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MEDEDELINGEN VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN,
NEDERLAND 59 (11) 1-12 (1959)

PRELIMINARY OBSERVATIONS ON THE EFFECT OF LIGHT INTENSITY AND PHOTOPERIOD ON TRANSPIRATION AND GROWTH OF YOUNG TOMATO PLANTS UNDER CONTROLLED CONDITIONS

by

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(Received 1.8.'59)

1. INTRODUCTION

This paper is the third of a series concerning the relations between transpiration, growth and water requirement of tomato under different environmental conditions. In the previous papers the effect of air temperature and irrigation regime (1) and air and night temperature (2) are discussed, in this paper the effect of light intensity and photoperiod on transpiration and growth will be described.

Many investigations have been made on the effect of light intensity on growth and fruit production of tomatoes (*e.g.* 4, 7), partly carried out under controlled conditions (8, 11). On the contrary, there are only very few data on the effect of light on the transpiration of tomato plants, and for this reason it may be valuable to investigate the relation between transpiration and growth of tomato plants under different conditions of light intensity and photoperiod.

2. MATERIAL AND METHODS

Tomato seeds of the variety "Ailsa Craig" were sown in a seed box in coarse sand in a glasshouse. The seedlings were transplanted 12 days afterwards in metallic pots with a height of 20 cm and a diameter of 10 cm. These pots were filled with 2 kg air-dry loam soil, the pF-curve of which was known. Fifteen days after transplanting the experiment started.

The plants were placed in a compartment at a mean air temperature of 25.2 °C and a mean relative humidity of 49 %. The air temperature varied between 24.6° and 25.5 °C and the relative humidity between 40 and 55 per cent during the

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experimental period of 4 weeks. The plants were illuminated from above with a set of fluorescent daylight tubes, "TL 55". The experimental set-up was surrounded by white curtains to keep conditions homogeneous and to increase light intensity and homogenity of illumination. In the experiment on different light intensities the duration of the illumination was 14 hours a day.

The light intensity was measured with a spherical lightmeter (10) in order to measure direct light as well as reflected light. These measurements were taken at the tip of the plant. In this way relative values were obtained for the quantity of light given to the plant. In the experimental equipment the light reflected from the white curtains etc. contributed to about 20 % of the total light intensity. The light intensity thus measured was resp. 1.15, 2.4, 5.1, and 6.5×10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere during the experimental period. An exact measurement of the energy absorbed by a tomato plant is difficult, since the variation in distance between the successive leaves and the light source is large. Moreover the effect of mutual shading of the leaves is not negligable.

The duration of the light period in the experiment with different photoperiods was 8, 11, 13.5, and 16 hours a day respectively. In this experiment the light intensity was the same in all treatments, namely 5.1×10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere, measured at the tip of the plant.

The soil moisture was maintained optimal for growth, and varied between 100 % and 80 % of the available soil moisture content.

The pots were weighed daily in order to determine the evapo-transpiration in the course of the experiment. Once a week the soil in the pot was covered with a nylon sheet to eliminate evaporation of the soil so that then the transpiration rate was measured directly. This cover was not maintained permanently in order not to interfere with aeration of the soil. The height of the shoot was recorded 8 times during the 4 weeks experimental period. At the end of the experiment measurements were made on dry and fresh weight of shoot and root, number of leaves, leaf area, chlorophyll content of the leaves, etc. The results of these measurements are given in tables 1 and 2.

At the beginning of the experiment, fresh and dry weight of the shoot of some plants were determined as initial values.

3. Experimental results

1. *Transpiration and growth at different light intensities*

It is evident from the results represented in table 1, that the light intensity has a large effect on transpiration and water loss of the plant. The total amount of water, transpired by the plants during the experimental period varies from 839 g. (100 %) at the highest light intensity to 373 g. (44 %) at the lowest light intensity (fig. 1). This large decrease is due to the cooperation of different factors. In the first place light intensity affects the transpiration rate, which is expressed in our case in $g.h^{-1}$. 100 cm^{-2} leaf surface. Secondly light intensity influenced the appearance of the plant with regard to the number of leaves, the leaf area, and other morphological characters which are important for transpiration. These factors will be dealt with below.

The mean transpiration rate has been calculated from the measured transpiration rate and the leaf area at the end of the experiment.

It is clear from fig. 2 that the transpiration rate is largely affected by light intensity. With exception of the transpiration at the lowest light intensity a

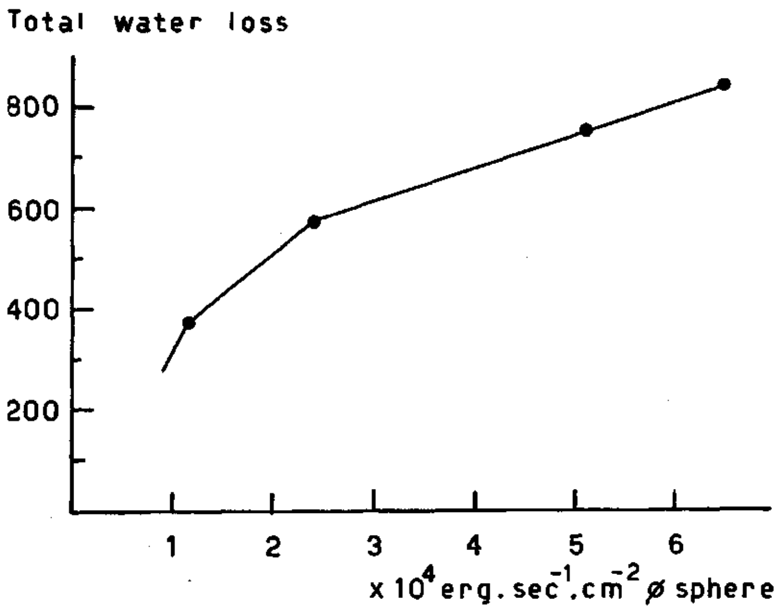

FIG. 1. The effect of light intensity on the total water loss in g by transpiration of the plants during the experimental period of 4 weeks.

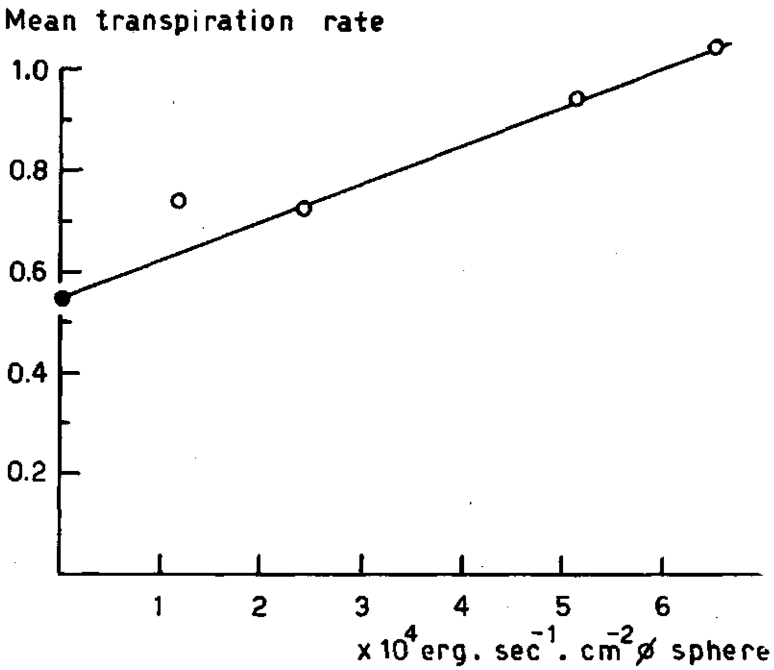

FIG. 2. The effect of light intensity on the mean transpiration rate, expressed in g. h^{-1}. 100 cm^{-2} leaf surface, of young tomato plants grown at the same light intensity (o——o). The dark value • has been obtained from potometer experiments (litt. 3) with cut tomato leaves, of plants grown at a light intensity of 2×10^4 erg. sec^{-1}. cm^{-2} ø sphere.

linear increase in transpiration with an increase in light intensity is observed. An observation on transpiration in dark is added in fig. 2. Unfortunately, no data pertaining to the experimental plants themselves were available so that this observation has been taken from potometer experiments with cut tomato leaves at the same temperature and relative humidity (3). The linear increase in transpiration with light intensity may be due to two different effects of light.

1) The increase in leaf temperature caused by the irradiation.

2) The increase in aperture of the stomata with increasing light intensity.

It was shown in an earlier publication (3) that, under our experimental conditions, the linear increase in transpiration owing to a rise in leaf temperature is at most 14 % of the dark value. For this reason the stomatal reaction is

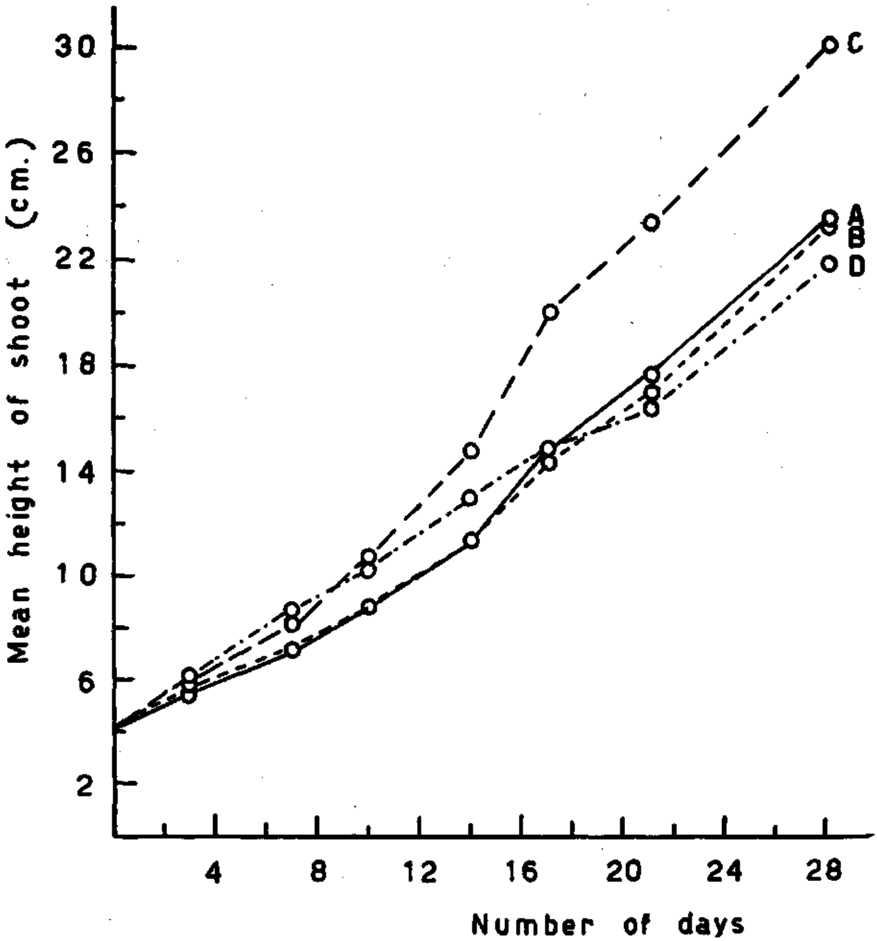

FIG. 3. The effect of light intensity on the height of the shoot in cm.

o——o, A = 6.5 × 10^4 erg. sec^{-1}. cm^{-2} ø sphere,
o------o, B = 5.1 × 10^4 erg. sec^{-1}. cm^{-2} ø sphere,
o – – o, C = 2.4 × 10^4 erg. sec^{-1}. cm^{-2} ø sphere,
o-.-.-o, D = 1.15 × 10^4 erg. sec^{-1}. cm^{-2} ø sphere.

responsible for the greater part of the effect of light intensity on transpiration, within the range of light intensities studied.

One may observe in fig. 2, that transpiration at the lowest light intensity applied in this experiment deviates from the linear curve. This deviation of the curve may be due to two morphological factors:

1) At low light intensities the leaf area is much smaller than at higher intensities (table 1). Preliminary observations have indicated that the stomatal index, *i.e.* the number of epidermis cells per stoma is the same for leaves of tomato grown at different light intensities. Therefore, the smaller leaves contain more stomata per unit leaf area than the larger leaves, as produced under higher light intensities. This may explain why the transpiration rate is found relatively higher at the lowest light intensity.

2) On the other hand it should be observed that the light absorption of pale green leaves, as grown at weak light is lower than that of leaves, grown at higher light intensities. This is illustrated by the observations on chlorophyll content of the leaves (table 1), while also preliminary measurements of the light absorption of leaves in an ULBRICHT sphere, showed that the absorption of the leaves grown in weak light (*e.g.* at 10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere) was lower than the absorption of leaves grown at a higher light intensity ($\sim 2.10^4$ erg. sec^{-1}. cm^{-2} ⌀ sphere). This effect would give rise to a lower transpiration rate, due to lower light absorption of the leaf. Our results indicate that this effect is more than compensated by the increase in number of stomata per unit leaf area, as discussed above.

The effect of light intensity on the height of the shoot is remarkable (fig. 3). It remains constant at the two highest light intensities applied and increases at the relative low light intensity of 2.4×10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere. It is obvious that this elongation of the stem is characteristic of the etiolation. Other characteristics of etiolation, like a decrease in leaf area, smaller leaves and a pale green colour of the leaves are visible at still lower light intensities *e.g.* at 1.15×10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere. It thus seems, that different characteristics of etiolation react differently to light intensity which is not surprising since these morphogenetic effects are the result of complicated biochemical chains involving the synthesis of several types of substances.

The number of leaves shows no significant variation (table 1). It is possible, that it is slightly higher at the highest light intensity.

The length of the mature leaves also shows only a very small variation. There is some indication, however, that it is slightly higher at 2.4×10^4 erg. sec^{-1}. cm^{-2} ⌀ sphere, the same intensity at which also the maximal height of shoot was observed.

The gain in dry weight shows a fairly linear increase with light intensity (fig. 4). Under conditions of light limitation, as prevalent throughout our present experiment, dry matter production depends on the light absorption of the plant, and thus also depends on the leaf area. Plotting dry matter production per unit leaf area against light intensity gives also a linear relationship and this is also found in the case of dry weight of 1 cm^2 leaf surface (fig. 4, table 1). One may conclude, that there is a linear relation between dry matter production per unit leaf area and light intensity, within the range of light intensities studied, just as holds for photosynthesis.

Since there is also a linear relation between the rate of transpiration and the light intensity, one may expect a linear curve for the relation between total

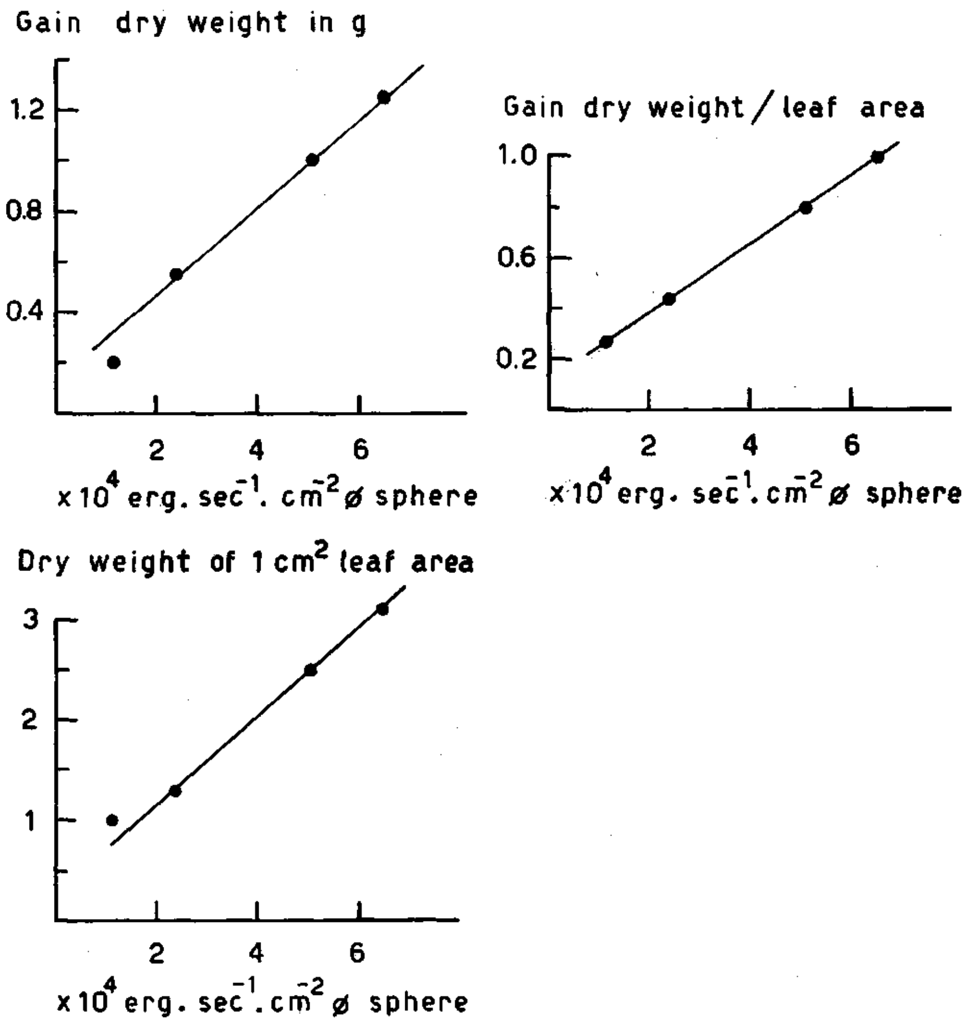

FIG. 4. The effect of light intensity on gain in dry weight of the whole plant in g, on gain in dry weight in g/100 cm^2 leaf surface, and on the dry weight of 1 cm^2 leaf area in mg.

water loss and total gain in dry weight. This indeed is found (fig. 5a). Fig. 5b represents the relation between the water requirement, expressed in g water transpired per g dry matter produced, and the light intensity. The water requirement is very high at a low light intensity, and decreases rapidly with increasing light intensity. It may be observed that the initial part of this curve runs asymptotically towards $+\infty$ at the compensation point of assimilation and dissimilation (zero gain in dry matter); below the compensation point it comes back from $-\infty$ to real negative values. We do not yet have experimental data in this region.

The observed decrease in water requirement with increasing light intensity is due to the fact that dry matter production rises more rapidly than transpiration. This rise is from 100 per cent at the lowest light intensity to 625 and 225

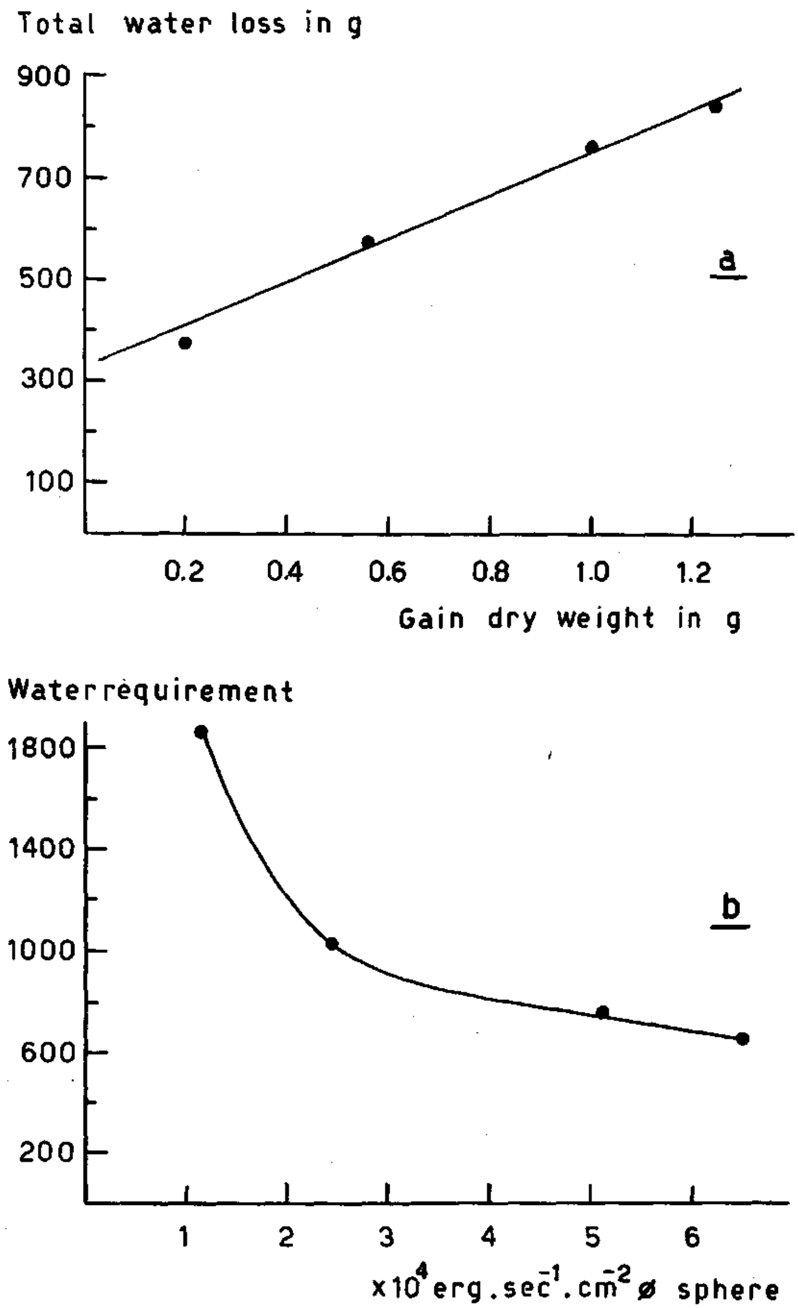

FIG. 5*a*. The relation between total water loss by transpiration in g and the gain in dry weight in g of young tomato plants, grown at different light intensities.

b. The effect of light intensity on the water requirement, the latter expressed in g transpired water/g dry matter production.

per cent at the highest light intensity, from dry matter production and transpiration respectively.

The water requirement may be expected to reach its lowest value when the stomata are fully open and dry matter production had just reached light saturation. At still higher light intensities dry matter production will provisionally remain the same, whereas transpiration will continue to increase. Also for this region we hope to be able to collect pertinent data in the near future.

The root/shoot ratio increases with light intensity (table 1). This may be explained by assuming that the products of photosynthesis are mainly used for growth and development of leaves and stem, and that a transport of sugars and other products to the roots only takes place above a certain level of photosynthesis. At higher light intensities the root/shoot ratio is somewhat irregular.

The fresh weight of the shoot increases with the light intensity in a similar way as the dry weight of the shoot but relatively less quickly, *viz.*, only about 2.5 times in the range of light intensities studied whereas the dry weight increases about 6 times.

It, therefore, does not surprise that the data of table 1 show a linear decrease of the water content of the shoot with increasing light intensity.

2. *Transpiration and growth at different photoperiods*

Since the experiment on growth and transpiration of tomato at different photoperiods was carried out at the same light intensity for each treatment and during the entire light period, the effect of an increasing photoperiod is associated with an increase in absorbed energy/day. The experiments were carried out at a relatively high light intensity, *viz.*, 5×10^4 erg. sec^{-1}. cm^{-2} ø sphere.

The data from this experiment are given in table 2, some are represented in fig. 6.

We may ask if the effect of photoperiod on growth and transpiration may entirely be due to the amount of energy received per day. One then would expect that the effects of the following treatments at different photoperiods of 16, 13.5, 11, and 8 hours at 5×10^4 erg. sec^{-1}. cm^{-2} ø sphere would correspond to a light intensity of 5.7, 4.8, 3.9, and 2.85×10^4 erg. sec^{-1}. cm^{-2} ø spere at an equal photoperiod of 14 hours.

Fig. 6 shows that the data on gain in dry weight and total water loss by transpiration fairly well fit the curve, obtained from the data of the experiment on light intensity. Similar results are obtained in relations as *e.g.* water requirement of the shoot versus light intensity, and water content of the shoot versus light intensity. Within the range of light intensities studied and within the range of photoperiods studied, the effect of light on transpiration, growth and water requirement of tomato is due to the total amount of energy, received daily by the plant.

4. Discussion

We have seen in this article that the transpiration rate and the total amount of water transpired by the plants during the experimental period show a linear relation with light intensity. This observation is in agreement with results obtained in potometer experiments with cut tomato leaves (3). Thus the linear relationship between transpiration and light intensity also holds for measurements with entire plants, grown in soil with inevitable mutual shading of leaves.

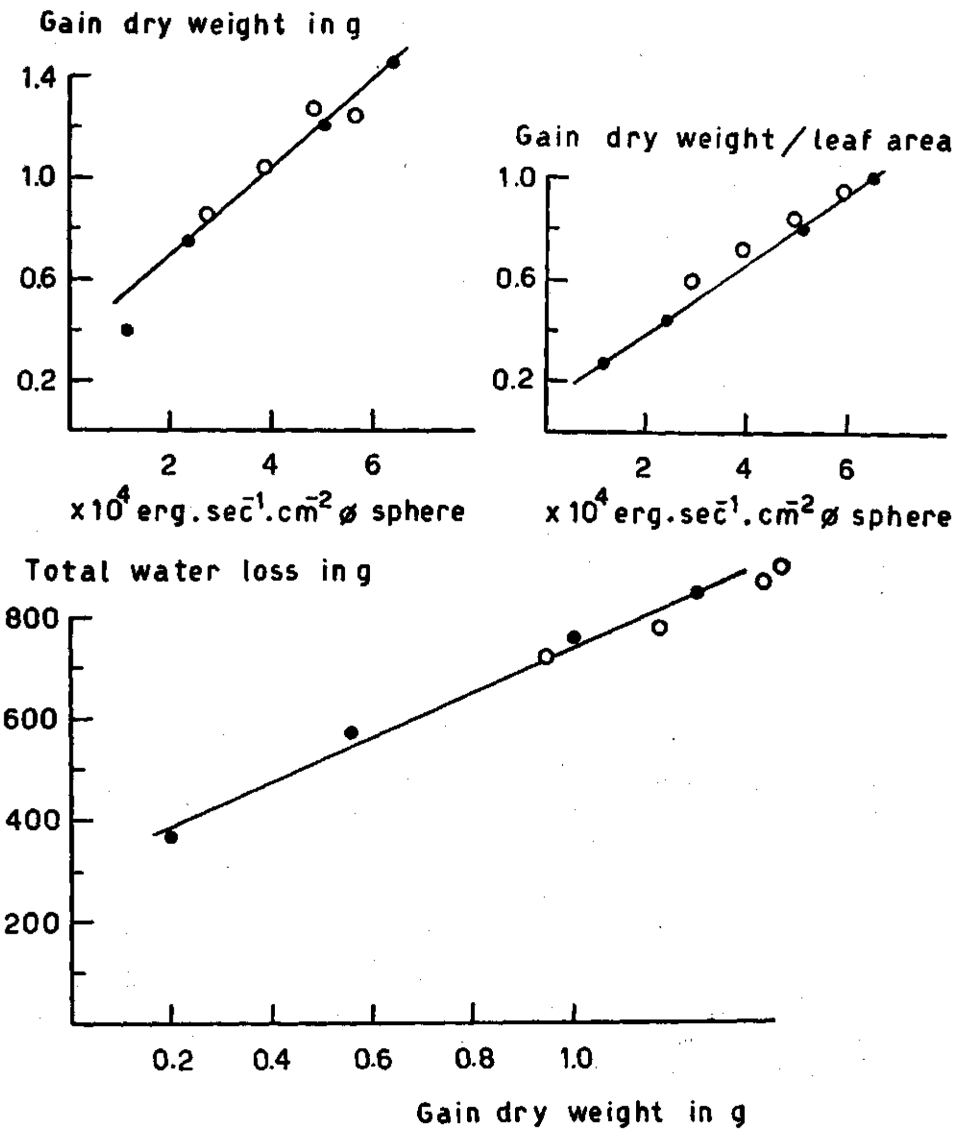

FIG. 6. Comparison of the results of the experiment at different light intensities (●—●), with those of the experiment at different photoperiods (o), showing that the effect of photoperiod is only due to an effect of total amount of energy daily received by the plants.

However, a deviation from the linear curve may occur owing to changes in the morphological appearance of the plant (e.g. etiolation). It was proved before (3) that linear relation between transpiration and light intensity mainly depends on the stomatal reaction to light. As this reaction is related with photosynthesis, it does not surprise to observe a linear relationship between dry matter production and light intensity. It should be noticed, however, that these conclusions only hold within the range of light intensities studied.

Our observations on growth in general agree with those in literature. WENT (11) *e.g.* also observed a nearly linear relationship between light intensity and growth rate of young San Jose Canner tomatoes at 26 °C day and night temperature. The decrease in water content of the leaves with an increase in light intensity and in dry matter production has been reported by MELVILLE (5).

The root/shoot ratio increases with an increasing light intensity in agreement with observations of WENT (12). It is of importance in this connection that, in various other conditions and with various plants, it has been observed in this laboratory during the last years that the shoot/root relationship is a sensitive morphogenetic feature. One may assume that this fact is due to an increase in carbohydrate supply to the root system with an increase in light intensity and photosynthesis. In this connection it is of interest that WASSINK and RICHARDSON (9), in young plants of *Acer pseudoplatanus* observed an effect of light intensity on root growth similar to that on photosynthesis.

The effect of photoperiod (8–16 h. daily illumination, equal energy throughout the entire period) on growth and transpiration of tomato could fully be explained as an effect of the total energy received by the plants. Recently, WENT (12) has reported that the growth rate of tomato decreases at a photoperiod less than 4 hours, perhaps owing to lack of carbohydrates produced in photosynthesis, while growth also is retarded at a photoperiod longer than 16 hours a day. Tomato plants need a dark period for healthy growth (12, 7). It should be stressed that such observations strongly depend on the light intensity at which the plants are grown.

5. SUMMARY

Young tomato plants were grown during 4 weeks at 25.3 °C and under different light intensities at a constant air temperature. The transpiration rate and the total amount of water transpired by the plants in the course of the experiment increase linearly with light intensity. Fresh weight and dry weight also increase linearly with light intensity and the same relation holds for the relation between total loss of water and gain in dry weight. The water requirement (g of water transpired per g dry matler produced) was high at low light intensities and decreased at higher light intensities. The effect of the length of the photoperiod (at equal light intensity), is due to the total amount of light received by the plants, as follows from a comparison between the data of the experiment at different photoperiods and those obtained at different light intensities.

ACKNOWLEDGEMENT

The experiments have been carried out in the Laboratory for Plant Physiological Research at Wageningen. The authors are greatly indebted to Prof. Dr. E. C. WASSINK for his stimulating interest and advice during the course of the work and his critical remarks on the results. Thanks are also due to miss J. BOS for experimental assistance.

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TABLE 1. The effect of light intensity on various aspects of growth and transpiration of tomato.

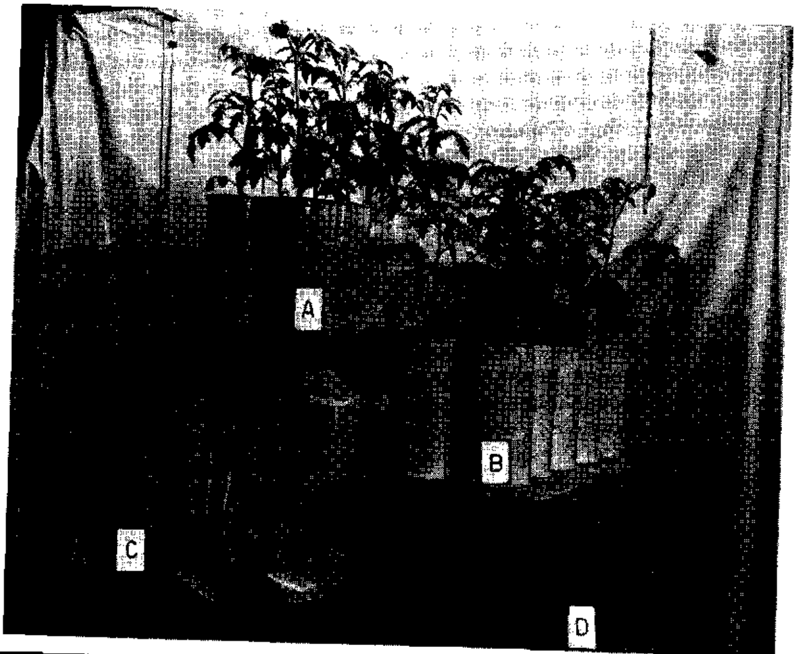
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Light intensity in 10^4 erg. sec^{-1}. cm^{-2} ø sphere	Total water loss by transpiration in g	Mean transpiration rate in g. $24h^{-1}$	Means transpiration in g. h^{-1}. 100 cm^{-2} leaf surface	Height of shoot in cm	Mean number of leaves/plant	Total leaf area at the end of the experiment in cm^2	Mean dry weight of 1 cm^2 leaf area in mg.	Relative chlorophyll content	Fresh weight of the shoot in g.	Gain dry weight shoot + root in g.	Gain dry weight shoot in g.	Ratio root/shoot	Water content of shoot in g/g dry weight	Water requirement in g water/g dry matter
6.5	839	31.1	1.04	23.9	10.1	253	3.1	0.126	10.5	1.25	1.13	0.11	8.3	675
5.1	760	28.2	0.94	23.7	9.2	255	2.5	0.121	9.7	1.00	0.89	0.12	9.9	760
2.4	575	21.3	0.72	30.45	7.9	253	1.3	0.118	8.2	0.56	0.51	0.09	15.1	1025
1.15	373	13.8	0.74	22.3	8.5	150	1.0	0.109	4.3	0.20	0.19	0.07	16.4	1870

TABLE 2. The effect of different periods of light on various aspects of growth and transpiration of tomato.

1	2	3	4	5	6	7	8	9	10	11	12
Light period in h/day	Total water loss by transpiration in g	Mean transpiration rate in g. $24h^{-1}$	Height of shoot in cm	Mean number of leaves/plant	Total leaf area at the end of the experiment in cm^2	Fresh weight of the shoot in g.	Gain dry weight shoot in g.	Gain dry weight roots in g.	Root/shoot	Water content of shoot in g/g dry weight	Water requirement in g water/g dry matter production
16	865	30.9	28.4	9.6	257	10.7	1.23	0.16	0.13	7.7	760
13.5	875	31.3	26.0	9.4	276	11.2	1.28	0.15	0.12	7.8	740
11	775	27.6	24.6	8.8	288	9.5	1.04	0.12	0.12	8.1	802
8	720	25.6	29.3	9.0	280	8.6	0.85	0.09	0.11	9.1	910

Plate 1.

1 A



1 B

Plate 1A. Tomato plants at 4 different light intensities, A, B, C, D, see text, p. 2. Age 4 weeks, photogr. 1.3.'58.

Plate 1B. Plants from Plate 1A, photogr. 3.3.'58. Light intensity A=6.5, B=5.1, C=2.4, D=1.15 (x 10^4 erg. sec^{-1}. cm^{-2} ø sphere).