

# THE EFFECT OF TEMPERATURE AND WATER SUPPLY ON GROWTH, TRANSPIRATION AND WATER REQUIREMENT OF TOMATO UNDER CONTROLLED CONDITIONS

by

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## 1. INTRODUCTION

Investigations concerning total water loss, water requirement and transpiration coefficient of a crop have been made on many occasions in the past. From the quantity of water transpired by the plant and the gain in dry matter produced, the water requirement in g water per g dry matter has been calculated. This ratio varies widely according to the plant species. However, wide variations even in the same species have been observed in different years and at various localities. This seems to support the supposition that dry matter production and transpiration behave differently with respect to the environment. Differences in behaviour may be expected e.g. with respect towards changes in the relative humidity of the air. The rate of transpiration depends largely on this factor, whereas the rate of photosynthesis – which process is the main source of dry matter production – remains unaffected to a large extent (1).

Estimations of supplementary irrigation based on water requirement values without considering such differences may lead, therefore, to erroneous results. In field experiments various climatic factors as temperature, light intensity, and relative humidity are intimately correlated so that it is difficult to analyze the effect of each factor separately on the various aspects of growth and transpiration.

For this reason, we have carried out experiments with tomato plants under controlled conditions in the laboratory. In this article the results on the effect of temperature, and availability of soil moisture will be presented.

The relation between temperature and plant growth is rather complex. Many processes, as germination, stem elongation, leaf initiation, and development generally increase with increasing temperature up to a certain optimum. At still higher temperatures, a rapid decrease in rate of growth was often observed, due

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to any reversible or irreversible damage of the protoplasm. The different temperature optima of the various growth-related processes result in an optimal temperature for the overall growth process. It has been found that such an optimum may occur at a relatively high temperature in young plants, and shifts to lower values with increase in age. In young tomato plants, WENT (6, 7) found optimal root growth at 30°C, while optimal stem elongation was observed at 25°C day temperature and 25°C night temperature. The latter optimum decreased with age to 20°C while in young plants the optimum even decreases to 8°C with a decrease in light intensity.

The effect of soil moisture on plant growth has been studied by several investigators (cf. VEIHMEYER (4), RICHARDS and WADLEIGH (2)). It is evident that growth is linked with the state of turgescence. The latter depends on the rate of water uptake as well as on the rate of water loss, while both processes are affected by various external factors. Within certain limits, plants can adjust themselves rapidly, in order to maintain a favourable water balance or turgescence under adverse conditions. This takes place either by cutting down the rate of transpiration by closure of stomata or by an increase in water uptake through increase in osmotic pressure, or by other means. In long periods of drought, the plant may also reach an effective adaptation by a change in its morphological character, e.g. by producing smaller leaves, a thicker cuticle, smaller and sunk stomata, etc.

## 2. MATERIAL AND METHODS

Seeds of tomato (*Lycopersicum esculentum* var. Ailsa Craig) were sown in a seed box. Two weeks later, the seedlings were transplanted in pots, 10 cm in diameter and 20 cm in height. Each pot was filled with 2 kg of air-dry loam soil, the field capacity of which was 21.2% (based on volume of soil), and the permanent wilting point 12.1%. When the plants were established (after a period of two weeks from transplanting), the pots were transferred to four compartments, adjusted at 26°, 20°, 15° and 10°C. No equipment was available to control the relative humidity in the compartments. The vapour pressure of the air was nearly the same in all rooms, causing a decrease in the relative air humidity and an increase in the vapour pressure deficit (V.P.D.) with increase in temperature. The average V.P.D. during the entire growth period was 17.8, 10.6, 6.4 and 2.6 mm Hg at 26°, 20°, 15° and 10°C respectively. The evaporation rate, measured by a PICHE evaporimeter and corresponding to the mentioned temperatures was 8.4, 5.2, 3.2 and 2.2 mm/day respectively. The compartments were provided with daylight fluorescent tubes, producing a light intensity at the top of the plants of approximately  $4.6 \times 10^4 \text{ erg. sec}^{-1} \cdot \text{cm}^{-2}$  sphere, measured with a spherical radiation meter (5). The plants were illuminated for a period of 12 hours a day. By interchanging the places of the pots every day, differences in light intensity were eliminated.

Before the pots were transferred to the compartments, 20 plants, similar to the experimental plants, were cut, and the fresh and dry weight were determined and considered as the initial weight.

In each compartment, 16 pots were placed at four different irrigation treatments (A, B, C and D), with four replicates. In the first group (A), water was added to bring back the soil to field capacity as soon as 20% of the total available water in the soil was used; in groups B, C, and D when respectively 40, 70

and 95 % of the available water were used. The duration of the experiment under these conditions was four weeks.

The pots were weighed every day to determine the water loss by evapo-transpiration. For the measurement of water loss through transpiration only, the pots were covered with plastic sheets one day every week. The water loss by soil evaporation was obtained from the difference between evapo-transpiration and transpiration, and the correction thus obtained was properly applied to all evapo-transpiration data. In the present series of experiments, no measurements of the dry weight of the root, and the root/shoot ratio have been carried out. In subsequent series, dealing with other environmental factors these aspects have been studied (to be published shortly).

### 3. EXPERIMENTAL RESULTS

#### A. Water loss

##### a) Evapo-transpiration

The total water loss by evapo-transpiration shows a wide range of variation under different conditions of temperature and irrigation, and varies between 4.33 and 0.44 mm/day (Table 1). It is evident that the evapo-transpiration de-

TABLE 1. The effect of air temperature, V.P.D., or Piche-evaporation, and irrigation regime on evapo-transpiration and evaporation (values in mm/day were calculated by dividing waterloss in day by 8.81, a „pot factor”).

Irrigation regime	Temperature °C	25.7	20.0	15.6	10.4
	V.P.D. (mm Hg)	17.8	10.6	6.4	2.6
		Piche evaporation (mm/day)			
		8.4	5.2	3.2	2.2
		Evapo-transpiration (mm/day)			
A		4.33 ± 0.14	2.53 ± 0.08	1.33 ± 0.02	0.59 ± 0.01
B		3.85 ± 0.03	2.20 ± 0.07	1.40 ± 0.07	0.52 ± 0.08
C		2.71 ± 0.02	1.64 ± 0.03	0.87 ± 0.02	0.44 ± 0.02
D		1.86 ± 0.02	0.97 ± 0.01	0.79 ± 0.01	
		Transpiration (mm/day)			
A		2.69 ± 0.17	1.58 ± 0.16	0.57 ± 0.02	0.17 ± 0.05
B		2.62 ± 0.05	1.37 ± 0.09	0.70 ± 0.03	0.14 ± 0.01
C		0.81 ± 0.06	0.77 ± 0.06	0.40 ± 0.01	0.14 ± 0.05
D		0.73 ± 0.05	0.48 ± 0.02	0.38 ± 0.02	
		Evaporation (mm/day)			
A		1.64 ± 0.03	0.95 ± 0.11	0.76 ± 0.02	0.42 ± 0.02
B		1.23 ± 0.01	0.83 ± 0.03	0.70 ± 0.05	0.38 ± 0.02
C		1.90 ± 0.08	0.87 ± 0.02	0.47 ± 0.03	0.30 ± 0.01
D		1.11 ± 0.03	0.49 ± 0.02	0.41 ± 0.01	

creases with a decrease in temperature, as well as with a decrease in water supply. The effect of temperature is indirect operating through the change in the vapour pressure deficit. The latter influences transpiration according to FICK'S law of diffusion:

$$E = k \frac{V.P.D.}{R}$$

$E$  = evapo-transpiration in g per unit time and unit leaf area.

$k$  = diffusion coefficient.

$V.P.D.$  = vapour pressure deficit, calculated from the data on air temperature and relative humidity, in mm Hg.

$R$  = diffusion resistance to the transport of water vapour from the plant to the surrounding air.

Plotting the rate of evapo-transpiration ( $E$ ) versus the vapour pressure deficit, a linear relation is obtained for the treatments A, B, C and D (fig. 1), the curves passing through the origin. The slope of the different curves depends

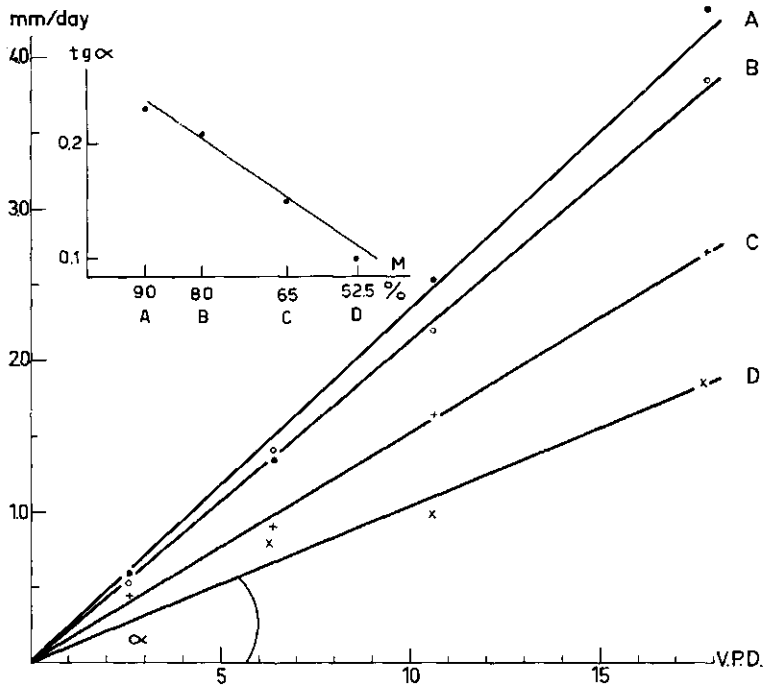


FIG. 1. The effect of the vapour pressure deficit (V.P.D. in mm Hg) on the rate of evapo-transpiration in mm/day (calculated by dividing loss of weight over 8.81) at various moisture levels. In the left corner the effect of available soil moisture content on evapotranspiration per day per mm Hg is represented.

on the water supply, and is 0.23, 0.21, 0.15 and 0.10 mm evapo-transpiration per day per mm Hg for A, B, C, and D respectively. As mentioned above, the availability of water varied between field capacity and a lower moisture content, e.g. between 100 and 80 % for treatment A. The average moisture content during

the entire growth period was in the middle of this range, and 90, 80, 65, and 52.5 % respectively for the treatments A, B, C, and D. The fraction of the available water used thus was 10, 20, 35 and 47.5 % respectively. Plotting these values versus the slope of the curves of fig. 1, a roughly linear relation was obtained (fig. 1, left corner). From these results a formula for the evapo-transpiration in mm/day was derived:

$$E = V.P.D. (pM + q),^1$$

$E$  = evapo-transpiration rate,

$V.P.D.$  = vapour pressure deficit,

$M$  = mean value of the available soil moisture content.

If we express  $E$  in mm/day,  $V.P.D.$  in mm Hg, and  $M$  in %, we have found:

$$p = 0.0036, \quad q = -0.09$$

With the PICHE evaporimeter, a linear relation between  $V.P.D.$  and evapo-transpiration is also observed. The curves, however, cross the abscissa at some distance from the origin. The same is observed plotting PICHE evaporation values *versus* vapour pressure deficit ( $V.P.D.$ ). This may be attributed to the fact that the surface temperature of the filter paper of the PICHE evaporimeter deviates from the air temperature (on which the calculations of  $V.P.D.$  were based) owing to the evaporation. Thus, the temperature of the PICHE evaporimeter, measured with thermocouples, was 22.5° at 26°C air temperatures which results in a large difference between the calculated  $V.P.D.$  and the actual  $V.P.D.$  as related to the temperature of the transpiring surface.

In this formula,  $pM + q$  represents  $1/R$ , in which  $R$  is the total diffusion resistance. It is clear that  $R$  depends largely on the availability of the soil moisture, which is due to a decrease in the stomatal aperture and possibly also to a reduction in size of the stomata with decreasing soil moisture. As a rule the surface temperature of a leaf shows smaller deviations from the surrounding air than that of the PICHE evaporimeter, since transpiration chiefly takes place through part of the surface only i.e. through the stomata. STÄLFELT (3) observed that the relative transpiration (ratio of leaf transpiration and evaporation of a blotting paper of the same size) is less than 70 % with fully open stomata. In the tomato, the stomata are present only at the lower side of the leaf. The deviation between leaf temperature and air temperature may, therefore, be less than  $0.5 \times 70 \% \times 3.5 = 1.2^\circ\text{C}$ .

#### b. Transpiration

The transpiration rate expressed in mm/day varies between 2.69 and 0.14 mm/day in the range of conditions of temperature and irrigation applied in our experiments.

Table 1 shows that the transpiration rate decreased with a decrease in air temperature or in  $V.P.D.$ , which decrease is more pronounced at higher levels of water supply. The transpiration rate at various temperatures with optimum water supply (A) were expressed as percentage of the *maximum* (fig. 2). Decrease in air temperature from 26° to 20°, 15°, and 10°C (corresponding to  $V.P.D.$ -values of 17.8, 10.6, 6.4, and 2.6 mm Hg) results in a fairly exponential decrease in transpiration rate to 63, 21 and 6 % of the value observed at 26°.

Table 1 shows furthermore that the effect of water supply on transpiration is more evident at higher temperatures. At the lowest temperature (low  $V.P.D.$ ),

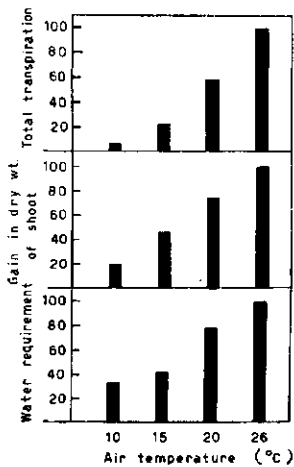


FIG. 2. The effect of temperature on total transpiration, gain in dry weight of shoot and water requirement at the highest level of irrigation (A). The values are expressed as percentage of maximum.

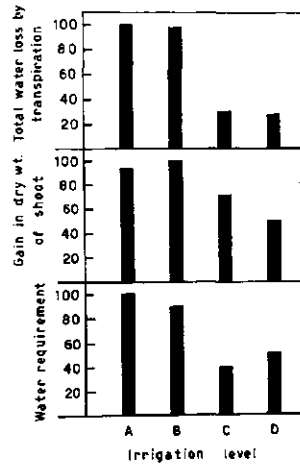


FIG. 3. The effect of irrigation regime on total transpiration, gain in dry weight of shoot and water requirement at 26°C. The values are expressed as percentage of maximum.

the difference among the values of the transpiration rate is nearly absent. For the study of the effect of water supply at 26°, the observed transpiration rates again were expressed as percentage of the maximum (fig. 3). It is obvious that there is only a small difference between the two high levels of available soil moisture (A and B). When, however, the mean level of available soil moisture drops to 65 % (C), the transpiration rate is reduced to approximately 30 %. At a still lower level of available moisture, the decrease in transpiration rate is smaller. This may be explained by the fact that at a higher level of available soil moisture, the moisture tension is low whereas below a certain level of available water, e.g. near the permanent wilting percentage, the moisture tension rises considerably. According to the formula for evapo-transpiration (see above), similar results may be obtained at temperatures, lower than 26°C.

### c. Soil evaporation

Table 1 shows that soil evaporation depends on conditions of temperature and irrigation regime. At the same irrigation level (A), the soil evaporation rate decreased from 1.64 mm/day at 26°C to 0.41 mm/day at 10°C. At the same temperature (26°C) the soil evaporation falls from 1.64 mm/day at A to 1.12 mm/day at level D.

In the period between sowing and emergence of seedlings, and in the early stages of germination, when the soil is approximately bare, the loss of water is almost only due to soil evaporation. It is interesting, therefore, to study the evaporation of a bare soil at different temperatures. Such study is important in the water economy of germinating seeds as it determines the moisture content of the soil layer in which the seeds and the young developing roots are present.

The pots used for this purpose were without plants. In fig. 4, the loss of water, starting at field capacity, is plotted versus time at various temperatures. At 26°C, the evaporation rate decreases rapidly in the first three days, followed by

a continued decrease until the 7th day. Then, the rate gradually becomes more or less constant. At 20°C, the drop in the evaporation rate is less rapid than at 26°C while it also becomes more or less constant after the 7th day. At 15°C, only a slight decrease in the evaporation rate is observed during the first day, whereas at 10°C the rate remains nearly constant during the whole period. During the first day, the evaporation rate at 26°C is 2.9 mm/day or nearly double that at 20°C, three times that at 15°C and about five times that at 10°C.

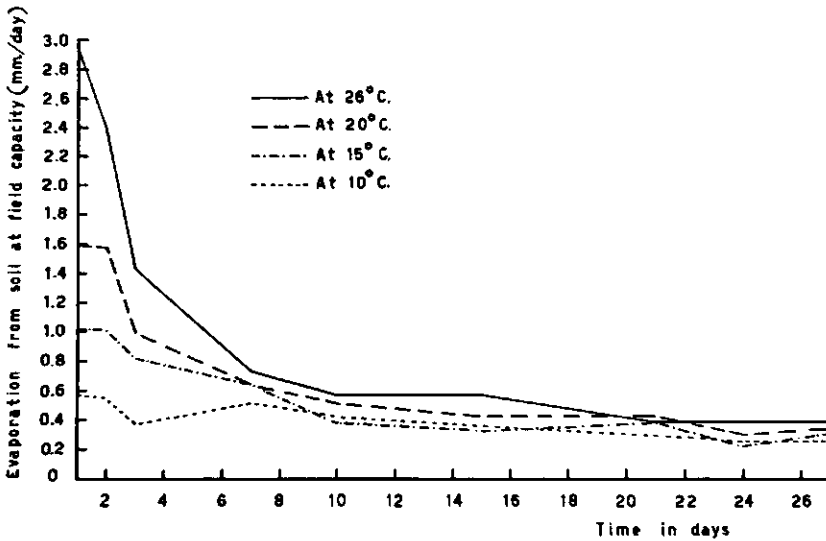


FIG. 4. Soil evaporation in mm/day versus time at various temperatures starting from field capacity.

After 7 days, the evaporation rate at the four different temperatures is approximately equal, and is between 0.5 and 0.7 mm/day. The large decrease in evaporation at 26°C and also at 20°C can be attributed to the formation of a thin dry surface layer, as a result of active evaporation in the beginning. The diffusion resistance of this dry layer reduced the evaporation rate to a low value, approaching the values obtained at the lower temperatures. The existence of such a dry layer is important in water economy as it protects the soil underneath from excessive evaporation, and keeps the soil moist for a prolonged period.

## B. Growth aspects

### a) Height of shoot

The height of the plant is very sensitive to changes in temperature and irrigation regime and varies between 4 and 21 cm (plate 1, Table 2). The height decreases with the decrease in water supply, as well as with the decrease in temperature. At the same irrigation level (A), for instance, the height of the shoot decreases from 21 cm to 11.2, 7.5, and 4.9 cm with a decrease in temperature from 26°C to 20°, 15°, and 10°C respectively which means a reduction to about one fourth. At 26°C, a decrease in water supply from the highest level

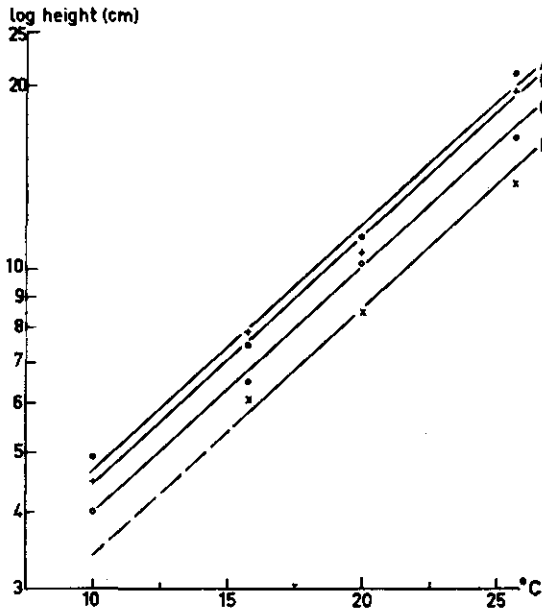


FIG. 5.  
The effect of air temperature on the height of the stem (log. scale) at various levels of water supply.

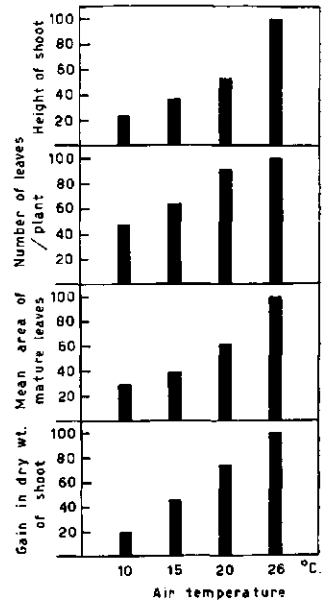


FIG. 6.  
The effect of air temperature on the height of shoot, number of leaves per plant, mean area of mature leaves and gain in dry weight of shoot. The values are expressed as percentage of maximum.

(A) to the lowest (D) causes a reduction in height from 21 to 13.8 cm or about one half.

The effect of air temperature on height is exponential, as shown in fig. 5. In plotting log height (cm) against temperature, straight lines are obtained, the curves for the various irrigation treatments are parallel. This may imply that the combined effect of these two factors is additive. Plotting log height versus the average water availability, calculated for each treatment throughout the whole growth period (A: 90 %, B: 80 %, C: 65 %, and D: 52.5 %) resulted in more or less straight curves also. From these data, represented in Table 2, the following formula is derived:

$$\log H = pT + qM$$

$H$  = height of stem,

$T$  = temperature,

$M$  = average available soil moisture.

If we express  $H$  in cm,  $T$  in °C, and  $M$  in %, we find:

$$p = 0.039, q = 0.0036$$

The temperature coefficient  $Q_{10}$ , computed from this formula is 2.44, and evidently is independent of the water regime.

b) Fresh weight of shoot

Temperature and irrigation regime exhibit a large effect on the gain in fresh



TABLE 2. The effect of temperature and water supply on water requirement, gain in dry weight of shoot, height of shoot and morphological characters in tomato

1	2	3	4	5	6	7	8	9	10	11
Tem- perature °C	Irrigation regime	Water requirement	Gain in dry weight (gms/plant)	Gain in fresh weight (gms/plant)	Water content (gms of water/ gm dry weight)	Height of shoot (cm)	Number of leaves/plant	Length of mature leaves (cm)	Length of basal inter- nodes (cm)	Dry weight percentage
25.7	A	847 ± 49	0.798 ± 0.088	8.23 ± 0.75	9.32 ± 0.02	21.0 ± 0.8	11.0 ± 0.4	14.6 ± 0.5	2.93 ± 0.15	9.7
	B	765 ± 32	0.852 ± 0.048	8.28 ± 0.27	8.72 ± 0.03	19.4 ± 1.0	11.0 ± 0.0	15.3 ± 0.3	2.85 ± 0.17	10.3
	C	335 ± 30	0.606 ± 0.015	5.62 ± 0.18	8.26 ± 0.02	16.2 ± 0.9	10.0 ± 0.0	13.7 ± 0.2	2.50 ± 0.13	10.8
	D	432 ± 17	0.422 ± 0.022	3.08 ± 0.13	6.38 ± 0.01	13.8 ± 0.7	10.8 ± 1.8	11.0 ± 0.6	1.80 ± 0.28	13.7
20.0	A	663 ± 39	0.591 ± 0.044	4.95 ± 0.33	7.38 ± 0.02	11.2 ± 0.4	10.0 ± 0.0	11.9 ± 0.4	1.70 ± 0.07	11.7
	B	672 ± 36	0.509 ± 0.048	3.91 ± 0.40	6.68 ± 0.02	10.6 ± 0.4	9.5 ± 0.3	11.2 ± 0.3	1.60 ± 0.09	13.0
	C	414 ± 8	0.460 ± 0.029	3.67 ± 0.27	6.97 ± 0.02	10.1 ± 0.2	9.0 ± 0.0	10.8 ± 0.3	1.60 ± 0.07	12.6
	D	388 ± 27	0.315 ± 0.031	1.81 ± 0.11	4.76 ± 0.03	8.5 ± 0.2	9.0 ± 1.0	8.7 ± 0.6	1.30 ± 0.11	17.4
15.6	A	355 ± 42	0.370 ± 0.028	2.98 ± 0.40	7.00 ± 0.15	7.5 ± 0.2	7.0 ± 0.0	8.5 ± 0.4	1.38 ± 0.05	12.4
	B	342 ± 18	0.516 ± 0.053	3.59 ± 0.34	5.96 ± 0.01	7.8 ± 0.3	7.8 ± 0.3	10.3 ± 0.3	1.35 ± 0.05	14.4
	C	333 ± 25	0.304 ± 0.007	2.29 ± 0.17	6.53 ± 0.04	6.5 ± 0.2	8.3 ± 0.6	8.0 ± 0.2	1.10 ± 0.17	13.3
	D	360 ± 22	0.267 ± 0.017	1.62 ± 0.12	5.06 ± 0.04	6.1 ± 0.1	8.0 ± 1.0	7.8 ± 0.2	1.08 ± 0.11	16.5
10.4	A	281 ± 28	0.154 ± 0.011	0.90 ± 0.08	4.84 ± 0.04	4.9 ± 0.3	5.3 ± 0.3	6.6 ± 0.3	0.93 ± 0.05	17.1
	B	256 ± 12	0.137 ± 0.006	0.75 ± 0.03	4.46 ± 0.03	4.5 ± 0.4	5.5 ± 0.5	6.3 ± 0.3	0.69 ± 0.11	18.2
	C	311 ± 12	0.119 ± 0.023	0.51 ± 0.13	3.19 ± 0.13	4.0 ± 0.3	6.3 ± 0.8	5.5 ± 0.2	0.58 ± 0.08	23.3
	D									

From the data of columns 1, 2, 4 and 5 respectively, the following empirical relations have been computed, in which  $y_A, y_B$ , etc. represent gain in dry weight,  $y'A, y'B$ , etc. gain in fresh weight for the treatments A, B, C, and D, respectively;  $x =$  temperature (°C).

$$yA = 0.043x - 0.29$$

$$yB = 0.043x - 0.27$$

$$yC = 0.032x - 0.20$$

$$yD = 0.012x + 0.05$$

$$y'A = 0.48x - 4.31$$

$$y'B = 0.47x - 4.25$$

$$y'C = 0.33x - 2.93$$

$$y'D = 0.15x - 0.87$$

weight (Table 2). A difference in temperature from 26° to 10°C for instance is accompanied by a decrease in gain in fresh weight from 8.23 to 0.99 g, or a reduction to about 11 %. At 26°C, the gain in fresh weight decreases from 8.23 to 3.08 g (reduction to 37 %) with a decrease in irrigation level from A to D.

Examination of the results reveals that the effect of temperature on gain in fresh weight is linear rather than exponential. The curves have been calculated from the data represented in Table 2. It is evident that the slopes of the different curves depend on the water supply. The initial temperature at which no gain in fresh weight will occur can be computed from these curves through extrapolation. Approximately the initial temperature is the same in all treatments, except D, and varies between 8–9°C.

### c) Dry matter production

The gain in dry matter production is greatly influenced by the difference in temperature and irrigation regime (Table 2). The maximum attained is 0.85 g and the minimum 0.12 g for the experimental period.

For studying the effect of air temperature, the values for gain in dry weight of shoot at optimal water supply and at different air temperatures were expressed as percentage of maximum (fig. 6). Also the height of shoot, the number of leaves per plant and the mean length of mature leaves were expressed as percentage of maximum, to find out their relation to changes in dry matter production of shoot.

Fig. 6 shows that, at the highest water supply, with a decrease in air temperature from 26° to 20°, 15°, and 10°C, a linear decrease in gain in dry weight of shoot occurs viz., from 100 to 74, 46, and 19 % respectively.

According to the complete data on gain in dry weight of the shoot, given in Table 2, this also holds for lower soil moisture conditions. The temperature at which no gain in dry weight occurs anymore is between 6° and 7°C.

The mentioned growth aspects, viz. the height of shoot, the number of leaves per plant, and the mean area of mature leaves which affect the gain in dry weight of shoot, thus exhibit approximately a regular decrease with decrease in air temperature (fig. 6). The difference in air temperature between 26° and 10°C is associated with a reduction in height of shoot to 26 %, in number of leaves per plant to 48 % and in mean area of mature leaves to 30 %. The combined considerable reduction in the growth aspects due to fall in air temperature from 26 to 10°C causes the great reduction obtained in the dry matter production which is about 19 %.

At the optimum temperature (26°C), a decrease in irrigation level from A to D is accompanied by a reduction in the gain in dry weight of shoot to about 53 % (Table 2, column 4). The change in dry matter production due to decrease in irrigation level from A to B is insignificant, but the fall in irrigation level from B to C and D leads to a remarkable reduction in dry matter production. This may be explained, as mentioned already above, by the fact that at higher levels of available water, the values of moisture tension are low. Below a certain level of available water, e.g., near permanent wilting, the moisture tension rises considerably. The change in dry matter production at different conditions of irrigation is caused by changes in height of shoot and in the area of the leaves, but the number of leaves per plant shows no significant variation.

### C. Water requirement

The water requirement, expressed as grams of water transpired per g dry matter

produced, varies widely under different conditions of temperature and irrigation, viz., in a range between 847 and 256 (Table 2). It decreased with decrease in air temperature and water supply, whereas the effect of each of these factors is more noticeable at optimal conditions of the other. Examination of the relation between water requirement and air temperature at the optimum irrigation level A (fig. 2) shows that at air temperatures of 26°, 20°, 15° and 10°C, the water requirement is 100, 78, 42, and 33 % respectively.

The variation in water requirement at different air temperatures is due to the differences in dry matter production and transpiration. This is shown in fig. 3, in which the decrease in temperature from 26° to 10°C. is accompanied by a reduction in the total transpiration to about 6 %, and by a reduction in the gain in dry weight of the shoot to about 19 %. The curve representing the variation of transpiration at different temperatures which is linear with V.P.D. (Fig. 1) and thus nearly logarithmically related to air temperature, is quite different from that representing the variation in gain in dry weight of shoot which is linearly related with temperature (fig. 6).

It is evident from Table 2 that the effect of water supply on the water requirement is noticeable at high temperatures and disappears at the lower ones. Comparing the irrigation levels A and B (Table 2) the water requirement decreases from 100 % to 90.5 % at the highest temperature; a very remarkable decrease from 90.5 % to 40 % is recorded comparing the irrigation levels B and C, while from C to the still lower irrigation level D an increase from 40 % to 51 % was noticed.

#### D. Water content

The values of the water content expressed as g water per g dry weight are presented in Table 2. The air temperature has a considerable effect on the water content. At the irrigation level A, for instance, the water contents are 9.32, 7.38, 7.00, and 4.84 at 26°C, 20°, 15°, and 10°C. respectively, so that the water content at 10°C is nearly half that at 26°C. A reduction in the water content to about 68 % occurs as a result of the fall in irrigation level from A to D at 26°C. At lower temperatures the effect of water supply is less pronounced.

It was observed that the water content depends not only on the treatment applied throughout the experiment, but also on the soil moisture content at the harvest.

#### E. Morphological characters

The number of leaves produced by the plant during the experimental period is greatly affected by temperature but does not show significant differences at various levels of irrigation. The relation with temperature is roughly linear. The number of leaves produced at 10°C is about half that at 26°C (Table 2).

It is clear from plate 2 that the length of mature leaves decreased with decrease in water supply as well as with decrease in temperature. The effect of the latter is more pronounced than that of the former. At the same irrigation level (A), a difference in temperature from 26° to 10°C is accompanied by a reduction in the leaf area to 30 %, whereas it is reduced to 50 % when the irrigation level falls from A to D at 26°C.

The length of basal internodes is also affected by water regime and temperature. The effect of the latter is more pronounced.

#### 4. SUMMARY AND CONCLUSIONS

Tomato plants were grown in metal pots, containing 2 kg of loamy soil, and kept in compartments at different air temperatures (26°, 20°, 15° and 10°C). In each compartment, four different irrigation treatments (A, B, C, D) with decreasing water supply, were applied. The compartments were illuminated with daylight fluorescent tubes, the intensity of which was  $4.6 \times 10^4$  ergs. sec.<sup>-1</sup> cm<sup>-2</sup>  $\varnothing$  sphere. The rate of evapo-transpiration, transpiration and soil evaporation were determined by means of weighing. Various growth aspects were measured and from the obtained data on transpiration and gain in dry weight, the water requirement was calculated.

The total water loss by evapo-transpiration exhibits a wide range of variation between 4.33 and 0.44 mm/day under different conditions of temperature and irrigation. Plotting the rate of evapo-transpiration versus the vapour pressure deficit, the curves are linear for the different irrigation treatments A, B, C and D. The slopes of these curves, show an approximately linear relation to water supply from A to D.

The transpiration rate varies between 2.69 and 0.14 mm/day. At optimum conditions of water supply, a reduction in the transpiration rate down to 6% occurs, owing to a difference in temperature from 26 to 10°C. (or from 17.8 to 2.6 mm Hg in V.P.D.). The decrease in transpiration rate with decrease in temperature and in V.P.D. is less pronounced at lower irrigation levels than at higher ones. At the highest temperature (26°C), the largest reduction in water supply results in reduction in the transpiration rate down to about 30% while at the lowest temperature (10°C), the effect of water supply nearly disappears.

At the maximum water supply, the soil evaporation rate decreases from 1.64 mm/day at 26°C to 0.41 mm/day at 10°C. At the maximum temperature (26°C), a reduction from 1.64 to 1.12 mm/day was found upon the difference in irrigation level from A to D. As the soil remains nearly bare during the seedling and young stages of plant development, the soil evaporation was studied at different temperatures in pots without plants. The moisture content of the soil in these pots was raised to field capacity at the beginning. In the first day, the rate of soil evaporation at 26°C is 2.9 mm/day or nearly double that at 20°C, three times as much as that at 15°C and about five times that at 10°C. After 7 days, the evaporation rate is approximately equal in the different treatments owing to the formation of a thin dry surface layer at higher temperatures which hinders evaporation and brings its rate down to a level, approaching that at the lower temperatures. The existence of such a dry layer is important in water economy, as it protects the soil underneath from excessive evaporation, and thus keeps it moist for a longer period.

Under conditions favouring good development of the shoot, the rate of transpiration is much higher than that of soil evaporation. The reverse holds true under adverse conditions. At optimum conditions of temperature and water supply, the transpiration rate approximately doubles that of soil evaporation. Under adverse conditions e.g. low temperature and water supply, the transpiration rate is nearly half the soil evaporation rate.

The height of the plant is very sensitive to changes in temperature and irrigation regime. The effect of air temperature is exponential. At the optimum water supply, A, the difference in temperature from 26° to 10°C is accompanied by a reduction in height to about one fourth. At the maximum temperature,

26°C, the difference in irrigation from the highest to the lowest level causes a reduction in height to about one half. The computed temperature coefficient for the height of shoot is 2.44 per 10°C.

The fresh weight of the shoot is approximately linear with air temperature, whereas the slope varies with the water supply. Through extrapolation of these lines it was calculated that the lowest temperature for growth was between 8 and 9°C.

At optimum water supply, A, the gain in dry weight of shoot is reduced to about 19%, in the air temperature range from 26° to 10°C. This large reduction in dry matter reduction results from the combined reduction in several growth characteristics, viz., the height of shoot (26% reduction), the number of leaves per plant (48%) and the mean area of mature leaves (30%). By extrapolation, the lowest temperature at which any gain in dry weight may occur, was found to be between 6 and 7°C.

The gain in dry weight of shoot is reduced to about 53 per cent as a result of decrease in irrigation level from A to D, the decrease is especially obvious below the B level.

The values for the water requirement range from 847 to 256 under different conditions of irrigation and of air temperature between 26 and 10°C. The effect of temperature on total transpiration is different from that on gain in dry weight of shoot, so that the water requirement varies at the different air temperatures.

The effect of water supply on the water requirement is noticeable at higher temperatures and disappears at lower temperatures. At 26°C, the water requirement shows a very remarkable reduction to 40% from the irrigation level A down to the level C.

The morphological characters, such as the number of leaves per plant, the area of mature leaves, the length of mature leaves and the length of internodes are greatly influenced by air temperature. These characters, except the number of leaves per plant, are affected also by the water regime.

#### ACKNOWLEDGEMENT

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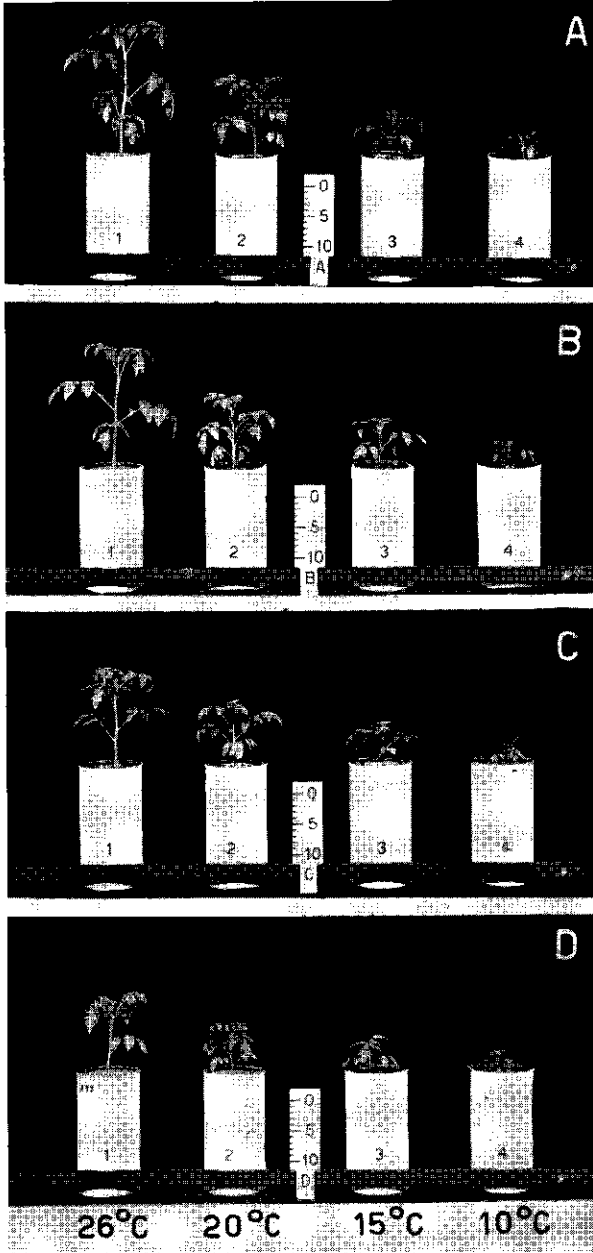


PLATE 1. The effect of temperature (26°, 20°, 15° and 10°C) and water regime (A, B, C and D) on the development of the tomato plant after a treatment of four weeks.

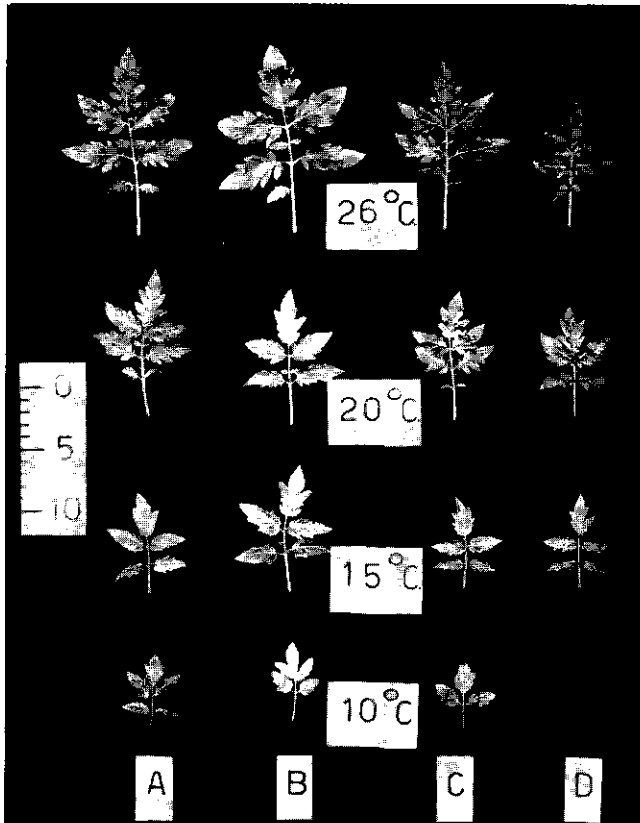


PLATE 2. The effect of air temperature and water regime on leaf area after a treatment of 28 days.



GROWTH AND TRANSPIRATION OF TOMATO  
IN RELATION TO NIGHT TEMPERATURE  
UNDER CONTROLLED CONDITIONS

by

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Wageningen, Netherlands, 189th Communication)**(Received 13.3.'59)*

## 1. INTRODUCTION

The effect of a constant air temperature on growth and water requirement of tomato was previously investigated. It is of special interest, however, to study separately the effect of day and night temperature since literature in connection herewith is not very extensive. It is also of importance to investigate the relation between transpiration and growth as influenced by night temperature.

## 2. MATERIAL AND METHODS

Tomato seeds were sown in wooden boxes and the seedlings transplanted 12 days afterwards into small metal containers, 20 cm high and 10 cm in diameter. Each of these containers was filled with 2 kg of loamy soil. Fifteen days after transplanting, the tomato plants were all exposed to the same day temperature (25.3°C) and, in series of four plants, to different night temperatures (25.3°, 20.0°, 15.6° and 9.2°C respectively). During 12 hours in every 24 hours the pots were in a compartment illuminated by "daylight" fluorescent tubes at an intensity of  $7.6 \times 10^4 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$   $\varnothing$  sphere, measured with a spherical radiation meter. Then each set of four plants was transferred to a dark compartment, kept at a constant temperature for the remaining 12 hours. The mean relative humidity of the air during the whole period of the experiment was approximately 60%. The soil moisture was maintained between 100 and 80 per cent of the maximal available water content which range previously had been shown to be optimal for growth (1).

The water loss was measured each day, by weighing. Once every week, the soil in the pot was covered with plastic sheets for 24 hours in order to measure the amount of water, transpired by the plants. For further methodical details see ABD EL RAHMAN and BIERHUIZEN (1). The height of the shoot was measured

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once a week, during the experiment (28 days). At the end, fresh and dry weight of shoot, total leaf area, number of leaves, and dry weight of roots<sup>1</sup>) were measured.

### 3. RESULTS AND DISCUSSION

#### A. Growth measurements

Some investigators have discussed the effect of night temperature on the growth of plants. According to WENT (5), the optimal temperature for stem elongation in young plants is 25°C during day and night. VERKERK (4) mentioned that under favourable light conditions the stem growth increased with increase of day and night temperatures. Under low light intensities this was less obvious. LOOMIS (2) observed that growth is often correlated with temperature during the night, and with the relative humidity during the day.

THOMAS (3) found translocation of sugar to increase with a decrease in temperature. Because of this, 18°C was considered a more favourable temperature than 26°C. Lower temperatures gave an unfavourable effect because they decreased too much the rate of other processes, involved in growth. According to WENT (5), so called thermoperiodicity in tomatoes is due to the interaction of two processes, one occurring in the dark, the other in the light, of which the dark process should have a much lower temperature optimum than the process in the light.

In the present investigation growth varies in relation to night temperature as is shown in plate 1. The height of shoot shows a reduction to 63 % with the night temperature falling from 25.3° to 9.2°C (fig. 2) which was due to a difference in rate of elongation (fig. 1). After seven days, the difference in height

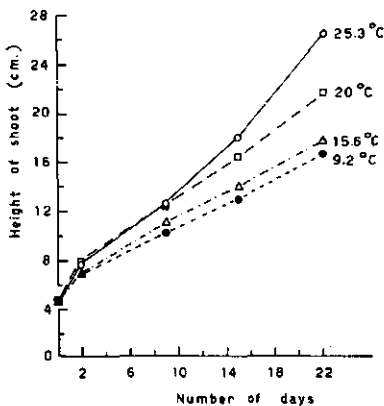


FIG. 1. The rate of stem growth of tomato plants at different night temperatures.

between the various treatments was not significant, it increased gradually with age (fig. 1).

The total leaf area varies irregularly with the different treatments. It seems that night temperature, in the range of temperatures studied, has only a minor effect on leaf area. The dry weight of the leaf decreases regularly – though rather

<sup>1</sup> Dry weight of roots was not measured in the experiments, described in (1), furtheron it has always been recorded.

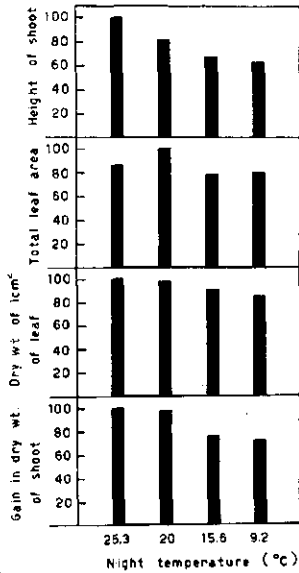


FIG. 2. The variation in height of shoot, total leaf area, dry weight of 1 cm<sup>2</sup> of leaf and gain in dry weight of shoot at different night temperatures. The values are expressed as percentages of maximum.

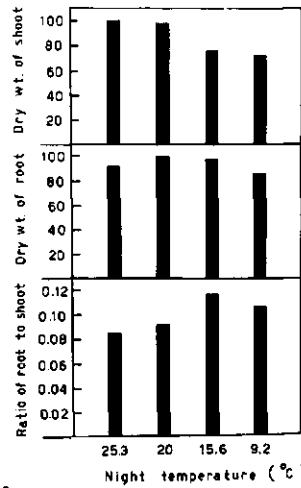


FIG. 3. The variation in dry weight of shoot, of roots, and of the ratio of roots to shoot at different night temperatures. The values are expressed as percentages of maximum, except the ratio of root to shoot.

little – with decrease in night temperature, it shows a reduction to 85 % in the night temperature range from 25.3° to 9.2°C (fig. 2).

The variation in total dry matter production of the shoot does not depend primarily on the variation in leaf area, but mainly on the growth of the stem and the dry weight of the leaf. The dry weight of the shoot decreases from 100 % to 98, 76, and 73 % in experiments at night temperatures of 25.3°, 20.0°, 15.6°, and 9.2°C respectively. The gain in dry weight of roots varies only slightly at the various treatments (fig. 3). It is evident, from these results, that low night temperature favours a high ratio of root to shoot (fig. 3 and Table 1). The rise in night temperature from 15.6° to 25.3°C is accompanied by a reduction in the ratio from 0.117 to 0.085 (or to about 73 %). The difference in ratio between 15.6° and 9.2°C is insignificant.

### B. Transpiration

During the last seven days of the experiment, transpiration was measured during day and night separately, while the obtained data were calculated per unit leaf area. It is evident from fig. 4 and Table 1 that a reduction in day transpiration rate is significant only in plants with a night temperature of 9.2°C. The night transpiration rate at 20.0°C night temperature is only 56 % from that at 25.3°C. At still lower night temperatures, the transpiration rate remains almost the same. The large decrease in night transpiration observed may be due to a decrease in the vapour pressure deficit at the lower temperatures. Since the transpiration rate during the day was roughly 5 times that during the night, the mean transpiration rate per 24 hours showed a significant reduction only at 9.2°C night temperature, viz., to about 76 %.

TABLE 1. Effect of night temperature on growth, transpiration and water requirement of tomato

Night temperature in °C	25.3°	20.0°	15.6°	9.2°
Height of shoot (cm) . . . . .	26.4 ± 0.7	21.7 ± 0.7	17.7 ± 0.3	16.6 ± 0.3
Mean length of inter-nodes (cm) . . . . .	3.8 ± 0.2	3.3 ± 0.2	2.7 ± 0.1	2.6 ± 0.1
No. of leaves . . . . .	10.4 ± 0.4	11.2 ± 0.4	10.4 ± 0.3	10.2 ± 0.2
Mean length of mature leaves (cm) . . . . .	17.3 ± 0.2	18.4 ± 0.5	16.6 ± 0.1	16.0 ± 0.4
Mean area of mature leaves (cm <sup>2</sup> ) . . . . .	60.9 ± 4.5	70.0 ± 3.1	58.7 ± 2.1	52.0 ± 2.1
Total leaf area (cm <sup>2</sup> ) . . . . .	344 ± 17	401 ± 19	314 ± 7	320 ± 14
Mean dry wt. of 1 cm <sup>2</sup> leaf surface . . . . .	3.73	3.65	3.41	3.18
Gain in dry weight of shoot (g) . . . . .	1.73 ± 0.15	1.70 ± 0.10	1.31 ± 0.08	1.26 ± 0.06
Gain in dry wt. of root (g) . . . . .	0.143 ± 0.005	0.155 ± 0.007	0.152 ± 0.008	0.133 ± 0.006
Gain in dry weight of shoot + root (g) . . . . .	1.88 ± 0.14	1.86 ± 0.11	1.46 ± 0.09	1.39 ± 0.06
Ratio of root(g)/shoot(g) . . . . .	0.085 ± 0.006	0.092 ± 0.005	0.117 ± 0.007	0.107 ± 0.008
Mean transpiration of a single plant (g/day) . . . . .	31.8 ± 3.3	31.2 ± 0.8	25.1 ± 1.0	21.6 ± 1.1
Transpiration by day (g/dm <sup>2</sup> .h) . . . . .	0.603 ± 0.030	0.597 ± 0.040	0.643 ± 0.017	0.522 ± 0.014
Transpiration at night (g/dm <sup>2</sup> .h) . . . . .	0.224 ± 0.015	0.126 ± 0.010	0.112 ± 0.005	0.110 ± 0.008
Mean transpiration rate of the whole day (g/dm <sup>2</sup> .h) . . . . .	0.414 ± 0.020	0.362 ± 0.025	0.378 ± 0.010	0.316 ± 0.007
Water requirement (shoot) . . . . .	512 ± 17	523 ± 42	600 ± 39	481 ± 9
Water requirement (shoot + roots) . . . . .	473 ± 17	479 ± 34	486 ± 26	435 ± 9

Although during the period of illumination (representing the day period), the plants belonging to different treatments were placed in a chamber at the same air temperature (25.3°C), the soil temperature in the pots exposed to lower night temperatures required some hours to attain the same temperatures as those continuously exposed to 25.3°C, and the more so, inasmuch as the difference in temperature was larger. This may be of considerable importance. The temperature of the soil in the former case was 24°C. The soil in pots exposed to night temperatures of 20.0°, 15.6° and 9.2°C required approximately 2, 5 and 6 hours, respectively, to arrive at a soil temperature of 24°C (fig. 5). Of course, it is also important that the soil subjected to a low night temperature took a similar period of adaptation to the low temperature. It is clear that the discussed effects have the largest amplitude at the night temperature of 9.2°C. On the other hand, relatively quickly the temperature of the soil is within only a few degrees from that of the air.

As the soil in the pots was 20 cm deep, it represents about the layer of soil in which the greatest number of the roots grow. It is evident from these data that the night temperature gives a large after-effect on the day temperature of the

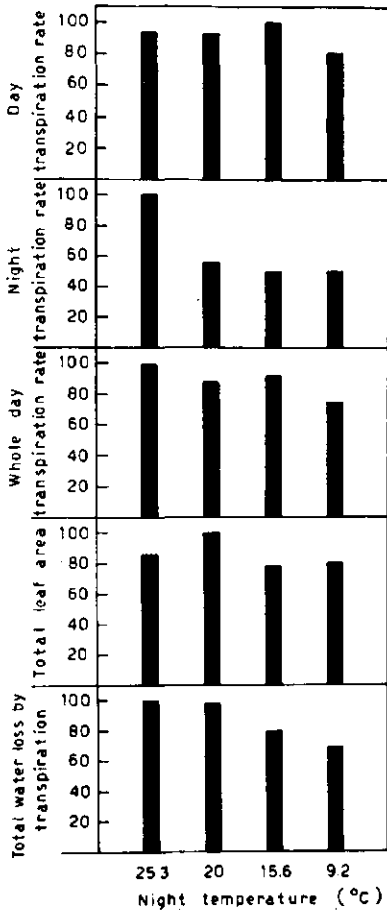


FIG. 4. The variation in day and night transpiration rate, and the transpiration rate during the whole day at different night temperatures. The values are expressed as percentages of maximum.

soil. Since the latter has a noticeable effect on the rate of water absorption, the night temperature may influence the day time transpiration by means of the soil temperature.

### C. Water requirement

The water requirement is determined by calculating the amount of water transpired in g per g dry matter produced. According to Table 1 and fig. 6 the total amount of water transpired, and the gain in dry matter produced at the different treatments show approximately the same procentual change. The difference in night temperature from 25.3° to 9.2°C is accompanied by a decrease in the total water transpired to 68 %, and in the gain in dry weight of shoot to 73 %. As the difference between the two percentages is not very great, the water requirement does not show appreciable variation.

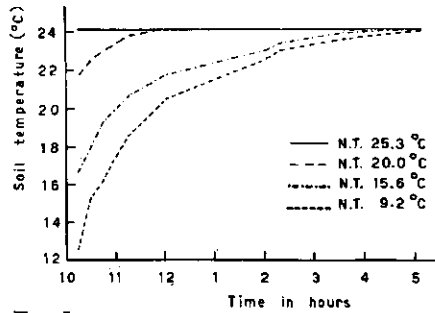


FIG. 5. The change in soil temperature of pots transferred from the different night compartments to the day chamber at 25.3°C, at 10 am.

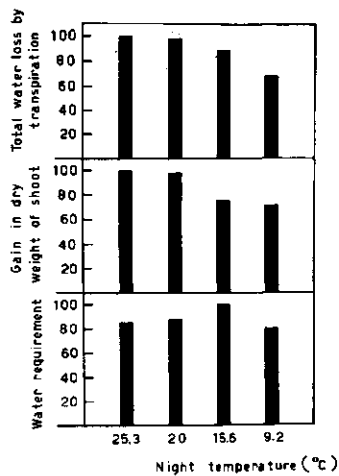


FIG. 6. The variation in total water loss by transpiration, gain in dry weight of shoot and water requirement, at different night temperatures. The values are expressed as percentages of maximum.

#### 4. SUMMARY AND CONCLUSIONS

Tomato plants were grown in metallic containers and, during a period of 28 days, placed at a constant temperature of 25.3°C under "daylight" fluorescent tubes for 12 hours in every 24 hours. In the night period (12 hours) one set was kept in the same chamber at 25.3°C and the others transferred to compartments of various temperatures (20.0°, 15.6° and 9.2°C respectively).

The growth rate of the stem is lower at lower night temperatures. A decrease in night temperature from 25.3° to 9.2°C resulted in a reduction to 63 % in the height of shoot. The total leaf area does not show a regular variation, but the dry weight of 1 cm<sup>2</sup> leaf shows a regular decrease to 85 % in the series with a night temperature of 9.2°C. The reduction in both the height of shoot and the dry weight of leaves result in a reduction to 73 % in total dry matter of shoot. The various effects of night temperature may, at least partly, be ascribed to the time lag of soil temperature occurring after lower night temperatures.

The transpiration rate per unit area during the whole 24 hours decreases significant only with a night temperature of 9.2°C, namely to 76 %, which was due to a decrease in day transpiration. The night transpiration was approximately one fifth of that during the day, and decreases to 56, 52, and 50 % with a decrease in night temperature from 25.3° to 20.0°, 15.6°, and 9.2°C respectively. The decrease in night transpiration may be due to a decrease in the vapour pressure deficit at the lower temperatures.

The water requirement does not show a regular variation in relation to night temperature, which may be attributed to similar procentual changes in transpiration and dry matter production.

#### ACKNOWLEDGEMENT

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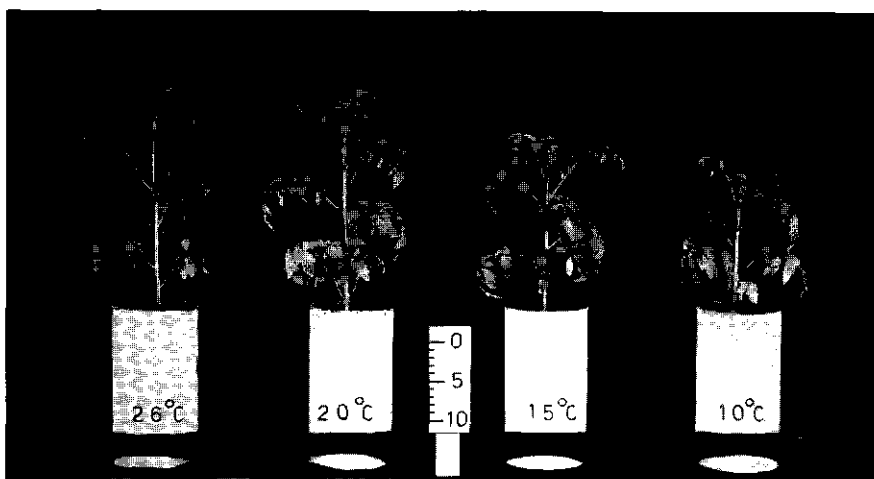


PLATE 1. Growth of tomato plants, kept for a period of 28 days at different night temperatures (From left to right: 25.3°, 20°, 15.6°, and 9.2° C).