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PRELIMINARY OBSERVATIONS ON THE EFFECT OF SOIL TEMPERATURE ON TRANSPIRATION AND GROWTH OF YOUNG TOMATO PLANTS UNDER CONTROLLED CONDITIONS

by

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1. INTRODUCTION

Several investigators have studied the effect of soil temperature on water uptake and transpiration. In general it has been found that plants from a warm environment show a greater reduction in water absorption by low soil temperature then plants grown in cooler soils and during the cooler seasons (KRAMER, 12, DÖRING, 10).

CLEMENTS and MARTIN (9) observed a rapid increase of water uptake and transpiration rate of sunflowers from low temperatures up to 12°C whereas a constant rate was observed above this temperature. In the latter case the evaporation conditions of their experiment did not claim for a higher amount of water supply of the shoot.

DÖRING (10) measured in short time experiments the effect of soil temperature on the rate of water absorption of 57 species from different habitats. Species from bogs, peat moors and other wet places generally showed small differences in water absorption, only some annuals with shoot development in summer were somewhat more sensitive. Arctic willow species showed no reaction to soil temperature at all. Woody plants with leaf development and flowering occurring early in spring like cornel, elm, hazelnut tree and larch show a low effect; on the contrary woody plants with a leaf development late in spring like oak, beech, acacia, ash, dogwood and lime tree show a large effect of soil temperature. CAMERON (8), BIALOGLOWSKI (5) and HAAS (11) found that cooling of the soil reduced water uptake and transpiration of orange, lemons and grapefruit, being crops of warm climates. BIALOGLOWSKI also observed a small decrease in water absorption of lemon cuttings at temperatures above

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30 °C. ARNDT (4) reported that cotton plants wilted at soil temperatures in the range between 15° and 20 °C. With cucumber a similar result was obtained. RALEIGH (14) observed that water uptake by muskmelon plants is very slow at 10 °C and increases rapidly from 18 °C up to 27 °C.

KRAMER (12, 13) studied the rate of water uptake by different species of plants in cold soil. He observed that some species wilted when their root systems were suddenly cooled. The plants recovered after some time, whereas transpiration always lags behind as compared with water absorption.

According to KRAMER (13) the main causes for a decrease in water absorption at lower soil temperatures, are a decrease in water flow from the soil to the root hairs, a decrease in root growth and in the water permeability of the cell membrane and an increase in the viscosity of water and protoplasm. The physiological activity of the roothairs, *e.g.* respiration, decreases at lower temperatures. This may be of importance in the process of active water absorption and in phenomena such as bleeding and guttation.

The effect of the viscosity of water may be observed in experiments with plants from low temperatures. The decrease in water uptake of Georgia cabbage and White Pine (12) in the range of soil temperatures from 25 °C till 5 °C seems to be mainly due to an increase in viscosity of water, as one may conclude from KRAMER's results.

In horticultural practice many phenomena on the cultivation of lettuce, strawberries, bulb flowers, lathyrus and other crops are ascribed to the effect of soil temperature. In the "Westland" *e.g.*, a horticultural district in Holland, harvest of lettuce in a cold glasshouse in spring on a sandy soil is about 14 days earlier than on clay soil. However, investigations on the effect of soil temperature in connection with other soil factors such as aeration on growth of these crops, on top/root ratio, etc. are scarce.

Soil temperature largely affects shoot growth through limitation of the water supply. The latter determines the state of turgescence and thus soil temperature regulates shoot growth within certain limits.

RIETHMANN (15) made an extensive investigation concerning the effects of soil temperature on growth, fruit production and fruit quality of the tomato under glasshouse conditions. He observed, that the height of the shoot increases regularly with an increase in soil temperature up to 33 °C. Above this temperature, the height decreases. A similar curve was obtained for the fresh weight of the plants, also with an optimum at 33 °C.

Our experiments aimed at obtaining more information on growth and water requirement at different soil temperature in tomato under controlled conditions.

2. MATERIAL AND METHODS

Seeds of the tomato variety "Ailsa Craig" were sown in a seed box in coarse sand. After 12 days, the seedlings were transplanted in tins, 20 cm high and 10 cm wide. They were filled with 2 kg air-dry clay soil, the pF-curve of which was known. Fifteen days after being transplanted, the plants were used in the experiment.

Before the experiment, the fresh weight and the dry weight of the shoot of some plants were determined and considered as initial values. The experimental plants were transferred to a constant temperature room (25.3 °C air temperature, mean relative air humidity during the experiment 44%). They were illuminated by daylight fluorescent tubes during 12 hours per day. The light intensity, measured at the top of the plant with the spherical radiation meter (WASSINK and VAN DER SCHEER (17)) was 5.4×10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere.

Different soil temperatures were obtained by placing the pots in thermostate baths. The temperature of the latter could be regulated with tap water and electric heating. The soil temperatures obtained in this way were 16.8°, 20°, 25.3° and 29.9 °C respectively. They remained constant during the experiment, with a total deviation of less than 1 °C. Eight replicates for every soil temperature level were used. The soil moisture was maintained at the optimal level, known from a previous experiment (1), and varied between 100 and 80 % available soil moisture.

The pots were weighed every day to determine the water loss by evapo-transpiration. Once a week the pots were provided with plastic covers in order to measure the transpiration rate. The height of the shoot was recorded every week, during the experiment, which lasted four weeks.

3. EXPERIMENTAL RESULTS

Transpiration

The total amount of water transpired by the plants during the experimental period shows a linear relation with soil temperature within the range of this experiment (16.8°–29.9 °C). It shows a large decrease from 969 gr at 29.9 °C soil temperature (100 %) to 263 gr at 16.8 °C soil temperature (27 %) (see fig. 1).

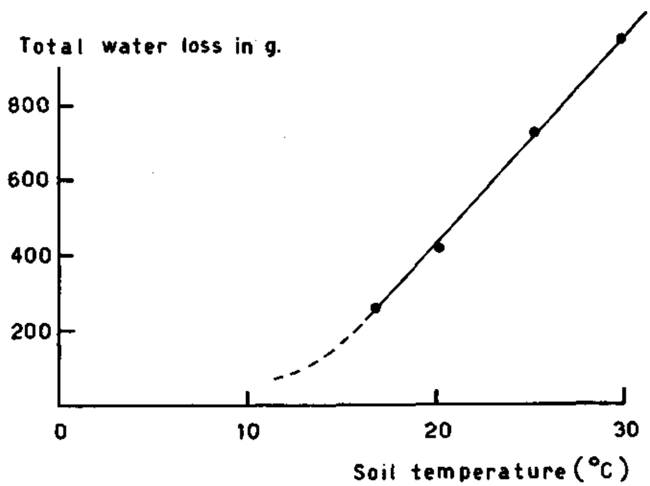

FIG. 1. The effect of soil temperature on the total water loss by transpiration during the experimental period in g.

Since transpiration per day and leaf area was measured at the end of the experiment, the effect of soil temperature on the transpiration rate per unit area, expressed in g.h^{-1}. 100 cm^{-2} leaf surface, could also be calculated (fig. 2); a linear relation between soil temperature and transpiration rate was found, the latter decreasing from 0.61 g.h^{-1}. 100 cm^{-2} leaf surface (100 %) to 0.37 g.h^{-1}. 100 cm^{-2} leaf surface (61 %).

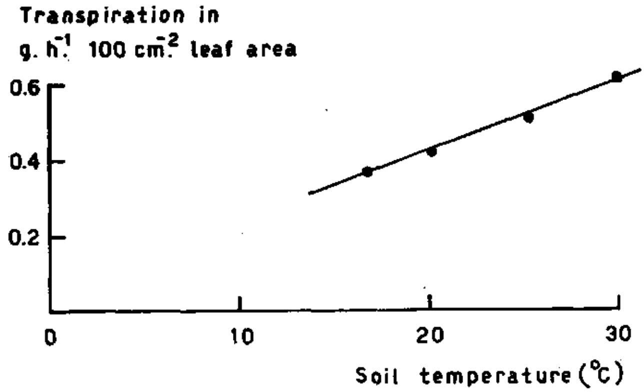

FIG. 2. The effect of soil temperature on the transpiration rate, expressed in g.h.$^{-1}$ 100 cm^{-2} leaf surface.

It is apparent, that transpiration is regulated to a large extent by soil temperature under the prevailing climatic conditions, since no maximum has been reached for the transpiration rate and the total water loss. This implies that the water uptake by the root system is the limiting factor for transpiration.

The effect of soil temperature on the rate of water uptake may be related to several factors, *e.g.:*

1. An increase in viscosity of water with decreasing temperature.

The fluidity of water decreases from 100% at 29.9 °C to 75% at 16.8 °C.

2. A decrease in the extent of the root system with decreasing soil temperature.

It is difficult to measure quantitatively the actual water absorbing root surface in pot experiments. No significant differences in dry weight of the root system were found in this experiment (table 3). Moreover, dry weight of roots does not seem a reliable basis for calculation of the root surface. However, variation in branching of the roots exists, the number of lateral roots increasing from 68 at 16.8 °C soil temperature (74.5%) till 94 and 95 (100%) at resp. 25.3 °C and 29.9 °C soil temperature.

3. An increase in "permeability" including all factors governing water uptake of the living root cells for water with increasing soil temperature.

We may obtain an idea about this relation from data on transpiration, on fluidity of water, and on the number of lateral roots, assuming that the latter gives a good information of the absorption capacity of the root system.

It is clear from fig. 3 and table 1 that the effect of the calculated water permeability of the root cells on transpiration is large; it increases from 51% at 16.8 °C soil temperature till 100% at 29.9 °C.

TABLE 1. The effect of soil temperature, analysed in different factors, on water uptake and transpiration of young tomato plants, expressed in % of the maximal value at 29.9 °C. See also fig. 3.

Soil temperature in °C	16.8	20.0	25.3	29.9
Water loss by transpiration (*a*)	27	43	74	100
Fluidity of water (*b*)	74.5	82	91	100
Number of lateral roots, assumed as parameter for the absorbing area of the root system (*c*)	71.5	82	99	100
Water „permeability" of the root cells, calculated from the data mentioned above (*x*) *)	51	64	82	100

*) x calculated according to $x = \frac{a}{bc}$, including all factors governing water uptake per root cell.

These date indicate that the effect of soil temperature on the "permeability" of the root cells is the most important factor in water uptake by the plant (see addendum).

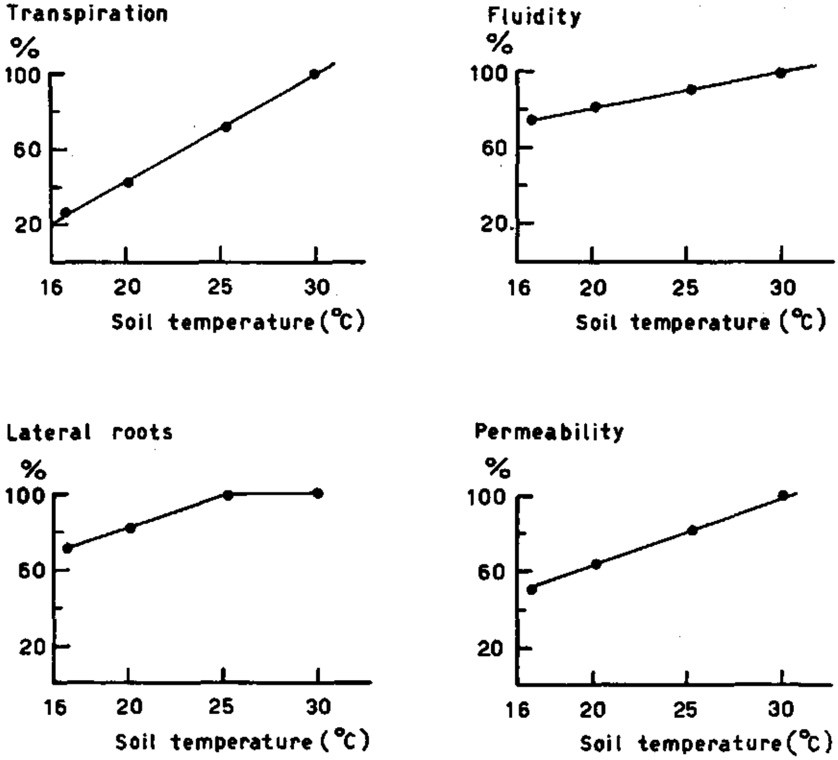

FIG. 3. The effect of soil temperature on total water loss by transpiration, analysed as fluidity of water, number of lateral roots and permeability of the root cells, expressed in % of the maximal value.

Growth aspects

Measurements have been made on total leaf area (1), mean area of mature leaves (2), number of leaves/plant (3), height of the shoot and fresh weight and dry weight of shoot and root (4), and root/shoot ratio (5).

1. The leaf area increases linearly with increase in soil temperature, from 133 cm^2 (34%) at 16.8 °C to 395 cm^2 (100%) at 29.9 °C soil temperature. The increase in total water loss is of the same order of magnitude, *viz.* from 27% at 16.8 °C to 100% at 29.9 °C. One would be inclined to conclude from these figures that the reaction of the tomato plant upon a low soil temperature merely consists in the reduction in leaf area, while the transpiration rate per unit leaf area is not affected. This conclusion however, is open to some doubt, since in the measurement of the actual rate of transpiration per unit leaf area on one day at the end of the experiment, this rate was found to increase from 61% at 16.8 °C to 100% at 29.9 °C (cf above and fig. 2).

The following additional remarks may be made: the figures 34% and 27% (cf. above) represent a transpiration figure per unit leaf surface of 80:100 referring to the lowest and the highest soil temperature respectively. If these figures were 37% and 24% (± 10%) the relationship of the transpiration rates actually found would be fairly well explained. Moreover, the transpiration figure refers only to one day at which a certain irregularity in moisture tension between the different treatments may not be fully excluded. Furthermore, the light conditions during the measurement necessarily differ for the smaller plant, at the low soil temperature, and the larger plant at the high one. For these reasons, not too much value should be attached to the figure for transpiration per unit area, and more data are needed to explain the apparent discrepancy, indicated above.

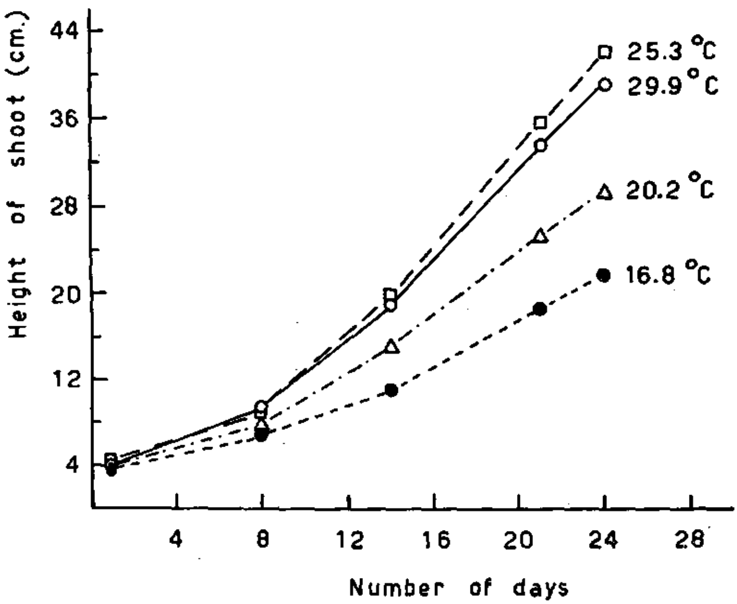

FIG. 4. The effect of soil temperature on height of the shoot in the course of the experimental period.

Also the linear relationships of total water loss and of total leaf area with temperature require a further analysis. This may point to the gradual increase with temperature of the importance of a limiting factor. An attempt to analysis of the water-loss figures has been made in table 1, but it is clear that "number of lateral roots" and "water permeability of root cells" as such are complicated items for which the gradual increase of the importance of a limiting factor is by no means excluded. Some data in literature suggest that physiological chains, if not interfered by limitations, show a constant Q_{10} over a large range of temperatures (WASSINK, 16, BOTTELIER, 7).

Unfortunately, we did not measure the initial leaf area, but we have found values between 50–90 cm^2 leaf surface of plants in other experiments after a similar pretreatment.

Assuming a leaf area of 75 cm^2/plant as initial value, and a linear increase in leaf area during the experiment, it is possible to compute the total amount of water transpired by the plants during the experiment from the transpiration rate and the leaf area at the end of the experiment. The values of the total water loss, calculated in this way, do not deviate appreciably from the measured ones (Table 2). They thus suggest the assumption of a linear increase in total leaf area during the experiment.

TABLE 2. Comparison between calculated water loss in g and measured water loss in g as affected by soil temperature.

Soil temperature in °C	Calculated water loss in g	Measured water loss in g
16.8	260	263
20.2	410	414
25.3	670	721
29.9	965	969

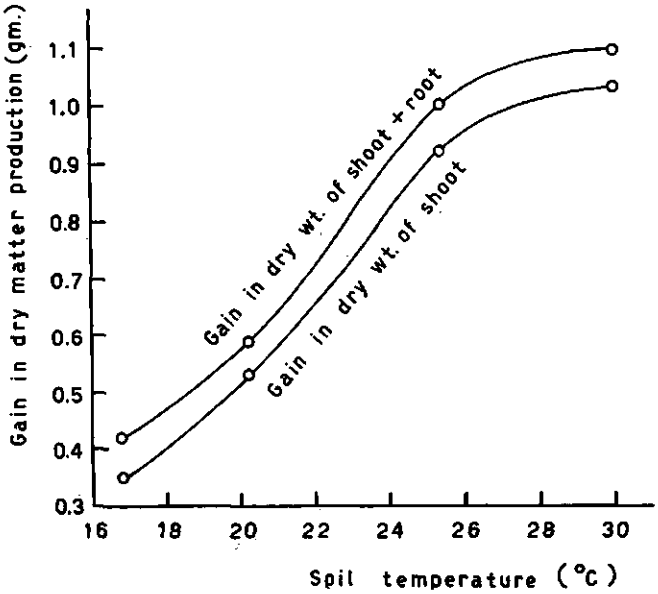

FIG. 5. The effect of soil temperature on the gain in dry weight of the shoot and on the gain in dry weight of the whole plant.

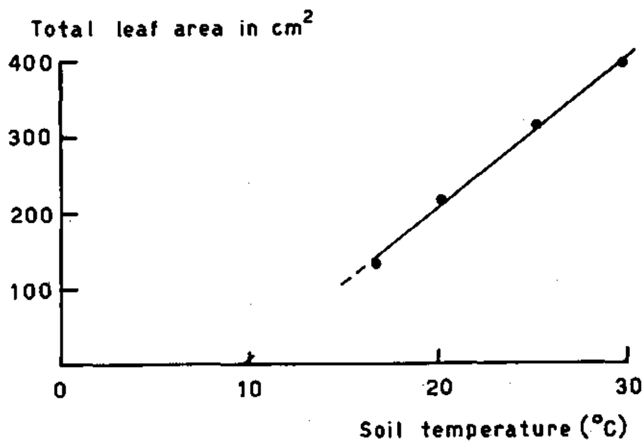

FIG. 6. The effect of soil temperature on the total leaf area measuredat the end of the experiment.

2 and 3. Similar results as mentioned above for the total leaf area are obtained for the mean area of mature leaves, since the number of leaves/plant is roughly the same for all treatments. The differences in number of leaves/plant are not significant; a slight increase in leaf number at higher soil temperatures may exist.

4. The height of shoot increases exponentially in the course of the experiment (fig. 4). After 24 days it was 21.8 cm at 16.8 °C, 42.1 cm at 25.3 °C, and slightly lower, *viz.*, 39.2 cm at 29.9 °C. An optimum is reached between 25.3 ° and 29 °C soil temperature. The reduction in dry weight and fresh weight is from 100% at 29.9 °C soil temperature to 38 and 35% respectively at 16.8 °C soil temperature. The reaction of fresh weight and dry weight of the plant to soil temperature resembles that of stem length (fig. 5). These observations suggest that above 25.3 °C a factor other than water supply limits the height of the stem; this may be the supply of assimilates to the stem, since dry weight of the shoot and stem length both approach optimum values. The effect of soil temperature on the height of the shoot within the range from 16.8 °C to 25.3 °C resembles its effect on dry weight of the plant, ranging from 100% at 25.3 °C to 52 and 42% respectively. However, it is quite sure, that the effect of soil temperature on stem height is complex.

As dry matter production depends on the process of photosynthesis, it is affected by the leaf area which shows much the same decrease from 100% at 29.9 °C soil temperature to 34% at 16.8 °C (table 3, fig. 6). It is therefore evident, that under the conditions of our experiments the gain in fresh weight and in dry weight are closely related to the light absorbing leaf area, within the range of soil temperatures from 16.8 ° to 29.9 °C.

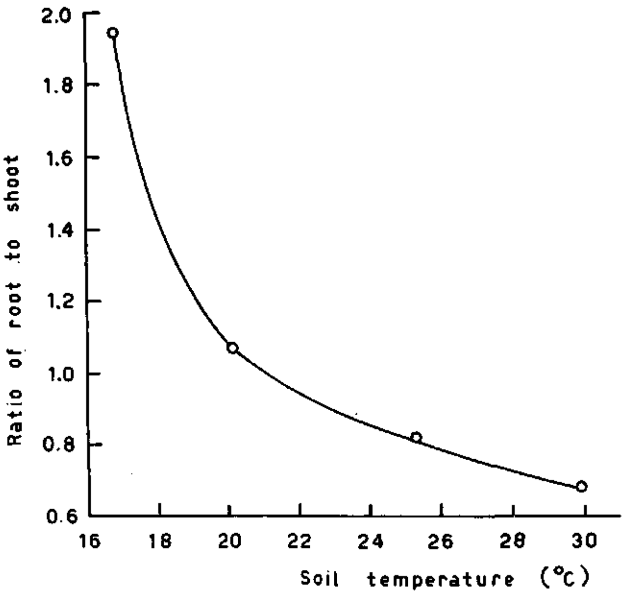

FIG. 7. The effect of soil temperature on the root/shoot ratio, the latter expressed as g. dry weight of root/g dry weight of shoot.

5. The ratio of root weight to shoot weight is greatly affected by soil temperature (fig. 7). It decreases from 0.194 at 16.8 °C soil temperature to 0.068 at 29.9 °C soil temperature.

If x represents soil temperature in °C and y dry weight of roots in g/dry weight of shoot in g, we found $xy = k$, and $k = 2.4 \pm 0.3$.

According to table 3, the temperature relationship of leaf area (col. 6) is about the same as that of shoot dry weight (col. 9) while dry weight of roots was hardly influenced, so that the temperature relation of shoot/root ratio appears mainly due to the soil temperature effect on leaf expansion.

Water economy

The total amount of water, transpired by the plants decreases considerably in the range between 25.3 °C and 16.8 °C soil temperature. This decrease is accompagnied by a similar decrease of the gain in dry weight so that the water requirement changes relatively little within this range of soil temperatures. At soil temperatures higher than 25.3 °C the transpiration rate and the leaf area still increase, causing an increase in water loss, whereas dry matter production is near its optimum at 25.3 °C soil temperature. For this reason the water requirement rises at soil temperatures is above 25.3 °C (table 3).

TABLE 3. The effect of soil temperature on transpiration and growth of young tomato plants.

1	2	3	4	5	6	7	8	9	10	11	12	13
Soil temperature in °C	Total water transpired/plant in g in 27 days	Transpiration rate in $g.h^{-1}$. 100 cm^{-2} leaf area	Height of the shoot in cm	Number of leaves/plant	Totalleafarea $(cm)^2$	Mean area of mature leaves $(cm)^2$	Fresh weight of the shoot in g	Gain in dry weight of the shoot in g	Gain in dry weight of roots in g	Root/shoot ratio (column 10/column 9)	Waier requirement in g water g/dry weight	Number of lateral roots/plant
16.8	263	0.37	21.8	8.6	133	22.8	5.2	0.35	0.07	0.195	635	68
20.2	414	0.42	29.2	8.6	217	36.5	8.35	0.53	0.06	0.11	704	78
25.3	721	0.51	42.1	10.0	315	49.6	13.4	0.92	0.08	0.08	726	94
29.9	969	0.61	39.2	11.4	395	58.0	15	1.03	0.07	0.07	874	95

4. DISCUSSION

Soil temperature largely affects the transpiration rate and the total amount of water transpired by the plants, which under our experimental conditions depend on the water uptake by the root system. The rise in water uptake with increase in soil temperature is due to several factors as fluidity of water, extension of the root system and permeability of the root cells. These factors all show a fairly linear relationship with soil temperature within the range studied.

BODE (6) and KRAMER (12) in experiments of 1 or 2 days found a much steeper curve for the relation between water uptake and soil temperature. This may be due to adaptation of the root cells to soil temperature during the 4 weeks of our experiment, but this needs further investigation.

An optimum height of shoot, dry weight and fresh weight was indicated at a soil temperature near 25°C, above which temperature these growth aspects are nearly constant, whereas the leaf area still increases.

One may observe from our data, that an increase in gain in dry weight of 1 g is correlated with an increase in water consumption of about 700 g in the range of soil temperatures of 16.8° to 25.3°C, which is in agreement with results obtained in a previous experiment at various light intensities (3).

It is of interest to compare our results obtained at a constant air temperature of 25.3°C and different soil temperatures with those from a similar experiment on growth and transpiration at different ambient temperatures (1). This comparison is possible, since the light intensity and the irrigation regime were nearly the same in both experiments. In fig. 8 the gain in dry weight of the plants of both experiments is plotted against temperature which is soil temperature in the present experiment (o) and general ambient temperature in the previous one (•). It may be concluded, that soil temperature is an important limiting factor for dry matter production at least up to above 25°C while about 25°C other factors may variously interfere, so that some aspects then may approach their optimum.

It would be interesting to investigate the effect of soil temperature (*e.g.* in the range of 15–30°C) at low air temperatures (*e.g.* 10–20°C). At a high soil temperature and low air temperature the limitation of water supply is removed and dry matter production and growth may be limited by air temperature. Preliminary observations indicate that this limitation of growth and gain in dry weight by low air temperatures at favourable soil temperatures (*e.g.* 29°C) is not clearly visible at an air temperature of 16.5°C. The growth of a plant at an air temperature of 16.5°C was about equal to that of a plant at 25°C air and soil temperature. This observation may be of interest for growers of tomatoes in hot glasshouses.

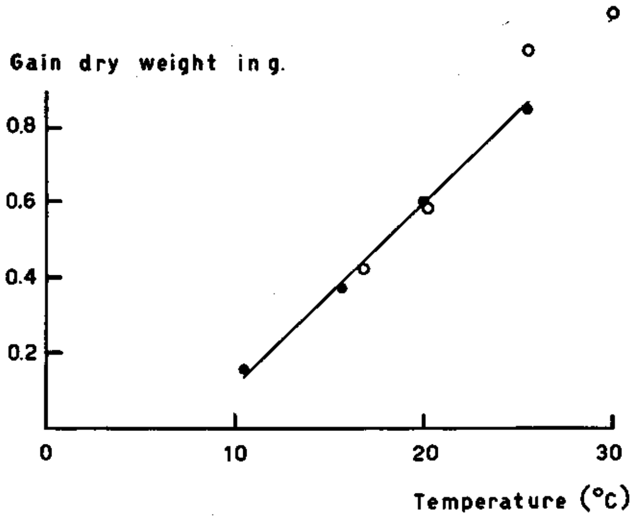

FIG. 8. The effect of soil- and air temperature on gain in dry weight. Data of the described experiment (o) are plotted versus soil temperature, the air temperature being 25.3°C, whereas data of a previous experiment (•) (litt. 1) are plotted against air temperature, soil and air temperature being the same.

Contrary to our results, WENT (18) in general did not find a large effect of soil temperature on growth of tomato. This may be due to low transpiration conditions in his experiments, but WENT does not give information on this subject.

RIETHMANN (15) observed a large effect of soil temperature on growth of tomato plants between 6 and 20°C, which agrees with our results. Evidently, the effect of soil temperature is more pronounced in experiments under high transpiration conditions than under conditions for low transpiration, as could be expected.

5. SUMMARY

Young tomato plants were grown, for a period of 4 weeks, at different soil temperatures (16.8°–29.9°C) and equal air temperature (25.3°C).

Different soil temperatures from 29.9°C to 16.8°C produce a decrease in transpiration rate with decrease in temperatures as well as a large reduction in the total amount of water transpired by the plants during the period of investigation. This large decrease in water loss may be explained by an effect on the fluidity of water, on the extent of the root system and on the "water permeability" of the root cells. It could be shown, that probably the latter is the most important factor, it includes physiological aspects.

The total leaf area increases with soil temperature in the entire range applied, whereas height of the stem, gain in dry weight approach their optimum at 25°C soil temperature. For these reasons, the water requirement changed little in the soil temperature range from 16.8° to 25.3°C and increased more sharply above 25.3°C.

The increase in dry weight and fresh weight from 16.8°C to 25.3°C soil temperature was found to be related to the increase in total leaf area, which is understandable, since the latter determines the amounts of light energy absorbed by the plant.

Comparison of the results of the present experiments with those obtained earlier, indicated that soil temperature was an important limiting factor for growth and dry matter production also in previous experiments at different ambient temperatures, under our experimental conditions.

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ADDENDUM (added in proof)

In the calculation of x in Table 1 we had used integrated values for a, and final values for c. Since *e.g.*, the leaf area had differently increased at the different temperatures during the experiment, one might wonder whether, x might turn out to be 100 at all temperatures if the time course was duely considered. We, therefore, have calculated x also for the direct transpiration measurements, one day each week. The data thus obtained are collected in the following table (p. 12). They do not suggest that the x-values should all have been 100 in the beginning when plants still were equal.The result seems in favour of the suggestion that in water uptake by the root cells temperature sensitive processes play an important role.

TABLE. The effect of soil temperature on the "permeability" including all factors governing the water uptake of the living root cells (x-value) in the course of the experiment. The number of lateral roots has been assumed to increase linearly in the course of the experiment.

Soil temperature in °C	16.8	20.0	25.3	29.9
x-value in:				
1st week	52	53	98	100
2nd week	47	64	97	100
3rd week	34	54	73	100
4th week	38	57	74	100

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PLATE 1. Growth of young tomato plants, as affected by soil temperature. (A: 29.9°C, B: 25.3 °C, C: 20.2 °C, D: 16.8°C) Air temperature 25.3°C. light intensity 5.4×10^4 $erg.sec^{-1}.cm^{-2}$ ⌀ sphere, measured at the tip of the plants.