIMENT V. *Response to root temperature of plants growing in dilute solutions*: Plants previously grown in 1.0 Hoagland's solution, 15° C in tem-

TABLE V

INFLUENCE OF VARIOUS DILUTE SALT SOLUTIONS & ROOT TEMPERATURE UPON RATE OF PLANT GROWTH & SHOOT-ROOT RATIO*

	% FR WT INCREASE**		% DRY WT SHOOT		SHOOT-ROOT RATIO***	
ROOT TEMP (C):	15°	25°	15°	25°	15°	25°
Solution						
KCl	37	46	12.8	12.9	2.72	2.40
KH_2PO_4	37	44	13.7	13.0	2.71	2.53
NaH_2PO_4	40	46	13.5	13.0	2.45	2.70
0.01 Hoagland	45	52	13.3	13.4	2.18	2.31
Significant levels of mean diff., %						
Root temperature	99		N.S.		N.S.	
Solution	94		N.S.		N.S.	

* Experiment V.

** Gain in fresh weight as a per cent of the initial fresh weight.

*** Fresh weight basis.

perature, were placed in 0.25 Hoagland's solution 5 days before beginning treatment. In treatment, they were grown at 15° or 25° root temperature, and in one of the four nutrient solutions whose characteristics are shown in table IV. Also shown, for reference, are some properties of the Hoagland's solution. One-half the plants were taken for weight measurement at the end of 48 hours. The nature of their responses was identical to that of the remaining plants, which were taken for weighing and analysis after an additional 72 hours. Plants were composited within treatments for chemical analysis.

Plants grew proportionately faster in the warm than in the cool dilute solutions, as shown by the data on per cent increase (table V). Since temperature treatment caused no shift in shoot-root ratios, it may be assumed that warm root media promoted shoot and root growth to the same degree.

Nitrate reserves were nearly depleted in all plants, particularly in faster growing warm-rooted plants, being about 100 ppm in shoots and 400 ppm in roots on a dry weight basis. The influence of treatment on concentrations of potassium and acetic acid-soluble phosphorus are shown in table VI. Shoots of warm-rooted plants were invariably higher in potassium and soluble phosphorus than their cool-rooted counterparts, even when these elements were not present in the nutrient solution. Evidently the warm root temperature stimulated the accumulation potential of shoot cells preferentially over that of root cells. In all solutions, the concentration of potassium in the root declined at the warmer root temperature. With phosphorus this occurred only when there was no phosphate in the nutrient medium.

Table VI also presents the absolute amounts of potassium and acetic acid-soluble phosphorus in whole plants, corrected for initial differences in plant weights. Warm-rooted plants contained more of these elements, even when they were not supplied in the external solution. This suggests that they were lost preferentially to the cooler solution. The differences amounted to 8 % of the potassium and 17 % of the soluble phosphorus. To what extent the soluble phosphorus fraction is indicative of total phosphorus is of course subject to doubt.

Experiment VI. *Response to root temperature of plants growing in distilled water*: Plants were preconditioned in a manner designed to make them typical of neither warm-root nor cool-root plants at time zero. During the final pre-treatment phase they were grown in standard Hoagland's solution at 25° for 3 days. During treatment, plants were grown in aerated distilled water, 15° or 25° C in temperature, and either at 35 % or 50 % minimal relative humidity. After 68 hours at treatment, plants were weighed and combined in groups of two for chemical analysis.

A slight response in shoot growth to root temperature was observed (table VII). Two preliminary experiments resulted in responses of the same level of significance (90–92 %). Final shoot weights as a per cent of the plants' original weights take initial differences into account. Such corrected quantities may more precisely portray the true responses, since growth was slow in distilled water and the treatment period was brief. The probability is fairly high that higher root temperature and higher humidity enhanced shoot growth even under these conditions of severe nutrient limitation. The shoot-root ratios indicate that the warm root temperature promoted shoot growth less than root growth.

In general, plants attaining a greater rate of growth, due to treatment, had lower concentrations of potassium, phosphorus, calcium, and nitrate in both root and shoot (table VIII). As estimated by several quantities or ratios abstracted from the data, on an absolute basis, differential shoot-root shifts in phosphorus and potassium, due to treatment, were too small to be detectable, nor were they lost to the medium in greater amounts at one temperature than at another. In contrast, calcium was lost from the shoot preferentially at the warm root temperature, and to a greater degree from the root, with the result that warm-rooted plants significantly contained from 5 % to 10 % less calcium than cool-rooted plants.

Table VI

Influence of Various Dilute Salt Solutions & Root Temperature on Concentration & Absolute Amounts of Potassium & Phosphorus**

	g K/100 g Dry wt				K/Plant***		g Sol. P/100 g dry wt				Sol. P/Plant***	
Root temp, C:	15°		25°		15°	25°	15°		25°		15°	25°
Solution	Shoot	Root	Shoot	Root	mg/g		Shoot	Root	Shoot	Root	mg/g	
KCl	3.4	3.8	3.5	2.8	5.1	5.3	0.14	0.27	0.16	0.24	0.23	0.27
KH_2PO_4	3.0	3.6	3.2	3.1	4.8	5.0	0.21	0.38	0.28	0.57	0.36	0.50
NaH_2PO_4	2.8	3.1	3.2	2.6	4.5	4.9	0.20	0.41	0.27	0.46	0.36	0.47
0.01 Standard	2.9	3.5	3.4	2.6	4.7	5.4	0.15	0.30	0.17	0.21	0.27	0.29

* Experiment V.

** Acetic acid soluble phosphorus.

*** Milligrams element per plant divided by the initial fresh weight per plant.

TABLE VII

EFFECT OF ROOT TEMPERATURE & RELATIVE HUMIDITY ON GROWTH OF SHOOTS & ROOTS OF PLANTS GROWING IN DISTILLED WATER*

REL. HUM.	ROOT TEMP	PER 2 SHOOTS			PER 2 ROOTS		SHOOT-ROOT RATIO***
		FR WT	ADJ. FR WT**	DW/FW	FR WT	DW/FW	
%	° C	g	%	%	g	%	
35	15	5.7	96	11.2	2.0	5.4	6.0
	25	6.2	96	11.6	3.4	5.7	3.8
50	15	6.4	98	11.6	2.2	5.5	6.5
	25	6.5	102	11.5	3.3	5.5	4.2
Significant levels of mean diff., %							
Root temp		92	92	N.S.	99	N.S.	99
Rel. hum.		92	97.5	N.S.	N.S.	N.S.	N.S.
Interaction		95	90	N.S.	N.S.	N.S.	N.S.

* Experiment VI.

** Fresh weight of shoot as a per cent of the initial fresh weight of the entire plant.

*** Dry weight basis.

DISCUSSION OF EXPERIMENTS V & VI: The fact that increased humidity (experiment VI) promoted shoot growth when nutrition was severely limited makes it improbable that water and nutritional relations exerted an interchangeable limiting role in root temperature responses. This substantiates the results of experiments I and IV.

In experiment VI, shoots responded slightly to warm distilled water, although concomitantly experiencing a net loss in nitrate and calcium, and without gaining phosphorus and potassium. Apparently the initial stimulation was due to some factor other than mineral supply. The stimulus, in this case, was not sustained by an adequate supply of mineral ions, and shoot growth was not vigorous. The relationship of the stimulation and the mineral supply is demonstrated by these observations on shoot-root ratios: in 1.0 Hoagland's solution (expt. IV), shoot growth was stimulated more than root growth by warm root temperature; in extremely dilute solutions (expt. V), shoot and root growth were stimulated equally; in distilled water, warm root temperature stimulated root growth more than shoot growth.

In experiment V, phosphorus and potassium apparently were lost to the medium in greater amounts at the cooler root temperature. In experiment VI, calcium was lost in greater amounts to the warmer root medium. These directional variations compare favorably with results obtained under conditions of normal nutrition; i.e., it was originally reported by

TABLE VIII

EFFECT OF ROOT TEMPERATURE & RELATIVE HUMIDITY ON CONCENTRATION OF POTASSIUM, PHOSPHORUS, CALCIUM, & NITRATE IN SHOOTS & ROOTS OF PLANTS GROWING IN DISTILLED WATER*

REL. HUM.	ROOT TEMP	K		SOL. P		TOTAL P		Ca		NO_3 AS N	
		SHOOT	ROOT	SHOOT	ROOT	SHOOT	ROOT	SHOOT	ROOT	SHOOT	ROOT
	° C	*% Dry Weight*								ppm	ppm
35	15	3.3	4.2	0.20	**	0.36	0.67	1.8	0.97	930	1700
	25	3.2	2.8	0.20	**	0.35	0.41	1.7	0.47	330	500
50	15	3.1	4.2	0.18	**	0.34	0.64	1.7	0.84	780	1700
	25	2.9	2.6	0.19	**	0.34	0.42	1.6	0.47	340	400
Significant levels of mean difference, %											
Root temperature		N.S.	99	97	...	N.S.	99	99	99	99	99
Relative humidity		95	N.S.	95	...	N.S.	N.S.	97	N.S.	N.S.	N.S.
Interaction		N.S.	N.S.	99	...	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

* Experiment VI.

** Not analyzed.

Lingle and Davis (29) that cooler rooted plants contained less potassium and phosphorus, while the warmest rooted plants contained less calcium. It is possible that the quantitative effect of ion loss to the medium upon the mineral content of the shoot is not negligible, even when nutrition is normal.

One additional observation upon intra-plant movements of minerals deserves comment. In experiment V, the shift of phosphorus and potassium from root to shoot was greater at warmer root temperature. The apparent loss of phosphorus and potassium to the medium was greater at cooler root temperature. This may indicate an effective barrier between the free space and a portion of the root-shoot path. The exudation phenomenon must, of course, rest upon just such a basis (8, 20). Its importance in the overall transport scheme is being evaluated at present (26, 37, 40). (It is emphasized that the above-mentioned differential movements of phosphorus and potassium were not evident in the distilled water experiment.) Ion loss to the medium and ion release to the shoot may involve fundamentally different mechanisms, even structures.

Discussion

If shoot response to root temperature has a degree of independence from its nutritional and hydrational states, an endogenous mechanism must be proposed. Variations in root temperature may, for instance, induce differential production of root-produced substances having shoot regulatory activity. Evidence of such substances has been reported for tomato (21, 42). Consideration of this type of mechanism probably will not be neglected in future investigations. Another mechanism is possible, however. It is easily overlooked, and, for this reason, will be emphasized in this discussion. Whenever shoot-root relationships are being studied, this mechanism remains a possibility until discounted. This is particularly true when experimental procedures involve ringing, or girdling, or severing of the root from the shoot.

Relatively low temperature may retard the rate at which materials are transported in the phloem (14). It would be reasonable to suspect that low root temperature might diminish the root's effectiveness as a "sink" for phloem transported material (7). Indeed, cool root temperature decreases shoot growth and mineral accumulation in a manner which recalls the ringing of branches (9, 31). Similar results have been produced by cooling a portion of a branch (10). In cooling and ringing treatments, procedures were used in which root activities were not curtailed nor transpiration primarily affected. Results of ringing were interpreted as indicating a significant upward transport of mineral elements in the phloem—a widely contested conclusion.

A different interpretation is possible. In the normal functioning of shoot cells, a large number of compounds are produced of which many may be classified as growth substances (17). Several known growth substances have been shown to accumulate at girdles (5). Should the shoot experience an alteration in the concentration of such compounds, due to an interruption or depression of phloem transport, a partial inhibition of shoot cell metabolism might result.

Endogenous mechanisms have been shown to cause wide fluctuations in the intensity with which cells accumulate mineral ions (3, 28, 32, 43). Such accumulation is known to depend on metabolic activity (1, 18, 37, 41). When shoot activity is comparatively low, mineral elements which have been taken up and not accumulated are probably subject to phloem export, or, in girdled stems, to a backward diffusion along purely physical gradients within the free space of the plant body (26).

Many of the responses reported herein, with regard to mineral concentrations in the shoot, are difficult to account for on the basis of a unidirectional (upward) transport (20, 40) alone. The mineral composition of the xylem exudate and that of the shoot did not vary similarly in response to root temperature, nor did the shoot display similar long and short-term variations. Doubling the standard Hoagland's solution did not increase the salt content of shoots, nor did elevated humidity decrease it, contrary to prediction on the basis of passive transport. Losses of ions from the shoot and from the entire plant, presumably to the rooting medium, are to be inferred from analyses of tissues of plants which were grown in dilute salts and distilled water.

These observations are more consistently explained if the mineral content of the shoot is assumed to be at least partially attributable to a selective accumulation by the shoot cells (20). Penston (36), Alberda (1), and Helder (18) propose a return of excess ions to the roots and to the root medium. Recirculation of ions has been thoroughly demonstrated (4). Mineral excretion to the root medium has been extensively reviewed by Loehwing (30) and Helder (18), and more recently demonstrated by Kylin (27) and Emmert (13), among others. Quantification of such mineral retranslocations may be essential in a strict accounting of the shoot's mineral content at a given time.

Should cool root temperatures actually retard movement in the phloem, resulting in a congestion of substances in the shoot which can depress metabolic activity and salt accumulation, a basis may be provided for understanding some of the effects of cool root temperature on shoot growth and mineral accumulation in tomato plants.

Summary

Tomato plants were grown under partially controlled environmental conditions in nutrient culture, the main treatments being variations of root temperature in the range 13° to 27° C.

In nutrient solutions graded in concentration from

0.2 to 1.0 times the standard strength of Hoagland's solution, each increment in nutritional level enhanced shoot growth of warm-rooted plants, but not of cool-rooted plants, although phosphorus and potassium concentrations were increased in both warm and cool-rooted plants. An increase of atmospheric humidity promoted the shoot growth of warm-rooted but not of cool-rooted plants. When plants were growing in distilled water, a weak but significant promotion of shoot growth was observed in response to increased root temperature and increased humidity. In this situation, the faster shoot growth occurred without a more rapid net movement of phosphorus and potassium into the shoot, and despite an absolute decrease in nitrate and calcium. It was concluded that the control of shoot growth by root temperature does not reside primarily in rates of mineral or water supply to the shoot. Over-all evidence did not favor an important role for nitrate reduction in this connection.

In response to root temperature, variations in mineral contents of the xylem exudate were not similar to variations in mineral contents of intact shoots, nor were short-term responses similar to long-term responses. A nutrient medium concentration twice that of Hoagland's solution did not materially alter the salt status of the shoots, nor did moderately increased humidity. Observations made on plants grown in dilute salt solutions and distilled water demonstrated the necessity of considering ion movements out of the plant in accurately accounting for its mineral contents at a given time. It was concluded that the salt status of shoots in response to root temperature variations could not be accounted for entirely by estimations of uptake alone, but shoot export and plant loss of elements must also be considered.

In explaining the response of shoot growth and salt accumulation to root temperature, discussion centers upon a possible endogenous mechanism.

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