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ROOT TEMPERATURE AND
GROWTH OF YOUNG
TOMATO PLANTS

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H. HARSSEMA

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ROOT TEMPERATURE AND GROWTH OF YOUNG TOMATO PLANTS

(with a summary in Dutch)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS,
DR. H. C. VAN DER PLAS,
HOOGLEERAAR IN DE ORGANISCHE SCHEIKUNDE
IN HET OPENBAAR TE VERDEDIGEN
OP VRIJDAG 13 JANUARI 1978
DES NAMIDDAGS TE VIER UUR
IN DE AULA VAN DE LANDBOUWHOGESCHOOL
TE WAGENINGEN

STELLINGEN

1

De groeiremming bij lage bodemtemperaturen wordt bij de tomaat niet in de eerste plaats veroorzaakt door een verhoogde weerstand tegen watertransport in de wortel.

Dit proefschrift.

2

Bij een doeltreffende beschrijving van plantengroei processen met behulp van simulatiemodellen zullen kwantitatieve gegevens over de hormoonhuishouding onmisbaar blijken te zijn.

3

Bij de keuze van biologische indicatoren voor luchtverontreiniging zal meer aandacht geschonken moeten worden aan de vraag, in hoeverre zij model kunnen staan voor door luchtverontreiniging bedreigde systemen.

4

De definitie van luchtverontreiniging in de Wet inzake de Luchtverontreiniging biedt onvoldoende garanties voor een beleid dat ook gericht is op de bescherming van waarden die niet direct aan de mens ontleend zijn.

5

Zorg voor een efficiënt gebruik van energie en voor de kwaliteit van oppervlaktewater zijn vooralsnog belangrijker drijfveren voor het vermijden van overmatig kunstmestgebruik, dan vrees voor een mogelijke aantasting van de ozonlaag.

6

Op de praktijk gericht teeltonderzoek is moeilijk te verwezenlijken in promotie-onderzoek projecten, waarvan de duur tot drie jaar beperkt wordt.

7

Er dienen dwarsverbanden ontwikkeld te worden tussen de planologische en de milieuhygiënische opleidingen aan de Landbouwhogeschool.

8

Bij de maximalisering van de opnamecapaciteit van de L.H. dient, naast verhoging van de onderwijs efficiëntie, ook aandacht geschonken te worden aan handhaving of verbetering van de onderwijskwaliteit.

H. HARSSEMA

Wageningen, 13 januari 1978

FOREWORD

The research reported in this paper was carried out at the Department of Horticulture of the Agricultural University, under the supervision of Prof. Dr. Ir. J. F. Bierhuizen. I greatly appreciate his interest in defining the problems and his suggestions for solving them. His critical comments, both during the investigation and on reading the manuscript, were highly valuable. The vast knowledge on many aspects of tomato growing of the late Dr. K. Verkerk guaranteed a rapid introduction into the extensive literature on this crop. The many stimulating discussions with him are gratefully acknowledged.

The varying nature of the experiments necessitated the cooperation of many people in the Department of Horticulture, both of the glasshouse and the phytotron section. I never asked for this cooperation in vain and I would like to thank everybody for that. Mrs. W. A. Wagenvoort should be mentioned specially for her assistance in many measurements; thank you, Helma.

The manuscript was prepared when I was working at the Department of Air Pollution. I thank Prof. Dr. J. G. ten Houten for giving me the opportunity to finish this work, and my colleagues for the extra tasks they performed when I was 'writing'. Mrs. J. P. Kieffer-Smits and Mrs. C. L. Hölscher-van den Berg are acknowledged for their care in typing the manuscript. Special thanks are also due to Mr. H. van Lent who prepared the drawings for this publication.

Finally I take the opportunity to thank all, who showed their interest in my work, and who stimulated me with their opinion and criticism.

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1. INTRODUCTION

The tomato is one of the most important glasshouse crops in the Netherlands. Originally this fruit crop was mainly cultivated in cold frames in which sometimes additional heating was applied. In order to expand the growing season and to achieve optimum conditions for plant growth, modern technical facilities were introduced during the past 15 to 20 years. At the same time, new varieties were used with a high production of good quality fruits, and with a high resistance to diseases. The control of fungi diseases was feasible also with new methods in plant protection, even at high temperatures and humidities.

Nowadays sophisticated techniques are available to control air temperature and humidity in commercial glasshouses (STRIJBOSCH and VAN DE VOOREN, 1975). These factors can be regulated in dependence of the available light intensity (CALVERT, 1975) or by simulating photosynthesis with the aid of computers (TAKAKURA, 1975) in order to achieve optimum plant growth. CO₂-enrichment of the glasshouse atmosphere, enhancing photosynthesis and growth, is at present widely practised in tomato production with good results (VAN BERKEL, 1967; HAND and SOFFE, 1971; CALVERT and SLACK, 1975 and 1976). The use of artificial light during the dark winter months has been extensively studied in the past (e.g. VAN KOOT, 1958; GERMING, 1962; VERKERK, 1962 and CANHAM, 1974b), but the economic feasibility of application remains questionable because of the high costs involved. Recently, however, new lamps with a much higher efficiency have been developed (CANHAM, 1974a). Such a development may lead to application of artificial light in practice in the near future.

In contrast with the vast amount of information on control of the aerial environment, knowledge regarding the rooting medium of tomato plants is scanty. Improvement of the rooting medium, together with optimal cultural practices has shown a drastic increase in growth rate of tomato seedlings (DE LINT and KLAPWIJK, 1973).

Root temperature has long been considered as an important factor in the growth of tomato plants (RIETHMANN, 1933), but the information on this parameter is still incomplete and often contradictory. Therefore a study on this environmental factor seems necessary in order to determine, under which conditions control of root temperature might be an advantage in tomato production.

The first objective of this study, therefore, was to quantify the effect of root temperature on growth and development, earliness and fruit yield of tomato plants, in relation to other environmental factors. Main emphasis was given to young plants, since the application of root temperature control is likely to be more profitable during the early stages of growth than later on. The number of plants per unit area is much higher in the nursery, which reduces the cost

per plant, while large effects may be expected during the early stages because of the exponential growth rate during that period.

A second objective of this study was to obtain information on the mechanism which is primarily affected by root temperature and which is limiting the growth rate of tomato plants.

A review of the literature on the subject is given in Chapter 2. In Chapter 3 a series of experiments is described, in which young tomato plants were grown under natural glasshouse conditions throughout the year at various root temperatures. Plants were cultivated up to the stage of transplanting in these experiments. An extensive growth analysis in relation to the environment is presented in Chapter 3. In Chapter 4, experiments are described, in which plants, pretreated at different root temperatures, were cultivated in a glasshouse during winter and early spring as a commercial crop, in order to obtain information on the performance of plants after transplanting. Data on development, earliness and fruit yield are reported. In Chapter 5 some experiments under controlled conditions in a phytotron with artificial illumination are described. Special emphasis was given to leaf growth, which appeared to be the most sensitive growth parameter. Various air and root temperature combinations were applied. Chapter 6 deals with the physiological background of the observed responses and some additional experiments are reported there.

2. LITERATURE

2.1. GENERAL

Two terms are generally used in the literature to indicate the temperature of the rooting medium of plants, viz. root temperature and soil temperature. Although no reports were found, where the temperature of the root itself was controlled or measured, it should be emphasized, that the fluxes in the heat balance of the root system are extremely small compared with the heat conductivity of the medium, so that root and soil temperature may be assumed to be equal. This fact is in contrast to the situation of the aerial part of a plant, the temperature of which may be quite different from that in the ambient air. Throughout this paper the term root temperature will be used.

An extensive review of the literature on root temperature and plant growth has been given by RICHARDS et al. in 1952. They discussed the effect of temperature on a number of physiological processes in the root, such as translocation and respiration, mineral uptake, water uptake and root growth.

The decreased rate of translocation and respiration at low root temperatures causes an increased carbohydrate content of both root and shoot. Phosphate uptake is reduced at low root temperatures, but nitrogen uptake seems to remain the same between 13 and 20°C. Water uptake is reduced at low root temperatures in many plant species.

Apart from the fact, that root growth is influenced by other processes such as translocation of carbohydrates, growth itself is temperature dependent. WHITE (1937) studied the effect of temperature on the growth rate of excised tomato root tips and found a sharp optimum at 30°C: the Q_{10} -value between 20 and 30°C was approximately 3. Below 15°C the growth rate was almost zero.

RICHARDS, et. al. (1952) represented a large number of experimental data on minimum, optimum and maximum root temperatures for growth and development of many plant species. Despite the mass of data, they concluded that in general knowledge regarding the processes involved in root temperature effects is scanty.

Since their review, a number of papers related to root temperature effects appeared, but an overall picture on this subject is lacking. The subsequent paragraphs will deal with that literature, which is important in view of the two objectives mentioned in the introduction, viz. a) the effect of root temperature on growth of tomato plants and b) the processes involved in the root temperature response.

2.2. THE EFFECT OF ROOT TEMPERATURE ON GROWTH OF TOMATO PLANTS

The discussion on the effect of root temperature on growth of tomato plants will be divided into three sub-paragraphs. The first one will deal with root temperature during raising, the second one with that after transplanting and in the third one the after-effect of root temperature during raising on subsequent development and yield will be discussed.

2.2.1. *Root temperature during raising*

Many references deal with temperature effects on young tomato plants, but in only a limited number air and root temperature were controlled separately. Without root temperature control the temperature in the rooting medium may be assumed to be equal to air temperature when the latter is constant. However, with fluctuating day-and-night temperatures, even in relatively small containers root temperature may lag behind air temperature considerably (ABD EL RAHMAN, et. al. 1959a). The neglect of root temperature may be partly caused by the observation of WENT (1944a), that root temperature as an important environmental variable does not affect growth of tomato plants in case other environmental conditions are optimal. This result was valid only for plants which had reached a height of about 30 cm. It should be mentioned also, that the control of root temperature requires special facilities and equipment which are often not available.

ABD EL RAHMAN, et. al. (1959b) grew tomato plants for four weeks under controlled conditions at a constant air temperature of 25°C and at constant root temperatures of 16.8, 20, 25.3 and 29.9°C. They measured transpiration and a number of plant parameters at the end of the experiment, and observed, that the highest rate of plant growth and transpiration occurred at the highest root temperature. Shoot/root-ratio was much higher at the higher root temperatures, while root growth was slightly affected by root temperature.

For a number of years the effect of root temperature was studied at the E.R.A. Field Station at Shinfield Green (U.K.). The results were reported by BOXALL (1962) and CANHAM (1966). Tomato plants were grown under natural glasshouse conditions at root temperatures ranging from 7.2 to 38.3°C for four weeks throughout the year. Optimum growth was always observed between 20 and 30°C. In other experiments soil heating was combined with supplementary light and it was shown that there was a more than additive increase in growth by combining both treatments.

Reports from Japan show the same tendency. FUJISHIGE and SUGIYAMA (1968) grew young plants of tomato, cucumber and sweet pepper under controlled conditions at root temperatures between 10 and 35°C for ten days. For tomato the optimum for shoot growth occurred between 20 and 30°C, and for cucumber and sweet pepper between 25 and 35°C. HORI, et. al. (1968) combined different air temperature regimes with root temperatures between 13 and 28°C; again the optimal root temperature ranged between 23 and 28°C. At lower air temperatures (18°C by day and 13°C by night) the effect of root temperature was only relatively small.

A number of root temperature studies were performed at the Glasshouse Crops Research Institute at Littlehampton (U.K.) under controlled conditions (COOPER, 1968). The plants were grown in a nutrient solution at 5 to 35°C. Air temperature was kept constant at 20°C. CO₂-enrichment was applied at a level of 2 g CO₂/m³ (approximately 1000 ppm by volume). The highest growth rate was obtained at a root temperature of 25°C (COOPER, 1973). The main effect of root temperature was observed during the first two weeks after emergence. Later on the growth curves of the different root temperature treatments were almost parallel. In contrast to the observation of ABD EL RAHMAN, et al. (1959b) mentioned above, Cooper reported only a slight increase of shoot/root-ratio at the higher root temperatures.

Maximum growth of tomato plants at a root temperature of approximately 25°C was also reported by CHERMNIH (1971) and by CHU and TOOP (1975).

2.2.2. Root temperature after transplanting

Whereas in the nursery vegetative growth is the main concern, generative growth is the most important parameter after transplanting. For that reason other temperature regimes than those for vegetative growth may be optimal.

The earlier literature on this subject has been reviewed in 1957 by FRÖHLIG. He concluded that in general an increase of root temperature to 20–30°C resulted in an earlier and higher yield, except under the poor light conditions of January and February, when temperatures in the root medium of 14–17°C appeared to be optimal. In his own experiments (FRÖHLIG, 1959) he did not find any positive effect of soil heating, neither in the period January – March, nor between March and May.

This lack of a positive effect on yield was confirmed by CALVERT (1956a), PLOEGMAN (1964), BOXALL (1971) and ABDELHAFEEZ, et. al. (1971). VAN DE MUYZENBERG (1957) reported, that an increase to 20°C in soil temperature after transplanting was clearly disadvantageous for plants that had received supplementary light during raising.

2.2.3. After – effect of root temperature during raising

Only a few reports are available on the after – effect of a certain treatment during the early stages of growth. VERKERK (1962), discussing the results of experiments on supplementary light during raising, concluded that the earliness of the yield was strongly determined by plant size at the moment of transplanting. An earlier yield of 5 to 7 days was obtained when plants were three times heavier at the moment of transplanting. CANHAM (1966) compared the effects of different air and root temperatures and of supplementary light during raising on yield, and observed that the increased plant size resulting from additional illumination also lead to an increase in early yield. He also found, however, that plants raised at high air and low root temperatures, although being larger at transplanting, did not yield better than those grown at low air and high root temperatures. The latter treatment is much cheaper than the former. CHERMNIH (1971) did not observe any after-effect of root temperatures in the range of

17–25°C during raising on the yield of tomato.

The relation between plant size, earliness and yield was extensively studied by SPITHOST (1969 and 1975), who reported that there was a good correlation between plant size and early yield. Although the various parameters of plant size (dry weight, plant height, number of leaves, developmental stage of the first inflorescence) were all closely related, the highest correlation with early yield was observed when plant height was chosen as a parameter of plant size. The relationship between plant height and early yield was more evident for early crops than for plantings later in the season.

Early yield is not only determined by plant size, but also by the place and the number of flowers of the first inflorescence. Both place and number are influenced by the temperature during the first weeks after cotyledon expansion (CALVERT, 1957). PHATAK (1966) reported that air temperature during this period determines the number of leaves below the first inflorescence while root temperature during this sensitive period determines the number of flowers. This interaction between vegetative growth (plant size) and generative growth (flower initiation) makes a prediction of the optimal combination of conditions during raising difficult.

2.3. PROCESSES INVOLVED IN THE ROOT TEMPERATURE RESPONSE

Since the review of RICHARDS et. al. (1952) mentioned in Section 2.1., many questions concerning the processes affected by root temperature have been clarified by the extensive research into the mechanism of water and mineral uptake by root systems, carried out by Brouwer and co-workers. Root temperature as a factor in the physiology of roots was first studied with pea. It was concluded that the growth reduction of the shoot at low root temperatures is not primarily caused by a reduction in photosynthesis but by a reduced uptake of water and minerals (BROUWER, 1959, and BROUWER and VAN VLIET, 1960). Between 15 and 20°C potassium uptake appeared to be the limiting factor, below 15°C water uptake was controlling the growth rate of the shoot. Two years later BROUWER (1962) published data of minimum, optimum and maximum root temperatures for a range of crops. Reduced shoot growth was mainly caused by a decrease in leaf growth, which was almost entirely due to a decreased cell-elongation. The rate of leaf initiation, and thus the number of leaves, was only slightly reduced.

Experiments on root temperature were continued with bean plants with special emphasis on anatomical aspects and on plant behaviour after a sudden change in root temperature (BROUWER, 1964, and BROUWER and HOOGLAND, 1964).

The root temperature effect on growth was closely related to the distance between the root tip and the zone where the endodermal cells were completely suberized. At sub- and supra-optimal root temperatures root growth and suberization proceeded at such a rate, that suberization took place close to the

root tip. At optimum temperatures growth was enhanced more than suberization, leading to a larger root surface through which water and minerals could be taken up.

Possible interactions between phytohormones and root temperature were examined as well. Growth reduction by low root temperatures could not be compensated by addition of gibberellic acid, benzyl-adenine or IAA to the nutrient solution (BROUWER and KLEINENDORST, 1967). In a study with radioactive tracers (BROUWER and LEVI, 1969) the translocation of salts from the leaves to the roots appeared to be influenced by the root temperature prior to the application.

In experiments with corn the evidence that water uptake is the most important factor in the control of shoot growth by root temperature, was strongly confirmed (KLEINENDORST and BROUWER, 1970). The reduction of leaf growth almost exactly paralleled the changes in the water balance of the leaves. The same could be concluded from a comparison between the effects of drought and low root temperatures on leaf elongation and photosynthesis of corn (BROUWER, 1974).

Such clear evidence on the primary mechanism of root temperature responses has never been described for the tomato. Water uptake of tomato plants was shown to be reduced by low root temperatures (SHIRAZI, et. al., 1975), and this effect is often forwarded as the primary cause of reduced shoot growth.

The pigmentation of the leaves of tomato plants at low temperatures, which resembles symptoms of phosphorus deficiency has led to the assumption, that a reduced phosphate uptake at low root temperatures is the primary cause of the reduced growth rate. LOCASCIO and WARREN (1960) found, that the beneficial effect of phosphate application on growth of tomatoes was maximal at low root temperatures, but WILCOX, et. al. (1962) did not find such an effect. Such differences may be expected, since the effects of additional nutrients depends strongly on the nutritional status of the plants. LINGLE and DAVIES (1959) and LINGLE (1960) concluded from their experiments with phosphorus and root temperature: 'These data again demonstrate the effect of soil temperature on the growth of tomatoes and the close correlation of this effect with phosphorous concentration in the tissue..... which suggests, that the lack of growth at low temperatures was in part due to restriction of phosphorus uptake by the plants' (LINGLE, 1960).

One year later, however, the same authors (DAVIES and LINGLE, 1961), published the results of experiments from which they concluded, that, although lower root temperatures reduce both the uptake of water and nutrients, none of these factors is primarily responsible for the growth reduction at low root temperatures. They suggest, that possibly the transport in the phloem is hampered at low temperatures, because of the resemblance of the observed symptoms with those of ringing. In this way, hormone transport from shoot to root, or from root to shoot might be reduced and thus cause an inhibition of growth. Also the translocation of assimilates may be restricted, although

WENT (1944b) reported a Q_{10} -value lower than one for sugar translocation in tomato. In many other papers (e.g. BÖHNING, et. al., 1953) this observation is contradicted.

SCHWARTZ (1972) studied the effect of the root crown temperature on growth of roots and shoot of tomato plants. He found, that lowering the temperature of this region during the day increased root growth, whereas raising the root crown temperature increased shoot growth. Continuously cooling to 7°C or heating to 35°C reduced the growth rate of both roots and shoots. This suggests, that translocation is affected.

The suggestion that hormones are involved in the response of plants to root temperature has been made many times (DAVIES and LINGLE, 1961; BROUWER, 1974). Some evidence for this suggestion for tomato is presented by MENHENETT and WAREING (1975), who applied gibberellins and cytokinins to the shoot apex or to leaf discs of tomato plants grown at various root temperatures. Hormone application partly compensated the effect of a low root temperature.

Summarizing one may conclude, that many experiments on the effect of root temperature on plant growth have been reported. Data on tomato are far less available. In general the effect of root temperature on tomato seedlings is more pronounced than that on plants in the generative phase. The physiological mechanisms underlying the root temperature response of tomato plants, however, have not been demonstrated unambiguously.

3. GROWTH AT A CONSTANT ROOT TEMPERATURE UNDER NATURAL GLASSHOUSE CONDITIONS THROUGHOUT THE YEAR

3.1. INTRODUCTION

In the previous chapter (Section 2.2.) the need for data on the relation between root temperature and growth rate of young tomato plants was demonstrated. These data may be obtained either from experiments under controlled conditions in a phytotron or under natural conditions in a glasshouse. Under controlled conditions the results can be reproduced, while a certain factor of interest can be varied, keeping the other ones constant. Extrapolation of the results to a natural environment, however, is often difficult. Moreover, an artificial environment may cause certain undesired side-effects, e.g. when light intensity is relatively low (BEHBOUDIAN, 1977). On the other hand, under natural conditions many factors vary and it is often difficult to reproduce the results in general. Therefore, much more effort must be devoted to data sampling of the environment and to mathematical techniques for the interpretation of the results.

The latter approach was chosen in the present study. Young tomato plants were grown in a greenhouse throughout the whole year at a constant root temperature. Air temperature, relative humidity, incoming radiation and evaporation were continuously measured, while plants were regularly harvested. Growth analysis was applied to the results in order to assess general relationships between environmental variables and plant growth.

3.2. MATERIALS AND METHODS

3.2.1. Cultivation

Seeds of tomato, *Lycopersicon esculentum* Mill., cv. 'Moneymaker' were sown in a box filled with a peaty compost, which was kept in a glasshouse at a temperature of 25°C during germination. Generally some seedlings emerged the fifth day, and the majority the sixth day. To increase uniformity of the plants, all those emerging before or after the sixth day were removed.

During cotyledon expansion the seedlings were selected again and transplanted into 5 litre plastic pots. The pots were filled with a weighed amount of a soil mixture which contained sufficient nutrients to prevent any sign of mineral deficiency, even when plants were grown to a size far beyond that in the experiments. The pF-curve of the soil mixture was determined prior to the experiment and the water content was measured before filling the pots. From the weight of the soil per pot, its water content and the pF-curve, the required amount of water to obtain a pF of approximately 1.5 was calculated and added

to the pots. All the pots were placed in Wisconsintanks at a temperature of $20 \pm 0.5^\circ\text{C}$ for two days. Thereafter root temperatures of 12, 15, 20, 25, 30 and $35 \pm 0.5^\circ\text{C}$ were imposed. At this stage the second leaf was approximately 1 cm. long.

The Wisconsintanks were located in a small, East-West oriented glasshouse. The upper side of the tanks equalled the ground surface. Although air temperature could be controlled by a thermostat, connected to a hot-water-pipe system and a ventilator, the capacity of the system was too small to achieve constant air temperatures. Each Wisconsintank contained 15 plants. Air temperature, radiation and evaporation conditions were rather uniform throughout the whole glasshouse. To assure an equal exposition of each individual plant to its environment, the position of each set of 15 plants was changed twice a week according to a fixed scheme. The soil surface of each pot was covered with a white polystyrene disc of one cm. thick with a 2 cm.-hole in the center for access of the stem, in order to improve its isolation. In this way even at a maximum difference between soil and air temperature (12 and 30°C , respectively) the top layer of the soil deviated less than 1°C from that of the Wisconsintank. The disc also reduced evaporation from the soil considerably.

The pots were weighed at regular intervals. From these data the loss of water and the pF-value were calculated. When the pF increased above 2.0 the amount of water loss was added. Corrections for the increase in plant weight were made, using the data of periodic harvesting. It was assumed, that between pF 1.5 and 2.0 no water stress would occur.

Seven experiments were carried out throughout the whole year. The duration of each experiment varied between 28 and 42 days. Either three or four periodic harvests were made with intervals of 7 to 10 days (Table 3.1).

3.2.2. *Measurements of plant parameters*

Non-destructive measurements of plant length and leaf number were done at weekly intervals. Every 7 to 10 days 4 to 5 plants per treatment were harvested from which fresh weight of leaf blades, petioles and stem of each plant was determined. The area of the leaf blades was measured with an optical planimeter (Technical and Physical Engineering Research Service, Wageningen, 66-2014). Dry weight was obtained after drying the plant material for 3 days in a ventilated oven at 80°C . No data were collected on the root system because of the high organic content of the soil, through which a cleaning of the roots and a reliable weighing was hardly feasible. Since the analysis of 24 to 30 plants during each harvest is rather timeconsuming, special care was taken to prevent undesired systematic errors. The sequence of harvesting the plants was as follows: one plant of each treatment was taken first, within 5 to 10 minutes, then weighed and prepared for determination of leaf area and dry weight. Subsequently a second plant of each treatment was taken, then a third one and so forth. In this way daily trends in plant weight distribution were equally represented in each treatment. Fresh weight was determined in the

glasshouse immediately after cutting, in order to avoid evaporative losses.

During the first experiment, a non-destructive method to estimate leaf area was developed and from the second experiment onwards included in the measurements. This method is based on a correlation between leaf area (A) and leaf length (l). PORTER (1937) established for tomato leaves a relationship $A = a + b.l + c.l^2$, in which a, b and c are constants, depending on environ-

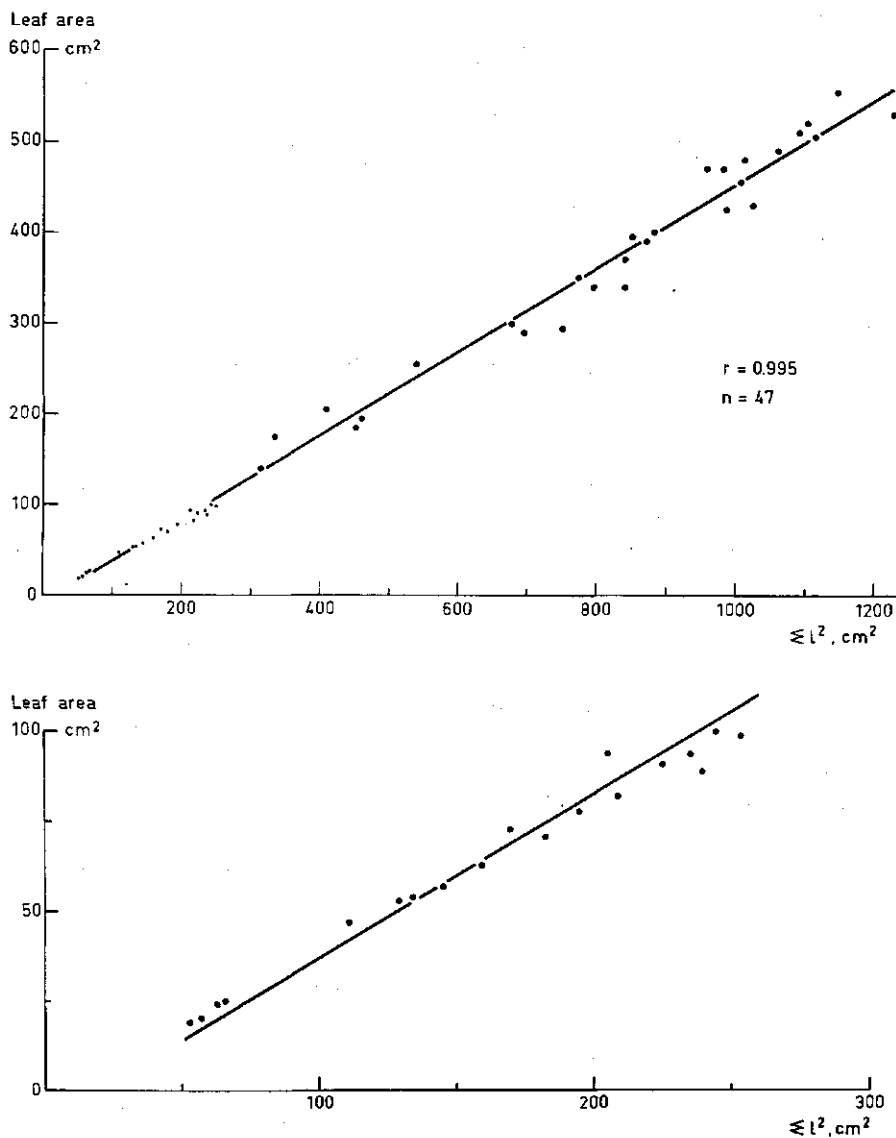


FIG. 3.1. Relation between the sum of the squared leaf lengths (Σl^2) and the leaf area of 47 plants varying in size, grown under equal environmental conditions. (In the lower part data for the smaller plants are enlarged).

mental conditions. LYON (1948) used another relationship: $A = a.l^2$ for single leaves, and COOPER (1959) represented the total leaf area of a plant by $A = a. \Sigma l^2$. The latter linear relationship between leaf area and the integrated squares of the length of individual leaves was applied to the data from 47 plants of various sizes from a preliminary experiment (Figure 3.1). The linear relationship is valid over a wide range in plant size, but does not exactly pass through the origin.

In order to obtain estimates of daily increases in leaf area, the length of all the leaves of two plants of the 12, 25 and 35°C treatments were measured at 9.00 A.M. each day. The leaf area of these plants was then obtained by using the ratio between A and Σl^2 . Since this ratio appeared to depend on environmental conditions, its value was determined at each harvest of all the experiments (I till VII), from measurements of the length of all the leaves of the harvested plants and their leaf area.

3.2.3. *Measurements of environmental parameters*

Air temperature and relative humidity in the glasshouse were recorded with a thermohygrograph. This instrument was calibrated at regular intervals against an Assman psychrometer. Mean values were obtained from the track by taking hourly readings, which were averaged.

Daily integrals of short wave radiation inside the glasshouse were obtained from an integrating light meter which was calibrated for direct and diffuse sunlight against a KIPP-solarimeter. Although the sensitivity of the instrument was slightly different for direct and diffuse light, only one average conversion factor was used. Radiation values reported in this paper thus represent the total shortwave radiation inside the glasshouse.

The evaporation in the glasshouse was measured with a Piche-evaporimeter. This simple instrument consists of a disc of Whatman filter which is pressed against the bottom-end of a glass tube filled with distilled water. In this way the disc remains saturated with water and the waterloss from the calibrated tube is a measure of potential evaporation. A detailed analysis of its performance was presented by DE VRIES and VENEMA (1954), who concluded, that the instrument simulates fairly well the waterloss of a single leaf exposed to the air, but for a crop canopy the effect of wind is overestimated and that of radiation underestimated.

3.3. RESULTS AND DISCUSSION

3.3.1. *Environmental factors*

Averages of air temperature (day, night and 24 h.-mean), radiation and evaporation for each period of the experiment are summarized in Table 3.1. Day temperature ranged from 18–20°C in winter to 25–30°C in summer: night temperature from 15–17°C in winter to 17–20°C in summer. Daily values of total short-wave radiation were about 80 Joule $\text{cm}^{-2} \text{d}^{-1}$ in winter

TABLE 3.1. Average air temperature, radiation and Piche-evaporation in the glasshouse during each experimental period.

Exp.	Period	Air temperature			Radiation	Evaporation
		day °C	night °C	24 hrs °C	J cm ⁻² d ⁻¹	mg cm ⁻² d ⁻¹
I	1. Sept. 24 – Oct. 12	23.3	18.2	20.8	361	668
	2. Oct. 12 – Oct. 22	21.5	17.3	19.4	260	482
	3. Oct. 22 – Nov. 2	20.6	17.4	19.0	147	350
II	1. Nov. 16 – Nov. 26	19.9	16.3	18.1	130	416
	2. Nov. 26 – Dec. 7	19.0	16.6	17.8	88	346
	3. Dec. 7 – Dec. 17	18.2	15.5	16.9	80	322
	4. Dec. 17 – Dec. 28	17.7	16.3	17.0	84	366
III	1. Jan. 14 – Jan. 25	17.8	16.1	17.0	76	388
	2. Jan. 25 – Febr. 4	19.0	15.9	17.5	101	362
	3. Febr. 4 – Febr. 15	19.9	17.5	18.7	147	365
	4. Febr. 15 – Febr. 22	19.5	16.7	18.1	172	393
IV	1. March 1 – March 11	20.5	16.4	18.5	374	533
	2. March 11 – March 18	22.0	17.0	19.5	411	558
	3. March 18 – March 25	21.1	18.4	19.8	273	522
	4. March 25 – April 1	27.5	18.4	23.0	471	528
V	1. April 8 – April 15	23.7	17.2	20.5	583	725
	2. April 15 – April 22	25.5	19.0	22.3	524	732
	3. April 22 – April 29	23.9	17.8	20.9	517	628
	4. April 29 – May 6	27.5	18.4	22.9	836	949
VI	1. May 28 – June 4	30.4	19.7	25.1	790	910
	2. June 4 – June 10	27.8	18.4	23.1	625	697
	3. June 10 – June 17	23.3	17.4	20.4	449	501
	4. June 17 – June 25	24.6	18.6	21.6	618	618
VII	1. Aug. 5 – Aug. 12	24.6	18.8	21.7	398	495
	2. Aug. 12 – Aug. 19	25.2	18.9	22.1	457	534
	3. Aug. 19 – Aug. 27	26.7	19.6	23.2	483	586
	4. Aug. 27 – Sept. 1	23.4	18.4	20.9	327	456

and 400–800 J cm⁻² d⁻¹ in summer. Evaporation ranged from 300–400 mg cm⁻² d⁻¹ in winter (3–4 mm d⁻¹) to 600–900 mg cm⁻² d⁻¹ (6–9 mm d⁻¹) in summer.

The values of daily radiation measured inside the glasshouse were compared with those from a nearby meteorological station (Department of Physics and Meteorology of the Agricultural University at Wageningen), at a distance of about 1 km. In general, there was a good agreement between both sets of data, but the structure of the glasshouse itself and the shading by the glasshouse to the South of the experimental one caused some variation, especially on sunny days. From these data the transmission coefficient of the glasshouse was calculated, which appeared to be 46% during autumn, winter and early spring (exp. I to IV) and 36% during summer (exp. V to VII). The low transmission

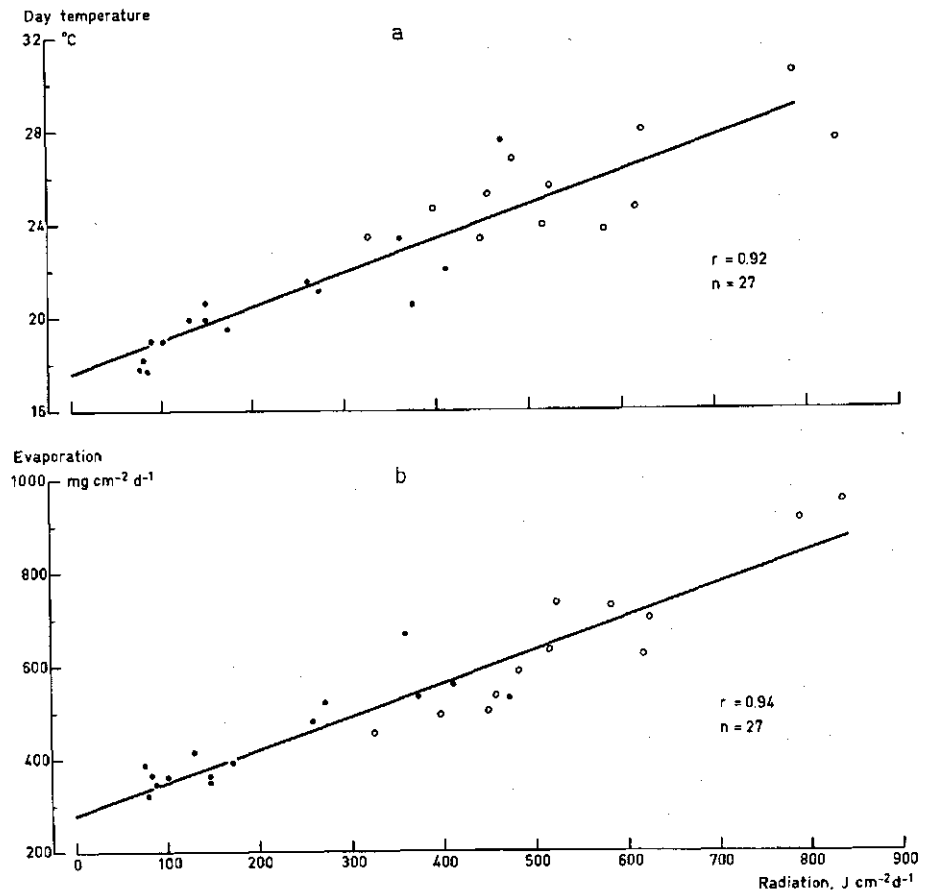


FIG. 3.2. Relation between day temperature (a), evaporation (b) and short wave radiation inside the experimental glasshouse.
 ● glasshouse not white-washed
 ○ glasshouse white-washed

during winter was, at least partly, due to the large angle of incidence of the light in this season, which caused a high reflectance. The shading from the nearby glasshouse was also noticeable during this period. In summer the glass had to be whitewashed to reduce excessive radiative heating, thus yielding the low transmission coefficient.

Both day temperature and evaporation were correlated with radiation inside the glasshouse (Figure 3.2). The relationships were not affected by white-washing the glasshouse (generally with radiation values above $400 \text{ J cm}^{-2} \text{ d}^{-1}$). Because of this correlation it is difficult to separate the specific effect of each of these climatic factors on plant growth.

3.3.2. Growth and development

3.3.2.1. General

Plant growth and development were favourable in all experiments at all root temperature treatments. Plant shape and structure were much more influenced by the annual variation of the environment than by root temperature. This is illustrated in Figure 3.3., where the typical winter-grown plants (upper) are compared with the more compact early-spring (middle) and the vigorous mid-summer plants (lower). The plants grown at the lowest and the highest root temperatures were fully normal in appearance, although their size was smaller than at the optimal temperatures of 20 and 25°C.

Leaf colour was affected both by season and by root temperature. Plants grown in summer were dark green, those in winter light green. The plants from the low root temperature treatments (12 and 15°C) were dark green and the first two to five leaves often showed pink to brown stained areas which usually disappeared when the leaves grew older. Sometimes, however, these areas changed into chlorotic spots in which later on leaf senescence started. In general, this senescence did not occur before the plants were twelve to fifteen leaves large. A root temperature of 35°C caused relatively dark leaves only during the summer months.

Stems and petioles, especially the lower part, were purplish at low root temperatures (12 and 15°C). Sometimes adventitious roots emerged from the basal stem part, which never reached a length of more than one or two millimeter.

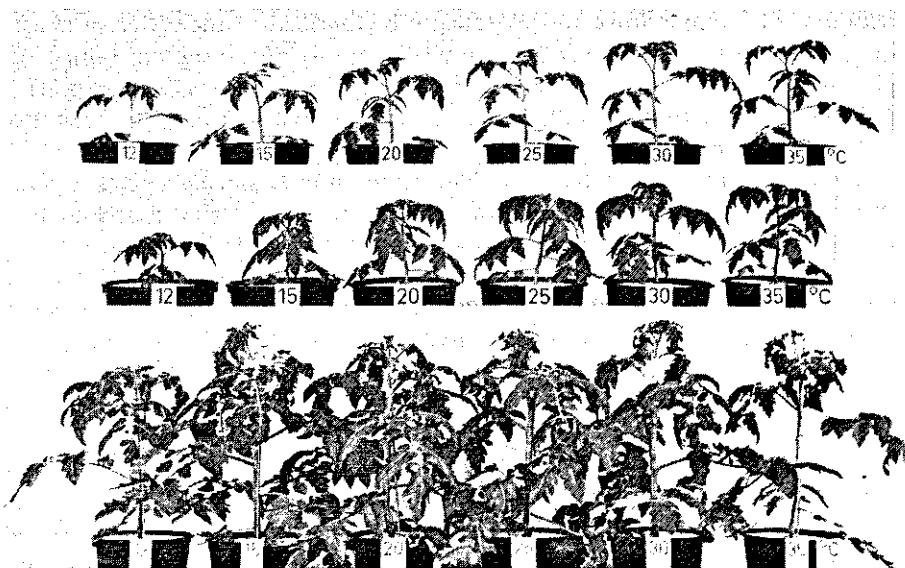


FIG. 3.3. Tomato plants after a treatment of four weeks at different root temperatures in winter (upper row), spring (middle row) and summer (lower row).

During summer the plants occasionally showed symptoms of wilting in the early afternoon. It occurred on sunny days, after a period of dull weather irrespective of the soil moisture condition. Apparently the plants were unable to adapt themselves to large changes in daily evaporation. The first symptoms were always observed at a root temperature of 35°C, which is probably caused by the enhanced suberization of the roots at this temperature (BROUWER, 1964).

3.3.2.2. Plant height

In Figure 3.4. plant height, between the cotyledons and the stem tip, was plotted against time for each treatment and each experiment. These curves show, that in general a period exists with increasing elongation rates, followed by a period with a more or less constant elongation rate. The period of increasing elongation rate is much longer at lower root temperatures. It depends also on the season. The critical plant height above which a constant growth rate is achieved, therefore, varies to a great extent. At 12°C *e.g.* it is about 20 cm in summer (exp. VI and VII). At 15°C it is 10 to 15 cm in summer and about 20 cm in spring and autumn (exp. I and IV). At root temperatures of 20 up to 35°C this critical value of plant height is as low as 10 cm in all seasons, except in winter, when the constant growth rate of 2 to 2.5 cm d⁻² was not reached in any of the treatments (exp. II and III).

In Table 3.2 the ratio between plant height at 25°C and that at 12°C root temperature, at a plant age of 25 days is represented for various seasons. The growth reducing effect of a low root temperature was large in autumn and spring, smaller in winter and quite small in summer. This apparent interaction between root temperature and season can be ascribed to the different stages of growth of the plants: in summer the growth rate of the stem at both temperatures had been linear for a long time already, in winter it was still exponential, whereas in autumn and spring the growth rate at 25°C was linear and that at 12°C still exponential.

The constant rate of increase in plant height after achieving a certain plant size, has often been used as a growth parameter in experiments to analyse growth rates at different conditions. Went (1944a) reported constant rates of 28 mm d⁻¹ under optimal conditions for plants larger than 30 cm. This value is close to that found in the present experiments (2.5 cm d⁻¹). In the same paper WENT (1944a) concluded from measurements of plant height, that root temperature did not affect the growth rate of tomato plants once they were larger than 30 cm, provided other conditions were optimal. The same conclusion may be drawn from our experiments.

3.3.2.3. Leaf number

The rate at which new leaves appear depends on the number of developing internodes. Flower primordia in tomato can only be initiated after a certain number of leaves or internodes has been produced by the apical meristem, and this fact is of importance for the earliness of flowering and fruiting.

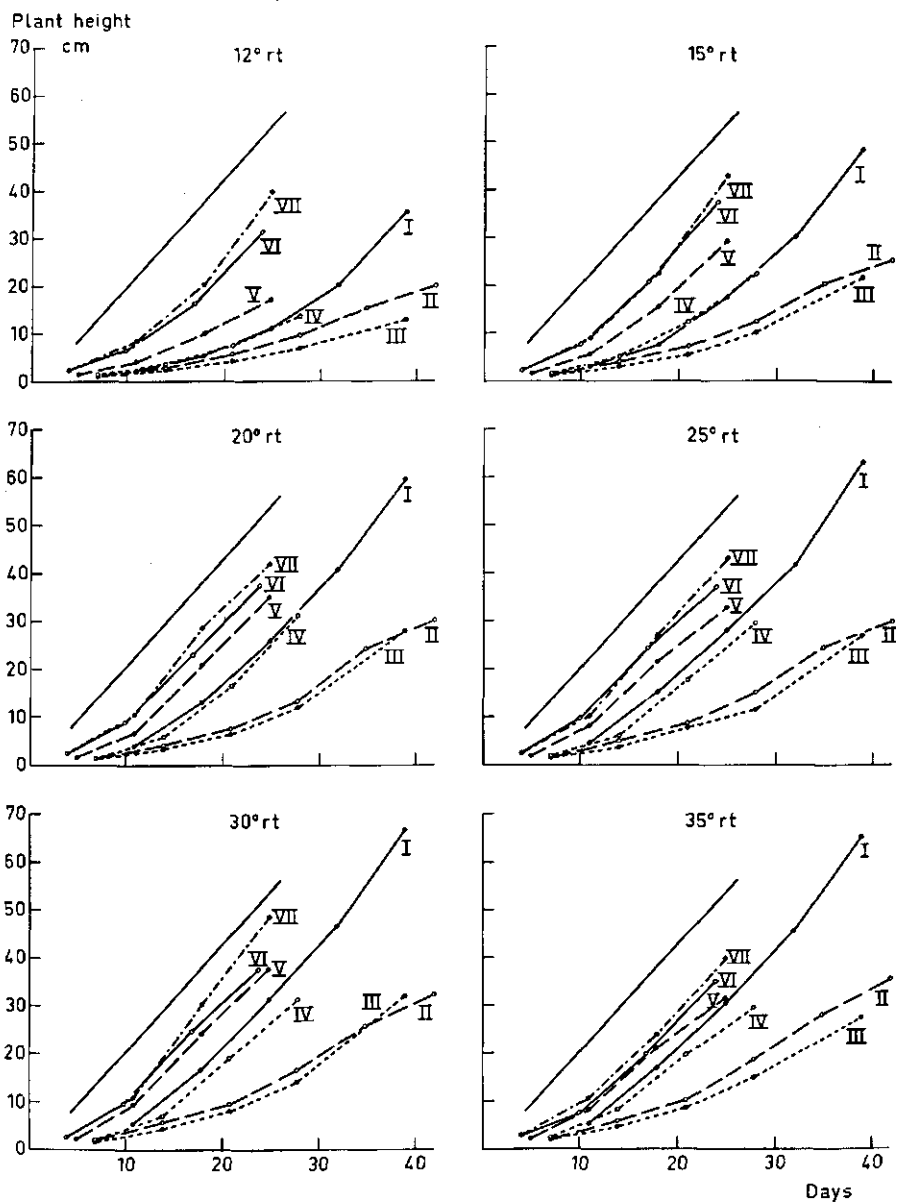


FIG. 3.4. Plant height vs. time in days after transplanting at various root temperatures (rt) during various seasons (I to VII, see Table 3.1).

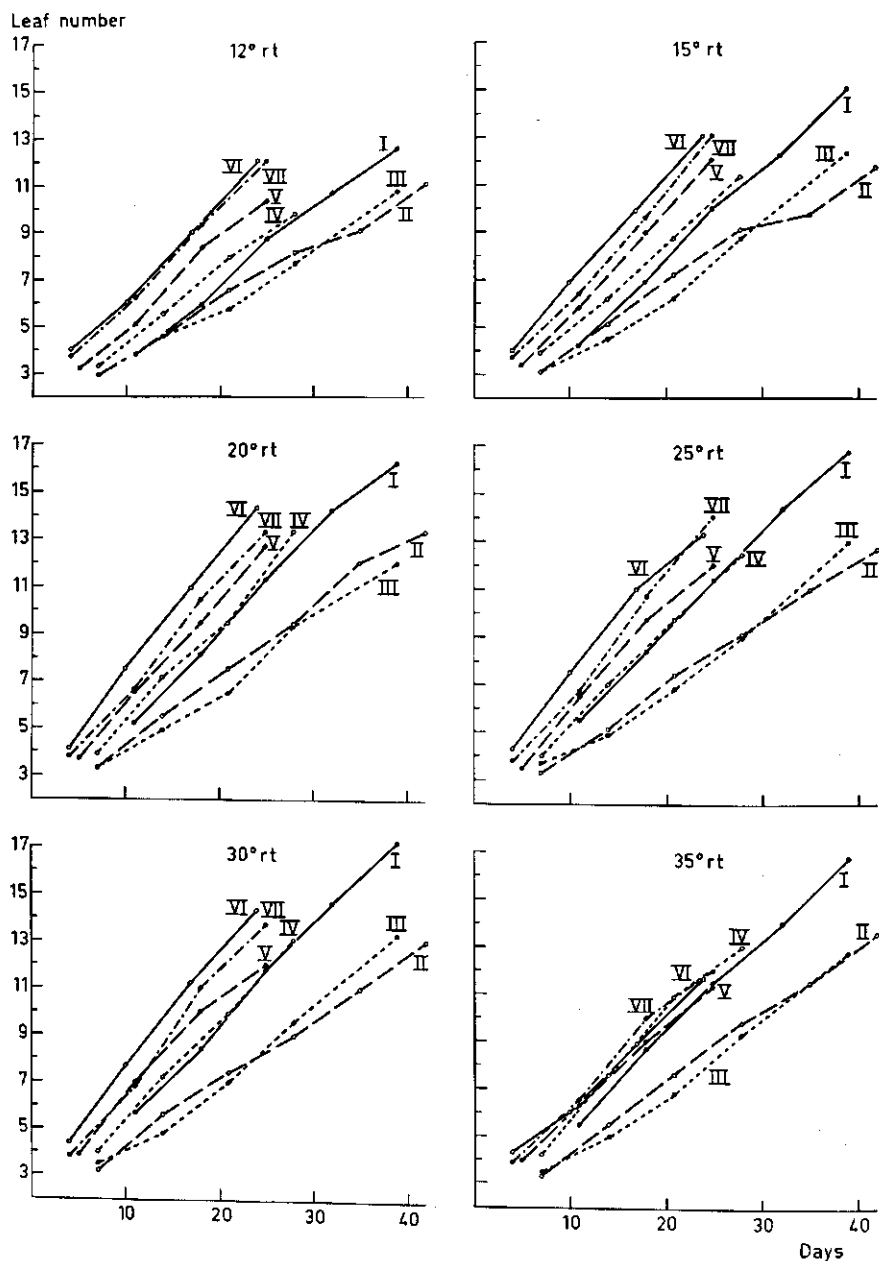


FIG. 3.5. Number of leaves larger than 1 cm. vs. time in days after transplanting at various root temperatures (rt) during various seasons (I to VII, see Table 3.1).

In Figure 3.5 leaf number is plotted versus time. The rate of leaf appearance was rather independent of plant age. It was affected by root temperature and by season. At 12°C it ranged from about 0.25 leaves per day in winter to 0.40 d⁻¹ in summer. At 25°C these figures were approximately 0.30 to 0.55 d⁻¹, and at 35°C from 0.30 to 0.45 d⁻¹, respectively. The rate at which new leaves appeared was thus somewhat reduced by low root temperatures in all seasons; at 35°C this rate was reduced only in summer.

BEAUCHAMP and LATHWELL (1967) reported a large effect of root temperature on the rate of leaf initiation in young corn. The position of the apical meristem in young corn plants, however, is quite different from that in young tomato plants.

The seasonal effect on leaf number is much smaller as compared with plant height. At a root temperature of 25°C, 25 days after transplanting *e.g.*, plant height was 42.5 cm in exp. VII (summer) versus 9 cm in exp. III (winter), while leaf number was only 14.0 versus 8.3 (Table 3.2). No apparent interaction between season and root temperature was observed with leaf number as was the case with plant height, since leaf number increases linearly with time.

HUSSEY (1963) studied the effect of air temperature and light intensity on leaf initiation of tomato in great detail. He found a steady rate of leaf formation at constant environmental conditions, which was higher at higher temperatures and higher light intensities. As already mentioned in Section 2.3, the site of the first inflorescence and its number of flowers may be influenced by air and root temperature. In the present experiment, however, the stage of flowering was only reached in summer, which prevented a complete counting of the number of flowers in the first truss. The number of leaves below the first inflorescence was counted in each run and varied from 9 to 11 in run III (early spring) to 7 to 9 in the other runs. Root temperature effects, if any, were small and inconsistent. Therefore, no further data on this aspect of growth will be presented.

TABLE 3.2. Plant height, leaf number and fresh weight, 25 days after transplanting at 25 and 12°C root temperature and the ratio between 25 and 12°C, in different months.

Exp.	Month	Plant height (cm)			Leaf number			Fresh weight (g)		
		25°C	12°C	ratio 25/12	25°C	12°C	ratio 25/12	25°C	12°C	ratio 25/12
I	October	28	11	2.5	11.4	8.7	1.3	65	13	5.0
II	December	12.5	7.5	1.7	8.3	7.4	1.1	8.5	4.6	1.8
III	February	9	5.5	1.6	8.3	6.8	1.2	8.6	1.8	4.8
IV	March	25	10.5	2.4	11.4	8.8	1.3	56	10	5.6
V	April	33	17.5	1.9	12.0	10.3	1.2	120	26	4.6
VI	June	39	32.5	1.2	13.5	12.4	1.1	168	80	2.1
VII	August	42.5	39.5	1.1	14.0	12.0	1.2	137	74	1.9

3.3.2.4. Fresh weight

Fresh weight of a plant is another parameter of plant size, in addition to plant height and number of leaves. While plant height is a one-dimensional representation of its size, the fresh weight quantifies its volume. It should be noted once more, that in the following total fresh weight of the plants stands for the fresh weight of the part above the cotyledons, since the weight of the root system could not be determined.

Fresh weight of the plants is plotted against time for each treatment and each experiment in Figure 3.6. The data were grouped in another way than in Figure 3.4 and 3.5. In Figure 3.4 the seasonal differences between the curves were the most interesting aspect and for that reason the curves from all 7 experiments were combined in one figure for each root temperature. Because of the relation between leaf number and plant height the same combinations were

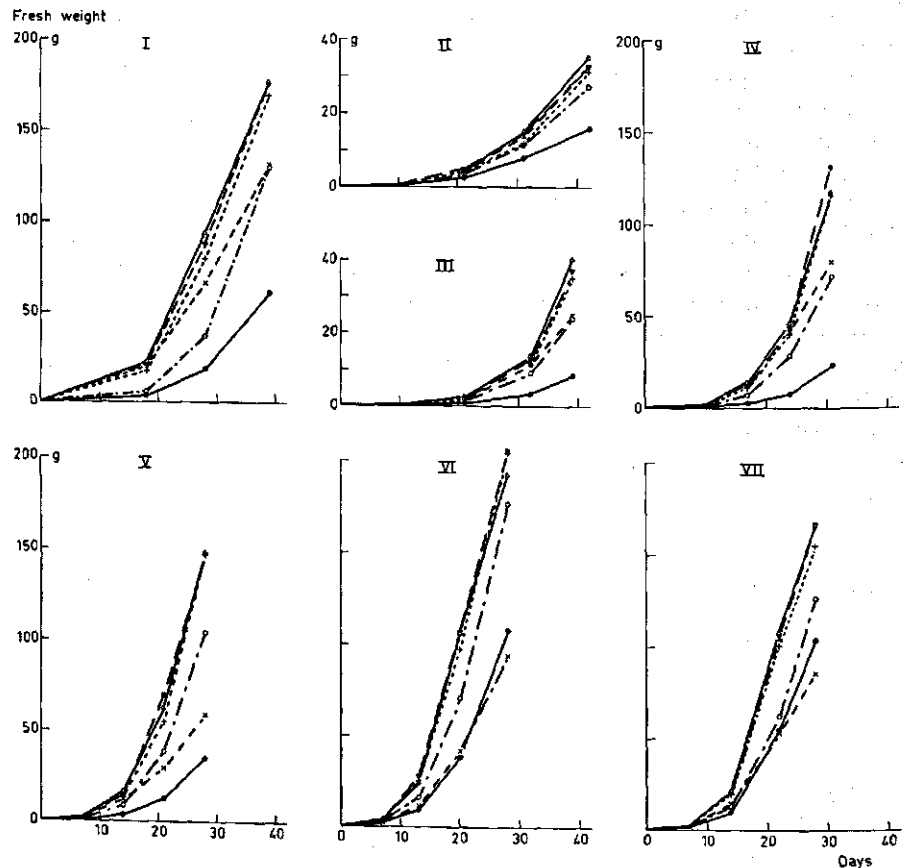


FIG. 3.6. Fresh weight of the plants vs. time in days after transplanting at different root temperatures during various seasons (I to VII, see Table 3.1). Note different scale for experiment II and III.

(● 12°C; ○ 15°C; + 20°C; ▼ 25°C; △ 30°C; × 35°C root temperature).

chosen for Figure 3.5. The very large seasonal differences in fresh weight, however, prevented a clear representation in the same way. Therefore, the data from each root temperature were combined in one figure for each experiment.

Root temperatures of 20 to 30°C yielded the largest plants in all seasons, while fresh weight at 15 and 12°C lags behind progressively. At 35°C there was a marked effect of season on fresh weight. In midwinter it was the same as that at 25°C (exp. II). In all other seasons it was equal to that at 25°C during the first weeks only. Later on growth declined gradually so that the final fresh weight was approximately the same as that at 15°C in autumn and spring (exp. I, III and IV), and close to that at 12°C (exp. V) or even lower in midsummer (exp. VI and VII).

Fresh weight of the plants, 25 days after transplanting (Table 3.2) depends largely on the season, being about 20 times higher in summer than in winter. The relative growth retarding effect of low root temperatures was expressed as the ratio of fresh weight at 25 to that at 12°C. This effect was large in autumn and spring, and small in mid-winter and mid-summer. The same was observed with plant height. It was previously discussed, that this apparent interaction with season was attributable to the different stages of growth in different seasons. For proper comparison, therefore, plants at the same stage of development should be used instead of plants at the same age. This equal stage, however, is reached at a different time, which means a different history of environmental factors in the varying conditions of a glasshouse. Therefore growth analysis is needed to assess the proper relationship between effects of root temperature and those of other environmental variables. Dry weight and leaf area are the important growth parameters in that analysis.

3.3.3. *Growth correlations*

3.3.3.1. *Introduction*

Plant growth can be expressed by a number of parameters, some of which, such as plant height, leaf number and fresh weight, have been discussed already in the previous sections. In these sections it has been shown that the effect of root temperature on various growth parameters was almost the same in the range between 20 and 30°C, and that at 15°C intermediate between 12 and 20°C. In the subsequent sections, therefore, comparison of growth correlations will be made only between low (12°C), optimal (25°C) and high (35°C) root temperatures.

3.3.3.2. *Fresh weight related to plant height*

The relation between fresh weight and plant height is important because the measurement of the latter is a non-destructive one. It can be used as an estimate for fresh weight at any moment, provided a firm relationship can be established. The ratio between weight and height also is a parameter of the shape of the plant, which may be either tall and tiny or firm and compact.

The relation between fresh weight and plant height depends on the season as

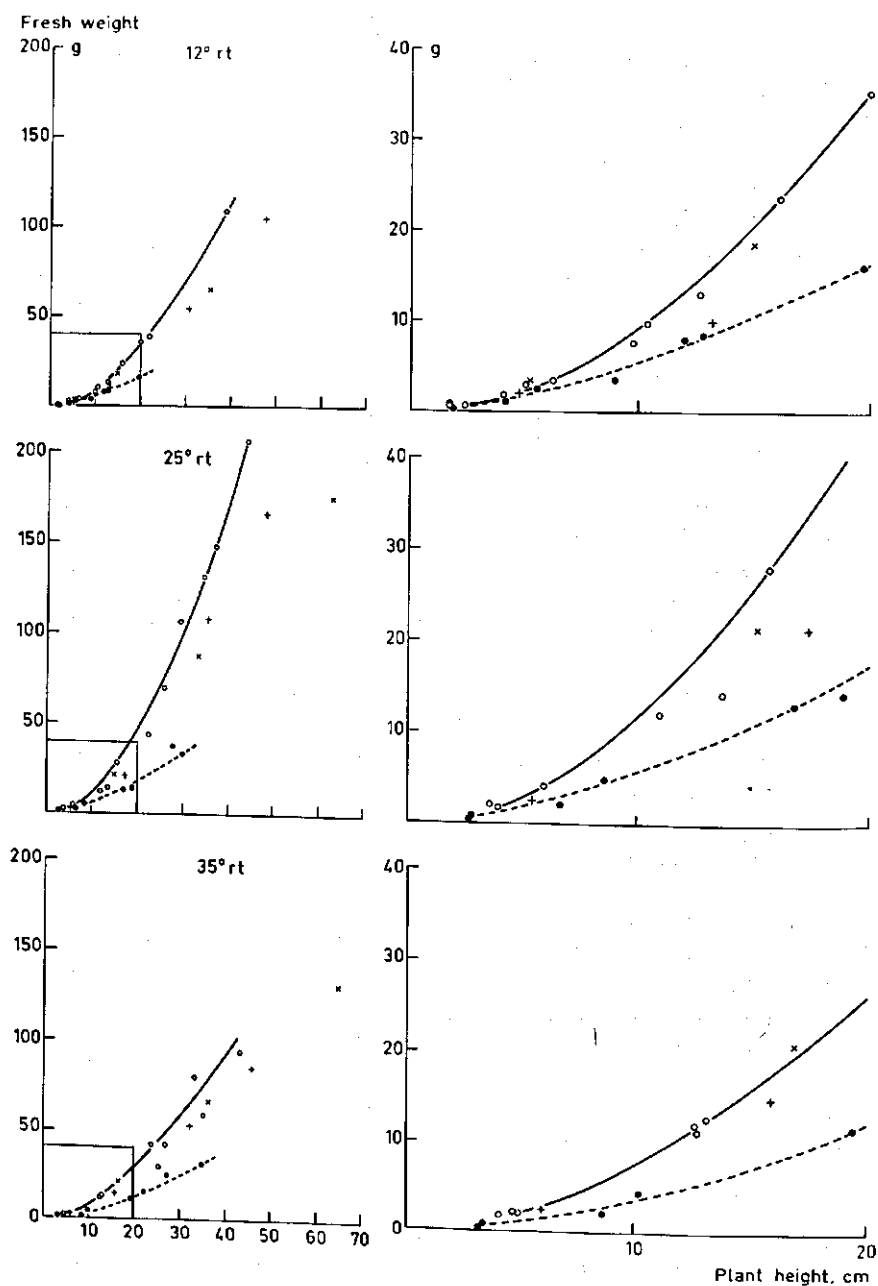


FIG. 3.7. Relation between fresh weight and plant height at 12°C, 25°C and 35°C root temperature (rt). The smaller values are enlarged on the right hand-side of the figure. (× exp. I; ● exp. II and III; ○ exp. IV, V and VI; + exp. VII, see Table 3.1).

TABLE 3.3. Coefficient (a) and exponent (b) in the equation $W_f = a \times H^b$, relating fresh weight (W_f) to plant height (H), for the curves in Figure 3.7.

Experiment Season		Root temperature (°C)	a	b	n	r
II, III	winter	12	0.134	1.60	8	0.984
		25	0.099	1.73	8	0.994
		35	0.071	1.73	8	0.992
IV, V, VI	summer	12	0.195	1.69	12	0.989
		25	0.126	1.94	12	0.995
		35	0.149	1.72	12	0.995

is shown in Figure 3.7. At a certain height, plant weight is low during winter (exp. II and III), high during early summer (exp. IV, V and VI) and intermediate in late summer and autumn (exp. VII and I).

The data for winter and summer were fitted separately to the equation $W_f = a \times H^b$ for each root temperature. The curves obtained in this way were drawn in Figure 3.7 and the constants a and b were listed in Table 3.3.

There appears to be a close relationship between fresh weight and plant height (high values of r), so the latter can be used for a non-destructive estimation of fresh weight. It should be kept in mind, however, that the constants a and b depend on the prevailing environmental conditions.

The coefficient a in the above-mentioned equation decreases with increasing root temperatures in winter but has a minimum at 25°C in summer. The exponent b is somewhat reduced by a low root temperature in winter and clearly reduced by sub- and supraoptimal root temperatures in summer. This means, that plants at low root temperatures are more compact than at optimal root temperatures during the first stages of growth, but gradually become more tiny. At high root temperatures plants are less compact than at optimal ones from the beginning onwards.

3.3.3.3. Dry weight related to fresh weight

The relation between dry and fresh weight of plants is usually expressed by the dry matter percentage, i.e. dry weight as a percentage of fresh weight. Although it is one of the most frequently determined ratios in the study of plant growth and development, the interpretation of this percentage is often difficult. Its numerical value depends on the water and the dry matter balance. The dry matter percentages of stems, petioles and leaf blades are listed in Table 3.4 for all experiments.

In general the dry matter percentages of stems and petioles were almost the same and that of the leaf blades twice as much. In winter stems and petioles ranged between 3 and 5%, and leaf blades between 8 and 12%. In summer these values were 4 to 10% and 10 to 20%, respectively. At an optimal root temperature, dry matter content was always lower than that at lower or higher temperatures and the differences were larger in summer than in winter.

TABLE 3.4. Dry matter percentage of stems, petioles and leaves of tomato plants at various root temperatures and harvesting dates (*: petioles included in stems)

Exp.	date	days after transpl.	Dry matter percentage of								
			stem			petiole			leaf		
			°C root temp.			°C root temp.			°C root temp.		
			12	25	35	12	25	35	12	25	35
I	Oct. 12	18	5.6	4.1	4.1	5.8	4.3	4.4	14.0	10.5	11.2
	Oct. 22	28	5.1	4.7	5.9	5.2	4.6	5.3	11.4	9.7	11.3
	Nov. 2	39	4.5	6.0	7.2	4.2	5.1	6.1	9.2	9.2	10.5
II	Nov. 26	10	6.5	4.5	4.3	5.7	4.4	4.7	11.4	9.7	10.2
	Dec. 7	21	4.1	3.6	3.6	4.2	3.7	3.8	9.6	8.6	8.8
	Dec. 17	31	4.1	3.3	3.6	4.1	3.5	3.8	9.9	8.8	9.4
	Dec. 28	42	4.5	3.7	4.1	4.3	3.8	4.2	9.5	8.8	9.5
III	Jan. 25	11*	4.5	5.0	4.7	—	—	—	9.2	8.0	8.4
	Febr. 4	21*	5.3	3.9	4.2	—	—	—	11.0	9.1	9.7
	Febr. 15	32	5.8	4.0	4.0	6.1	4.4	4.7	13.2	9.8	10.7
	Febr. 22	39	6.3	4.4	5.4	6.7	4.8	5.6	14.8	11.7	14.5
IV	Mar. 11	10*	7.3	4.8	5.4	—	—	—	13.3	10.7	11.6
	Mar. 18	17	7.0	4.3	5.2	7.2	4.8	5.5	15.4	10.9	12.2
	Mar. 25	24	6.4	4.4	5.1	6.6	4.5	5.2	13.8	10.2	12.1
	Apr. 1	31	7.4	5.6	8.0	7.1	5.5	7.4	14.8	10.7	14.5
V	Apr. 15	7*	7.0	4.9	5.1	—	—	—	14.9	10.8	12.6
	Apr. 22	14	5.7	4.2	5.3	6.4	4.7	5.9	14.0	10.6	13.4
	Apr. 29	21	7.5	5.8	8.3	7.6	6.1	8.1	17.7	13.3	17.1
	May 6	28	9.2	8.6	12.8	9.0	8.1	10.9	18.2	14.8	20.1
VI	June 4	7*	6.1	5.3	7.2	—	—	—	17.5	12.2	16.7
	June 10	13	5.6	4.8	5.3	6.3	5.3	5.9	13.6	11.0	12.8
	June 17	20	5.7	5.6	6.4	5.7	5.5	6.3	12.5	10.9	13.5
	June 25	28	7.7	9.4	9.4	7.4	8.4	8.6	15.4	14.9	16.1
VII	Aug. 12	7*	5.2	4.8	5.2	—	—	—	11.5	10.2	11.5
	Aug. 19	14	5.6	4.5	5.8	6.0	5.1	6.2	13.6	11.9	14.7
	Aug. 27	22	5.9	5.2	6.9	5.7	5.1	6.3	12.3	10.5	13.1
	Sept. 1	28	6.7	8.2	8.7	6.3	7.3	7.6	13.2	13.5	14.5
Average			6.04	5.19	6.16	6.08	5.19	6.02	13.1	10.8	12.6

Superimposed on these general trends diurnal variations in dry matter percentage occurred, which depend on short term fluctuations in the dry matter and water balance of the plants. As noted already in Section 3.2.2, fresh weights were determined in the glasshouse immediately after cutting (within one or two minutes), so that errors in the measurement of this parameter were negligible. As an illustration of the magnitude of these short term changes in dry matter content, some values of this parameter are shown in Table 3.5. During the first harvest of the experiment three plants per treatment were harvested in the morning and two in the afternoon. The increase in dry matter content is

TABLE 3.5. Dry matter percentage of leaves at various root temperatures in the morning and in the afternoon of the same day (October 12th).

Plants	time	Root temperature						Mean
		10	15	20	25	30	35°C	
6-8	10.00-10.45	13.5±0.6	11.9±0.2	10.2±0.1	10.0±0.1	10.0±0.1	10.5±0.1	11.0
9-10	14.30-15.00	14.7±0.3	14.0±0.3	11.8±0.1	11.1±0.1	11.4±0.2	12.3±0.1	12.6
Mean		14.1	13.0	11.0	10.6	10.7	11.4	

obvious at all root temperatures, which is a result of the progress of photosynthesis and the increasing water deficit of the plant during the day. Since the weather conditions were rather constant during this specific day, the pattern was quite regular. Larger differences were observed in summer, when sometimes periods of bright sunshine were alternated by heavy clouds or showers.

Remarkable high values of the dry matter content of all plant parts were recorded at the final harvest of exp. III, V, VI and VII (Table 3.4), and to a less extent at the last harvest of exp. IV and the third harvest of exp. V. The plants were large on these days and the weather was rather clear and sunny. The evaporative demand of these plants should be high and the root system of the plants was probably restricted by pot size. The high values of the dry matter percentage suggest, that in this case the plants were close to lack of water. No visible signs of wilting occurred on these days, however, except at the final harvest of the fifth experiment, immediately after an extremely warm and sunny weekend, when water supply was not adequate.

Summarizing, the relation between fresh and dry weight was found to be clearly affected by season, but also by root temperature. Large short-term fluctuations may occur, however, so that this relationship can not be generalized.

3.3.3.4. Dry weight of leaves related to total plant dry weight

Since no data on root weight could be collected, the total dry weight consists of the weight of stem, petioles and leaf blades. The function of leaf blades is important, because they determine the potential growth rate of the plant on account of their photosynthesis. Therefore, the relation between dry weight of the leaf blades and total dry weight will be considered here.

Plant dry weight, between 0.02 grams and 20 grams, demonstrated a linear relationship with dry weight of the leaf blades, when plotted on a double logarithmic scale, as is shown in Figure 3.8 for the data of the 25°C treatment.

The regression equation calculated from the 81 observations at 12, 25 and 35°C was:

$$\log L = 0.9285 \log W - 0.1710 \quad (r = 0.998) \quad (\text{Figure 3.8})$$

in which L is leaf dry weight and W is plant dry weight.

In a further analysis each value of leaf dry weight was expressed as a percentage of the value it should have according to the regression equation. The

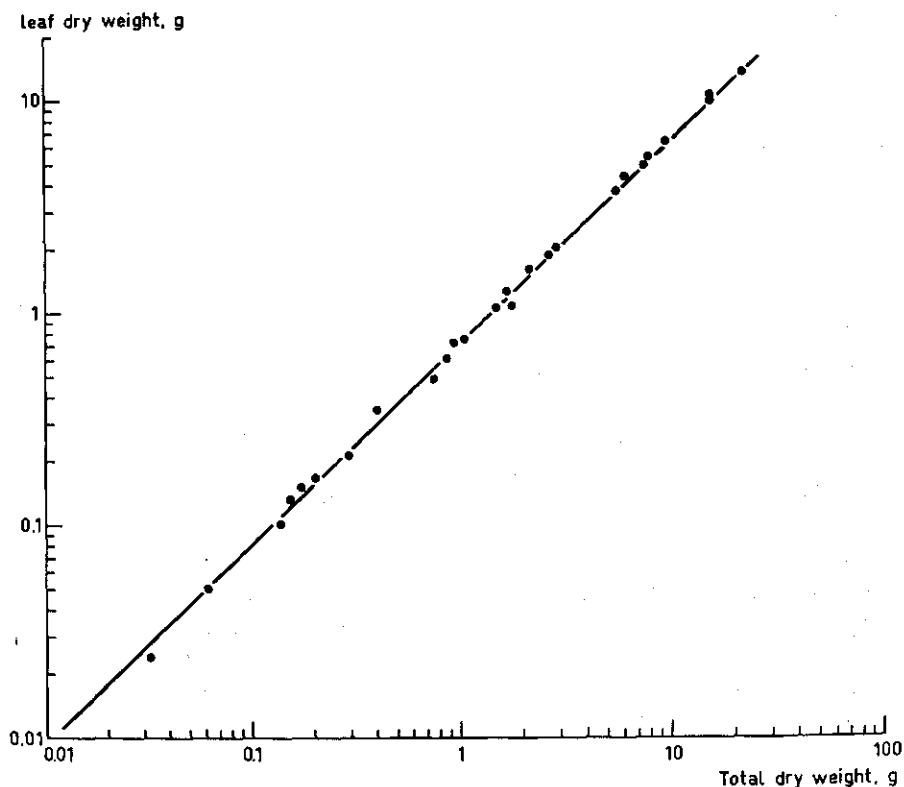


FIG. 3.8. Relation between leaf dry weight and plant dry weight (roots excluded). The straight line was calculated from all data at 12,25 and 35°C root temperature. The dots only represent the data at 25°C root temperature throughout the year.

standard deviation of these percentages was 7.8% only; the highest value was 115.7% and the lowest one 82.3%. The regression equation thus appears to give a fairly good description of the relation between leaf dry weight and total plant dry weight. The ratio between leaf dry weight and total plant dry weight (Leaf Weight Ratio or LWR) can be obtained from the regression equation :

$$\begin{aligned} \text{LWR} &= 10^{-0.1710} \times W^{(0.9285-1)} \\ \text{or } \text{LWR} &= 0.675 \times W^{-0.0715} \end{aligned} \quad (3.1)$$

which relationship is at least valid for plants between 0.02 and 20 grams dry weight. LWR thus decreases with increasing plant size, which can be considered as an ontogenetic drift. In order to assess, whether there was an effect of season or root temperature superimposed on this ontogenetic drift of Leaf Weight Ratio, the observed LWR values expressed as a percentage of those calculated according to equation 3.1 were plotted for each root temperature and each harvest separately in Figure 3.9a.

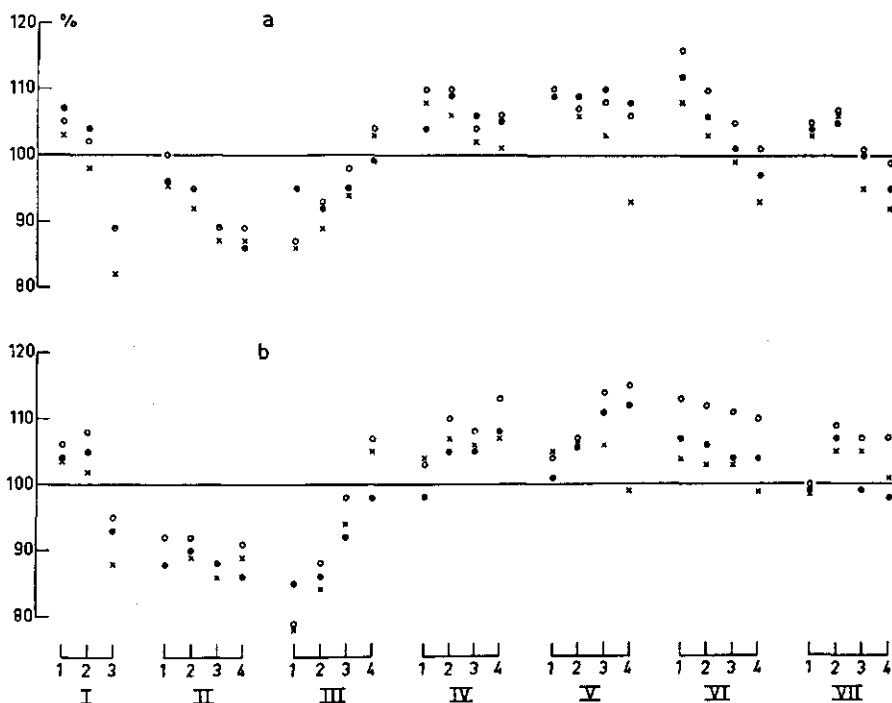


FIG. 3.9. The measured Leaf Weight Ratio at each harvesting date, expressed as a percentage of the calculated LWR according to Eq. 3.1 (a) or to Eq. 3.2 (b).
(● 12°C; ○ 25°C; × 35°C root temperature)

A small, but rather consistent root temperature effect seems to occur, but this effect was hardly significant.

Figure 3.9a also shows a seasonal fluctuation of LWR. During the winter period (between harvest I-3 on the 2nd of November and harvest III-2 on the 25th of January) it is 10 to 25% lower than that in summer.

A further analysis of Figure 3.9a shows, that in exp. I, II, VI and VII LWR decreased with age, which suggests that the ontogenetic drift of LWR was larger than that accounted for by equation 3.1. The slope of the regression line in Figure 3.8 may have been biased by the fact, that the relatively low values of LWR during winter were obtained with small plants only, whereas the higher values of LWR during summer were accompanied by much larger plants. It thus seems reasonable to suggest a slope of the regression line somewhat less steep. Assuming a slope of 0.9000 in stead of 0.9285, equation 3.1 changes into

$$\text{LWR} = 0.675 \times W^{-0.1000} \quad (3.2)$$

This relationship was applied to construct Figure 3.9b and it appears, that both the seasonal trend and the root temperature effect are shown more

clearly than in Figure 3.9a. During November, December and January Leaf Weight Ratio was 15 to 20% lower than during the rest of the year, with a very short transition period only.

The relative values of LWR at 25°C root temperature from Figure 3.9b were plotted against the average radiation during the week preceding each measurement in Figure 3.10.

Above 500 J cm⁻² d⁻¹ LWR is rather independent of radiation. From 500 to 200 J cm⁻² d⁻¹ it declines gradually from 110% to 100%, and between 200 and 50 J cm⁻² d⁻¹ a steep decline of LWR from 100 to 80% occurs.

This observation is in accordance with that of DE LINT and KLAPWIJK (1974). They reported an effect of season on the relation between the fresh weight of the leaves and that of the shoots for tomato. The weight of the leaves was relatively low during winter. In a discussion on the influence of light and temperature on leaf growth, BLACKMAN (1956) reported that light intensity did not affect the leaf weight ratio of *Helianthus*. If this is also true for tomato, it implies that the decrease of LWR during winter, observed in the present experiments and by DE LINT and KLAPWIJK (1974) is caused by the short days instead of the low light intensities during winter.

The partition of dry matter between various plant parts of tomato in relation to plant size was studied by COOPER (1972). In his experiments on nutrient solutions he observed that the ratio between root dry weight and plant dry weight

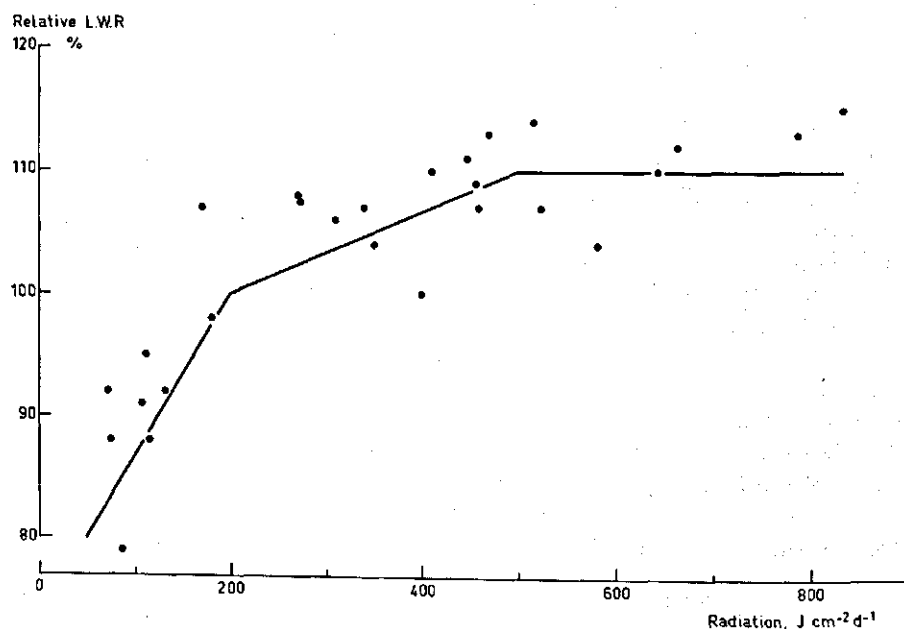


FIG. 3.10. Leaf Weight Ratio, expressed as a percentage of the calculated LWR according to Eq. 3.2, against average daily radiation during the preceding week (data for 25°C root temperature only).

gradually declined and that between leaf dry weight and plant dry weight increased with increasing plant size. This is in contrast with our observations, although in our case the dry weight of the root system was not determined. This, however, can hardly explain the discrepancy.

3.3.3.5. Leaf area related to leaf dry weight

Besides LWR it is important to analyse the ratio between leaf area and leaf dry weight, or the Specific Leaf Area (SLA). This quantity determines the amount of light which is intercepted by the plant for photosynthesis.

Values of SLA with their standard deviation are represented in Table 3.6. The variability of SLA was in general quite small within one treatment when determined on the same day. The standard deviation was 3 to 4% only. Large seasonal variations in SLA occurred, however, ranging from almost 1000 cm² g⁻¹ in winter to about 250 cm² g⁻¹ in summer. Root temperature too appeared to affect this ratio. In most cases it was lower at 12 than at 25°C, whereas at

TABLE 3.6. Specific Leaf Area in cm² g⁻¹ during the season at various root temperatures (mean of 4 to 5 plants and standard error of the mean, s.e.)

Exp.	Harvest	12°C		25°C		35°C	
		mean	s.e.	mean	s.e.	mean	s.e.
I	1	479	10	544	15	546	19
	2	540	23	554	18	524	9
	3	696	9	604	11	588	6
II	1	660	19	743	32	746	37
	2	748	28	837	22	848	28
	3	861	12	993	13	999	32
	4	841	15	850	35	873	18
III	1	892	19	989	47	988	32
	2	760	13	866	9	877	5
	3	639	35	801	27	832	27
	4	492	42	615	43	558	17
IV	1	438	4	473	10	462	14
	2	353	21	460	13	469	6
	3	382	10	532	21	471	3
	4	342	23	408	11	364	12
V	1	337	20	437	18	456	15
	2	363	13	483	6	391	8
	3	295	9	359	5	316	3
	4	216	11	264	5	227	11
VI	1	284	5	389	15	319	18
	2	341	13	395	11	347	15
	3	381	13	380	3	349	13
	4	288	4	265	4	277	10
VII	1	497	9	542	9	507	8
	2	435	1	457	18	399	13
	3	437	15	470	5	422	7
	4	398	14	339	14	373	23

35°C it appeared to be reduced only during summer. This ratio was not markedly depending on plant size.

The large seasonal fluctuation in SLA could depend on air temperature, radiation and evaporation. It appeared that the highest correlation was found with radiation. In Figure 3.11 SLA is plotted versus this climatic parameter for root temperatures of 12, 25 and 35°C. The values used in preparing Figure 3.11 are based on the average radiation conditions existing during 7 days prior to the measurement.

It is obvious, that a large decrease in SLA occurs between 50 and 200 J cm⁻² d⁻¹. The decline at higher radiation intensities is smaller. The data suggest a hyperbolic or logarithmic relation between Specific Leaf Area and radiation. Lines of best fit were calculated for both mathematical relationships for the root temperature treatment of 12°C only. The logarithmic expression appeared to yield the best fit as is shown in Figure 3.11, so that for the other treatments also a logarithmic regression was calculated and drawn in the figure. Although there is an appreciable scatter around the curves, 85 to 90% of the variance of SLA is explained by radiation in this way.

At 12°C the specific leaf area was lower than at 25°C, the difference being approximately 10% at low radiation intensities and about 20% at the higher intensities. The absolute difference was approximately 50 cm² g⁻¹ throughout the whole range in radiation. At 35°C SLA was equal to that at 25°C at low radiation and 15% or 40 cm² g⁻¹ lower at higher light intensities.

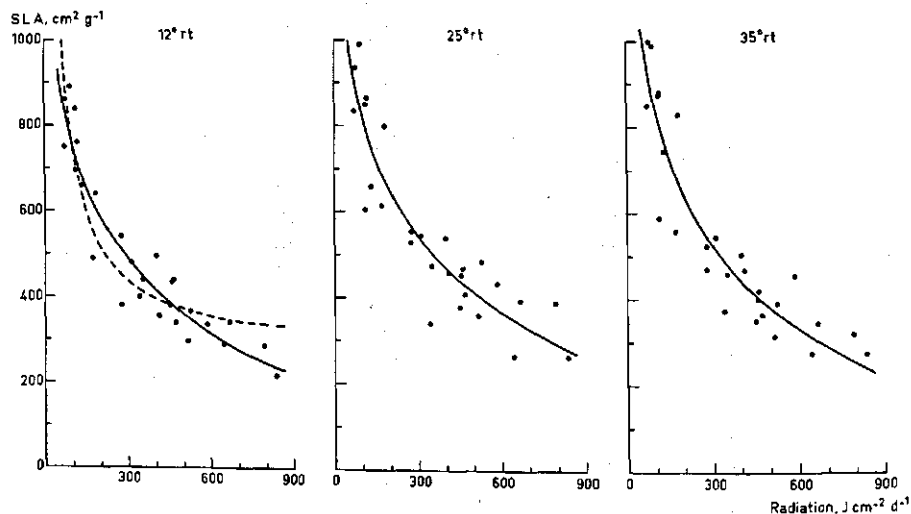


FIG. 3.11. Specific Leaf Area (SLA) against average daily radiation during the preceding week at 12, 25 and 35°C root temperature. The broken line represents a hyperbolic relation, the full drawn ones represent the logarithmic relationship:

at 12°C r.t. : $SLA = 1891 - 567 \times \log R$

at 25°C r.t. : $SLA = 1986 - 582 \times \log R$

at 35°C r.t. : $SLA = 2121 - 644 \times \log R$.

A further analysis of the data showed, that at 25 and 35°C there was a decrease of SLA with increasing plant size. This effect of plant size could be hardly detected from the data in Table 3.8, but when these values were expressed as a percentage of the values, which they could have according to the equations in Figure 3.11, a highly significant negative correlation between SLA and total plant dry weight was found at 25 and 35°C. The linear correlation coefficients were -0.71 and -0.62, respectively and based on 27 observations. At 12°C root temperature, however, this coefficient was only -0.19, which is not significant. The effect of plant size on SLA was approximately 1.7% per gram plant dry weight increase at 25°C and 2.6% per gram at 35°C. This effect of plant size accounted for another 6% of the total variance of specific leaf area at these temperatures. Thus the plants gradually reduced their leaf area per gram of dry weight in the leaves when growing larger, at least at optimum and high root temperatures. The increase of SLA with a decrease in light intensity is an indication of a more efficient interception of light when this factor is limiting. The efficiency was less at low root temperatures during the whole season, whereas high root temperatures reduced this efficiency only at higher light intensities.

Specific Leaf Area is of great importance in quantitative aspects of growth and appeared to be quite sensitive to environmental conditions. Because of its sensitivity it may be a useful indicator of the response of plants to environmental variables.

3.3.4. *Quantitative analysis of growth*

3.3.4.1. Introduction

A number of qualitative and quantitative aspects of the plant have been presented in the preceding paragraphs. In this section a growth analysis will be given in order to assess the importance of root temperature relative to other environmental factors.

In the beginning of this century already, some concepts of growth analysis were presented, of which the compound-interest-law, first recognized by BLACKMAN in 1919, was the most important one. A detailed review on the history of these concepts is given by EVANS in 'The Quantitative Analysis of Plant Growth' (1972). Therefore only some basic equations used in this section will be presented in connection with the results obtained. Growth is the increase in size or weight and it will be used here as the increase in dry weight of the plant. The relation between weight and size has been discussed earlier.

The weight of the plant at any time (W_T) depends on the initial weight (W_0) at $t = 0$, and the increase in weight per unit time (dW/dt), according to:

$$W_T = W_0 + \int_{t=0}^T \frac{dW}{dt} dt \quad (3.3)$$

Integration of eq. 3.3 is rather easy in two cases, namely at a constant growth rate (a) and with exponential growth (b).

- In this case dW/dt is a constant, so that upon integration of eq. 3.3 a linear relation between W and t will be obtained.
- In the case of exponential growth a linear relationship exists between dW/dt and W , or $dW/W \cdot dt$ is a constant. The quantity $dW/W \cdot dt$ is called the Relative Growth Rate (RGR) and is defined as the dry weight increase per unit weight and time. In this case equation 3.3 can be rewritten as:

$$\int_{W_1}^{W_2} \frac{dW}{W} = RGR \times \int_{T_1}^{T_2} dt$$

and integration yields

$$(\ln W_2 - \ln W_1) = RGR (T_2 - T_1) \quad (3.4)$$

where \ln means the logarithm to the base e . At any time $t = T$ the weight W_T is related to the initial weight W_0 at $t = 0$ by:

$$W_T = W_0 \cdot \exp (RGR \cdot T) \quad (3.5)$$

In young plants, under constant conditions, growth is often found to be exponential for some time. Subsequently a long period of a transition towards linear growth can be observed. During this period a good mathematical description of growth is difficult because RGR is time-dependant, through which integration of eq. 3.3 is highly difficult. When the time-interval ($T_2 - T_1$) or the weight-interval ($W_2 - W_1$) is not too large, one may consider an exponential growth during such an interval. RGR is constant then and different during the next interval. The choice of the maximum time interval during which an average RGR can be used without introducing large errors is arbitrary. It depends on the rate of change of RGR and on the accuracy aimed at. EVANS (1972) suggests a time interval in which W increases two to fourfold as the maximum time span between successive measurements of plant weight, in order to calculate RGR from eq. 3.4.

Although the calculation of RGR from data of successive harvests is quite easy with equation 3.4, the interpretation of the figures thus obtained is extremely difficult. Therefore it is often useful to separate RGR into a few other variables, which are more easily analysed.

Since $RGR = dW/W \cdot dt$,

also $RGR = (dW/A \cdot dt) \times (A/W)$,

where:

A is the area of the leaves

$dW/A \cdot dt$ is the change in dry weight of the plant per unit time and leaf area, often called Net Assimilation Rate, NAR

A/W is the ratio between leaf area and total plant weight or Leaf Area ratio, LAR.

EVANS (1972) argued, that the term NAR is somewhat misleading because it is not exactly the same as net assimilation or net photosynthesis. He proposed the term Unit Leaf Rate (ULR), but since the term NAR has been used for a long time already it will also be used throughout this paper.

RGR thus appears to be the product of NAR and LAR. LAR, in turn, depends on two parameters according to:

$$LAR = A/W = (A/W_L) \times (W_L/W),$$

where W_L is the dry weight of the leaves.

A/W_L is the area per unit dry weight of the leaves, which has been discussed already as the Specific Leaf Area (SLA), and W_L/W is the ratio between leaf dry weight and total dry weight (LWR). It thus appears, that the relative growth rate

$$RGR = NAR \times SLA \times LWR \quad (3.6)$$

SLA and LWR have been presented already, so that the next section will deal with the calculation of NAR.

3.3.4.2. Net Assimilation Rate

At each moment is:

$$NAR_t = \frac{dW}{A dt} \quad (3.7)$$

The average value during the period between T_1 and T_2 is:

$$NAR = \frac{1}{T_2 - T_1} \times \int_{T_1}^{T_2} NAR_t \cdot dt \quad (3.8)$$

substitution of 3.7 in 3.8 yields:

$$NAR = \frac{1}{T_2 - T_1} \times \int_{w_1}^{w_2} \frac{1}{A} dW \quad (3.9)$$

In case A is constant, the integration is simple, but leaf area generally increases. The relation between A and W should be known to integrate the function dW/A between the limits W_1 and W_2 . When a linear relationship exists between A and W, integration of 3.9 gives:

$$NAR = \frac{W_2 - W_1}{T_2 - T_1} \times \frac{\ln A_2 - \ln A_1}{A_2 - A_1} \quad (3.10)$$

In chapter 16.12 EVANS (1972) represented a method to calculate NAR according to equation 3.10, with subsequent correction for non-linearity of the

relationship between A and W. This method was used for the calculation of the NAR – values presented in Table 3.7. (Method I).

Application of this method is correct only, when the increase in plant size between two successive harvests is less than two to fourfold (see previous section). Therefore the data from the first period of each experiment were omitted, because of the much larger increase in size.

The use of data from two harvesting dates implies that different plants are used in the calculation. Since differences between plants were relatively large, this approach increased to a large extent the error in the calculated NAR. Therefore, another method of estimating NAR was used, referred to as method II. For each treatment two plants were not harvested but leaf length was measured during the whole experiment. NAR was estimated from these two plants. The method consisted of the following steps:

- Estimating the average leaf area of these two plants at each harvesting date, from their Σl^2 -values and the relationship between area and Σl^2 at that date and treatment (obtained from the plants harvested).
- Estimating the average dry weight of these two plants at each harvesting date, from their leaf area and the relationship between dry weight and leaf

TABLE 3.7. Net Assimilation Rate during the season at various root temperatures, calculated from the measurement of leaf area and dry weight of plant samples taken at each harvesting date (I) and from estimates of these parameters for plants grown during a whole experiment (II).

Exp.	Period	12°C		25°C		35°C		root temp
		I	II	I	II	I	II	method of calculation
II	2	0.231	0.215	0.248	0.215	0.232	0.224	
	3	0.186	0.167	0.168	0.165	0.186	0.170	
	4	0.119	0.152	0.147	0.160	0.147	0.170	
III	2	0.238	0.210	0.218	0.174	0.237	0.232	
	3	0.235	0.198	0.279	0.297	0.258	0.223	
	4	0.349	0.338	0.348	0.331	0.330	0.369	
IV	2	0.578	0.539	0.667	0.606	0.696	0.637	
	3	0.396	0.462	0.470	0.417	0.475	0.488	
	4	0.640	0.539	0.582	0.567	0.524	0.534	
V	2	0.749	0.580	0.741	0.695	0.808	0.814	
	3	0.836	0.833	0.697	0.742	0.675	0.719	
	4	0.854	0.920	0.718	0.827	0.853	0.817	
VI	2	0.902	0.896	0.951	1.003	0.861	0.875	
	3	0.703	0.744	0.714	0.700	0.816	0.844	
	4	0.787	0.881	0.701	0.758	0.747	0.788	
VII	2	0.714	0.780	0.834	0.745	0.874	0.862	
	3	0.665	0.629	0.579	0.572	0.566	0.616	
	4	0.485	0.660	0.504	0.580	0.465	0.557	
Mean		0.537	0.541	0.532	0.531	0.542	0.553	

- area at that date and treatment (obtained from the plants harvested).
- Application of equation 3.10.
- Correction for non-linearity as previously discussed.

Since no measurements of leaf length were available for the first experiment, no NAR-values for that experiment are presented in Table 3.7.

Differences in NAR between the two methods were large, but the average for each root temperature was only slightly affected by the method of calculation. The Net Assimilation Rate appeared to range between approximately $0.2 \text{ mg cm}^{-2} \text{ d}^{-1}$ in winter and $0.9 \text{ mg cm}^{-2} \text{ d}^{-1}$ in summer. Although NAR is determined by a number of physiological processes, photosynthesis is no doubt the most important one. Therefore, the values were plotted against the mean radiation intensity during each period for each of the two sets of data. Values for all three root temperatures were combined because of their small difference. The data were fitted to a hyperbolic equation which is often used to give the relationship between radiation and photosynthesis (see e.g. PEAT, 1970):

$$\text{NAR} = \text{NAR}_m \times \frac{R}{E + R} \quad (3.11)$$

in which:

NAR_m is the maximum net assimilation rate ($\text{mg cm}^{-2} \text{ d}^{-1}$)

E is the radiation at which half of NAR_m is reached ($\text{J cm}^{-2} \text{ d}^{-1}$)

and:

R is the average daily radiation during each period ($\text{J cm}^{-2} \text{ d}^{-1}$)

A reciprocal plot of NAR against R will give a straight line according to:

$$\frac{1}{\text{NAR}} = \frac{E}{\text{NAR}_m} \times \frac{1}{R} + \frac{1}{\text{NAR}_m},$$

with a tangent of $\frac{E}{\text{NAR}_m}$ and an intercept of $\frac{1}{\text{NAR}_m}$.

Both sets of data from Table 3.7 yielded almost exactly the same curve, the difference being less than 1% for radiation values smaller than $600 \text{ J cm}^{-2} \text{ d}^{-1}$ and less than 2% at the highest radiation values. The correlation coefficient based on 54 observations was 0.943 for method I and 0.969 for method II, which indicated that the latter method yielded values which showed less scatter. Only the data of method II are presented in Figure 3.12. The constants of eq. 3.11 for these data are:

$$\begin{aligned} \text{NAR}_m &= 1.76 \text{ mg cm}^{-2} \text{ d}^{-1} \\ E &= 765 \text{ J cm}^{-2} \text{ d}^{-1}. \end{aligned}$$

Radiation accounted for 90% of the total variance in NAR.

To assess, whether there was any effect of root temperature or plant size on NAR, each value of NAR was expressed as a percentage of that according to eq. 3.11 with the constants mentioned above. No significant difference between the figures from the root temperature treatments could be detected and there

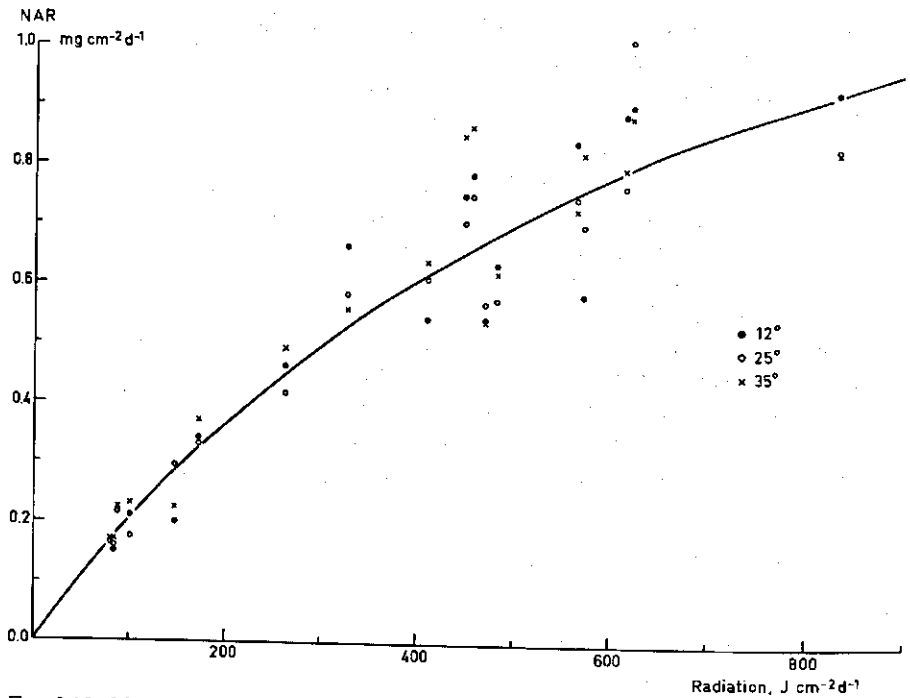


FIG. 3.12. Net Assimilation Rate (NAR), calculated by method II, vs. average daily radiation during the preceding period, for various root temperatures. The curve is based on all 54 observations, fitted to Eq. 3.11.

was no significant correlation between these percentages and plant size. Net Assimilation Rate thus appeared to be free from ontogenetic drift and independent of root temperature. The latter result is in accordance with the conclusion of BROUWER (1959) that photosynthesis of pea plants was not affected by root temperature. Net Assimilation Rate of corn was also reported to be independent of root temperature (GROBELAAR, 1963 and BROUWER, 1973).

The observed relationship with radiation indicated that even in summer the maximal dry weight increase per unit leaf area was not reached during this experiment. From his experiments on shading of tomato plants COOPER (1967) also concluded, that light saturation was not reached under natural glasshouse conditions in England during summer. He reported a net assimilation rate of $78 \text{ g m}^{-2} \text{ wk}$ ($1.11 \text{ mg cm}^{-2} \text{ d}^{-1}$) in June and $14 \text{ g m}^{-2} \text{ wk}^{-1}$ ($0.20 \text{ mg cm}^{-2} \text{ d}^{-1}$) in December. These values are slightly higher than those obtained in our experiment, which is at least partly due to the low light transmission of the glasshouse used for these experiments.

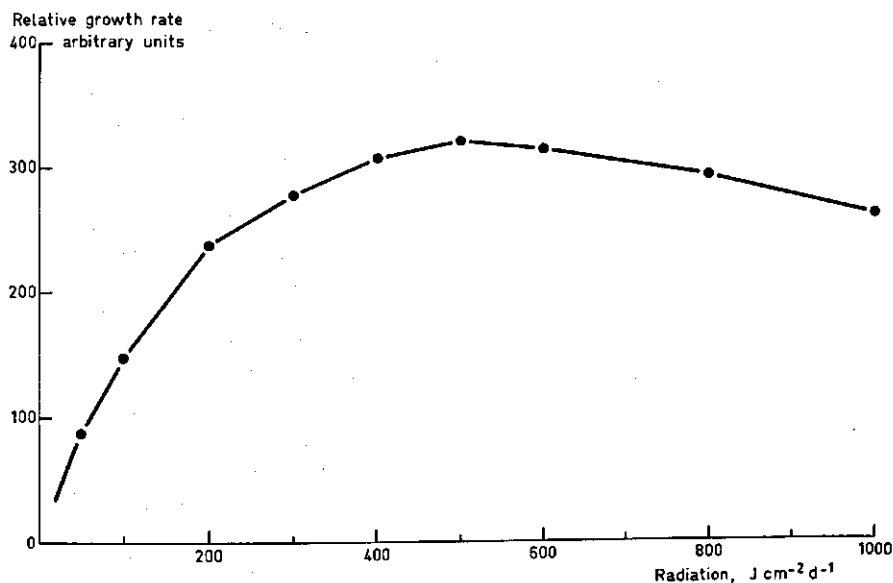


FIG. 3.13. Relative Growth Rate in arbitrary units, plotted against radiation. The curve was obtained by multiplication of the LWR, SLA and NAR-values from Figure 3.10, 3.11 and 3.12, respectively.

3.3.4.3. Relative Growth Rate

Since Relative Growth Rate (RGR) is the product of LWR, SLA and NAR (eq. 3.6), all factors which were found to affect these parameters will also affect the relative growth rate.

The most important variables appeared to be radiation, root temperature and plant size. Because day length, air temperature and evaporation were closely correlated with radiation, their effect could not be assessed separately.

At decreasing radiation values, LWR and NAR decreased (Figure 3.10 and Figure 3.12). The effect on RGR was partly compensated by an increase of SLA at low radiation (Figure 3.11). In Figure 3.13 these effects were combined to give RGR in arbitrary units as a function of radiation. A curve is obtained which shows an optimal radiation value of approximately $500 \text{ J cm}^{-2} \text{d}^{-1}$. Although in the relation between NAR and radiation no light saturation was evident, it occurred between RGR and radiation because of the gradually decreasing SLA. This means that at high radiation growth is not limited by photosynthesis but by processes which determine the increase of leaf area.

The apparent light saturation of RGR agrees with that reported by PLOEGMAN (1964) who observed no increase of the growth rate of tomato plants at higher light intensities between April and August.

Root temperature had a minor effect on LWR but a more pronounced one on SLA. NAR was not affected by root temperature at all. Radiation interacted with the root temperature effects on LWR and SLA. At low radiation the

negative effect of low root temperatures on LWR and SLA was smaller than at high light intensities. The reduction of LWR and SLA by a high root temperature was observed only at high radiation.

Plant size had a large effect on LWR. This ratio decreased at increasing plant size. SLA also depended on plant size, but much less than LWR and only at a root temperature of 25 and 35°C.

The decrease of LWR is thus the main cause of the often observed gradual decline in relative growth rate. DE LINT and KLAPWIJK (1973) reported that this decline could be delayed by improved cultural practices. It is not clear, however, whether this delay is achieved by retarding the ontogenetic drift in LWR or by a relative increase in SLA. Since SLA was found to be a sensitive parameter for environmental effects, the latter suggestion is possibly true.

Because of the complicated interactions mentioned above no general conclusions on RGR can be drawn, since LWR and thus RGR depends strongly on plant size. This means a negative feed-back mechanism. Decreasing growth rate results in relatively smaller plants with a higher LWR and thus a larger potential growth rate. This implies that the real response of plants to environmental variables may be overlooked by a direct comparison of relative growth rates. COOPER (1973) observed, that after some weeks of growth at low root temperatures, the relative growth rate of tomato plants was no longer different from those growing at optimum conditions. His conclusion that an adaptation occurred is not entirely correct, however, in view of the feed-back mechanism described above.

3.3.5. *Leaf growth*

As described in Section 3.2.2, daily estimates of the leaf area of two plants at a root temperature of 12, 25 and 35°C were obtained by measuring the length of each leaf. Analogous to the calculation of RGR (eq. 3.4) daily values of relative leaf growth rate (R_A) were determined.

Leaf expansion rate was generally reduced at low and high root temperatures, but large daily variations were observed. These variations may be ascribed partly to the inaccuracy of the measurements. From the duplicates of the measurements, the random variation of the measurements proved to be approximately 5%. Most daily fluctuations, however, were by far greater than this experimental error.

An attempt was made to relate these daily fluctuations to variations in air temperature, radiation and evaporation, but no systematic relationships could be established. Since leaf expansion is a function of plant weight increase, those factors which affect RGR will also affect R_A in general. The fact, however, that no clear relationship between these factors and daily R_A - values could be established suggests, that leaf expansion rate responds to the varying environment in a complex manner. Leaf expansion under constant conditions will be discussed in Chapter 5.

3.3.6. Transpiration

The plants were irrigated twice a week throughout the experiment with a known amount of water, from which the transpiration rate could be calculated. The evaporation of the soil, which was reduced by a polystyrene cover (Section 3.2), was determined separately from pots without plants.

The evaporation depends on the soil temperature and was negative at 12 and 15°C, rather small but positive at 20 and 25°C and larger at 30 and 35°C. This result is easily understood because at low soil temperature the vapour pressure near the soil surface is lower than that of the air, so that condensation occurs. The vapour pressure gradient is small at a soil temperature of 20 and 25°C, while at 30 and 35°C the vapour pressure at the soil surface is much higher than that of the ambient air. All data were corrected for the evaporation of the soil. This correction was relatively large at the beginning of each experiment and in the order of 20 to 70% of the total water loss. It declined with larger plants to less than 10%. For this reason transpiration values after the first harvest of each run will be presented only.

To obtain the transpiration rate per unit leaf area, the procedure was as follows:

Leaf growth of young plants is approximately exponential, or

$$A_T = A_0 \cdot \exp. (R_A \cdot T) \quad (3.12)$$

where A_T is the leaf area at any time $t = T$ and A_0 is the leaf area at $t = 0$ (compare eq. 3.5).

The average leaf area between $t = T_1$ and $t = T_2$, $A_{1,2}$, is then given by:

$$A_{1,2} = \frac{1}{T_2 - T_1} \cdot \int_{T_1}^{T_2} A_t \cdot dt$$

$$\text{or} \quad A_{1,2} = \frac{1}{T_2 - T_1} \cdot \int_{T_1}^{T_2} A_0 \cdot \exp (R_A \cdot T) \cdot dt$$

Since A_0 and R_A are constant

$$A_{1,2} = \frac{1}{T_2 - T_1} \cdot \frac{A_0}{R_A} \cdot \left[\exp (R_A \cdot T_2) - \exp (R_A \cdot T_1) \right] \quad (3.13)$$

Analogous to eq. 3.4

$$R_A = \frac{\ln A_2 - \ln A_1}{T_2 - T_1}$$

And according to eq. 3.12

$$A_0 \cdot \exp (R_A \cdot T_2) = A_2$$

and

$$A_0 \cdot \exp (R_A \cdot T_1) = A_1$$

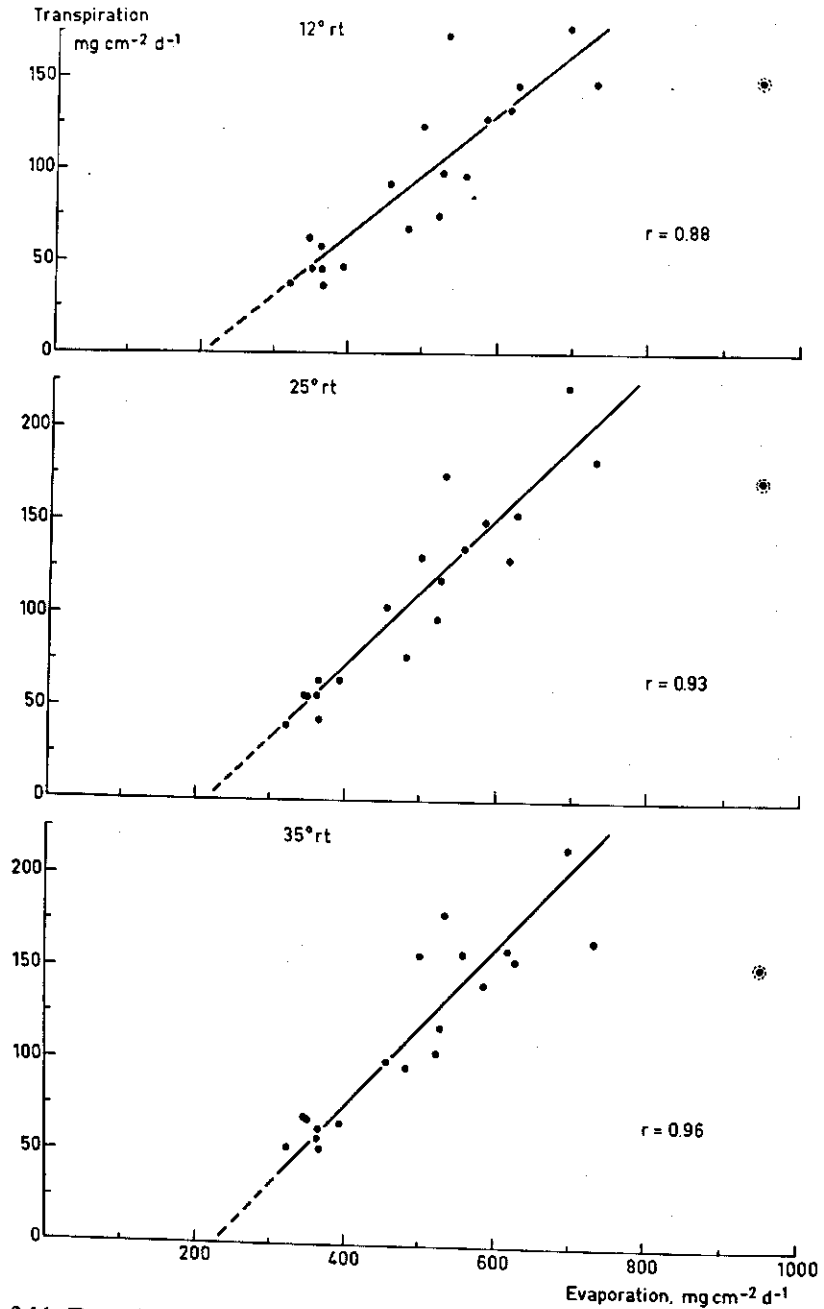


FIG. 3.14. Transpiration vs. Piche-evaporation at a root temperature of 12, 25 and 35°C. For encircled points, see text.

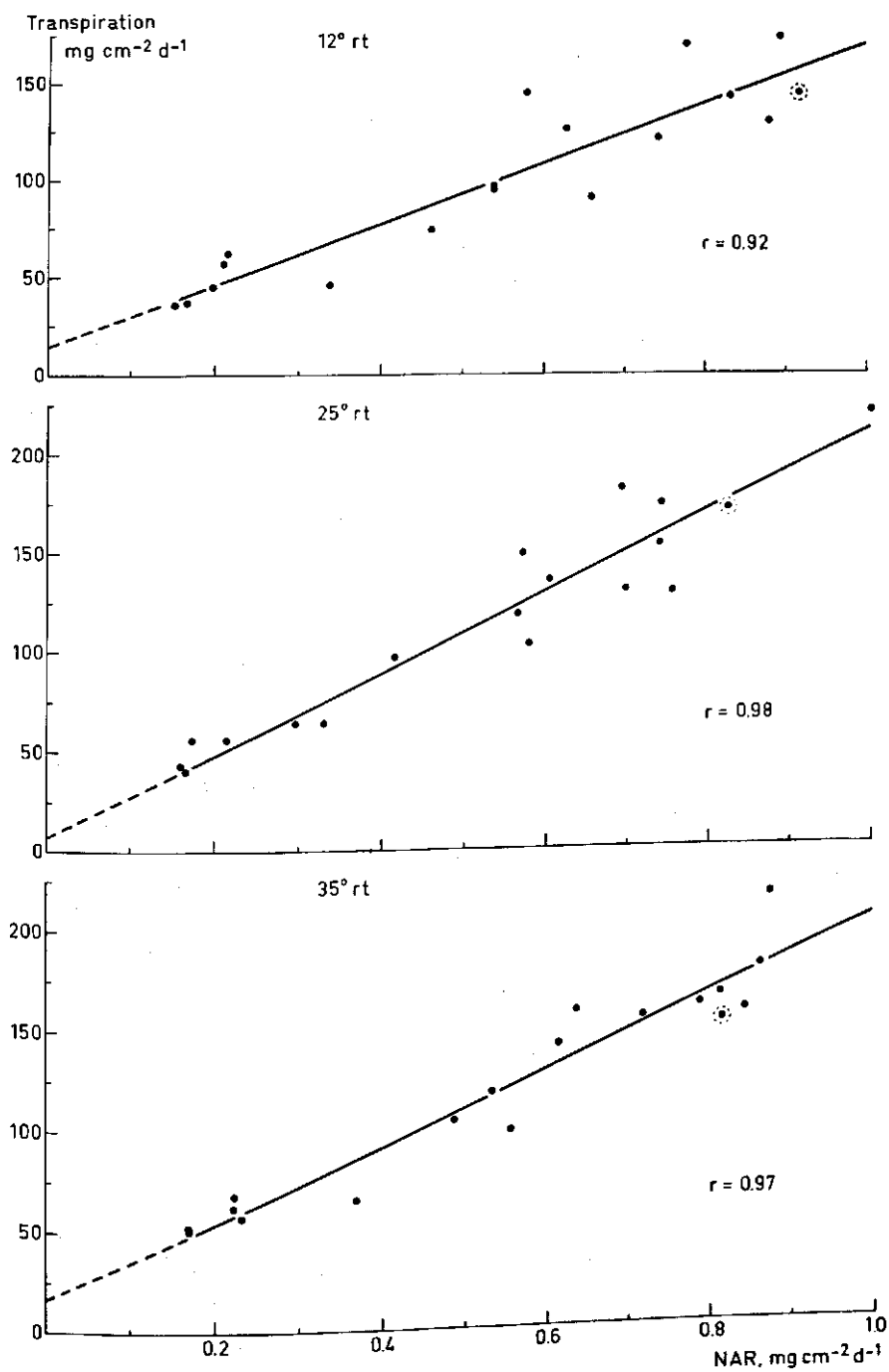


FIG. 3.15. Transpiration vs. Net Assimilation Rate at a root temperature of 12, 25 and 35°C.
For encircled points, see text.

Substitution into 3.13 yields:

$$A_{1,2} = \frac{A_2 - A_1}{\ln A_2 - \ln A_1} \quad (3.14)$$

For each period the average leaf area was determined from eq. 3.14 and used in calculating the transpiration rate per unit leaf area per day.

The values thus obtained were plotted in Figure 3.14 against the corresponding evaporation values measured with the Piche-evaporimeter. At each root temperature a linear relationship existed between transpiration and evaporation. The values from the last period of experiment V were far below this relationship for all treatments and are indicated with a dotted circle in the figure. As already noted in Section 3.3.3.3, the water supply at the end of this period was inadequate, so that probably the evaporative demand could not be met by the plants at any root temperature. These values were omitted in the calculation of the regression lines. Extrapolation of these lines indicates, that at each root temperature transpiration rate was zero at an evaporation rate of approximately $200 \text{ mg cm}^{-2} \text{ d}^{-1}$. This rate may represent the average evaporation during the night. The slope was 0.32, 0.39 and 0.43 at root temperatures of 12, 25 and 35°C , which indicates that the transpiration rate increased with increasing root temperature up to 35°C . As mentioned in Chapter 2 such an effect generally occurs in most plant species.

The ratio between transpiration and dry weight increase of plants (transpiration ratio) is often used as an indicator of the water use efficiency of plants. In Figure 3.15 the transpiration rate is plotted against the corresponding values of net assimilation rate. It shows a linear relation almost passing through the origin. The regression line at 12, 25 and 35°C is represented in the figure. It appears that the transpiration ratio decreases with decreasing root temperature, specially below 25°C . This is a consequence of the fact that transpiration is reduced at low root temperatures, while net assimilation rate remains the same.

The data for the last period of experiment V, although being low, are within the normal range in Figure 3.15. This either means, that NAR was also reduced by the inadequate water supply as was transpiration, or evaporation was overestimated in that period.

3.4. CONCLUSIONS

The aim of this series of experiments under natural glasshouse conditions was to obtain quantitative data on growth of young tomato plants in relation to root temperature and climatic factors. Plant size ranged from 1 to 100 gram fresh weight, 0.1 to 10 gram dry weight and 1 to 50 cm plant height. Seasonal effects on growth appeared to be much larger than root temperature effects. Due to the high correlation between day length, radiation, air temperature and evaporation it was impossible to separate the effect of each of these parameters

on growth. Radiation showed the best correlation with a number of plant parameters.

Growth in weight was exponential, but the relative growth rate decreased with increasing plant size, due to a gradual decrease in the ratio between leaf weight and total plant weight. Seasonal effects on growth were balanced, since an increase in radiation caused an increase in the assimilation rate, but a decrease in the specific leaf area. Leaf weight ratio was to 15 to 20% lower during winter. Root temperatures were optimal for growth between 20 and 30°C. At lower root temperatures growth was reduced throughout the year, and at high ones only in summer. In both cases the main cause of this reduction was the decrease of the specific leaf area. Leaf weight ratio was affected only slightly, while net assimilation rate was not influenced at all by root temperature.

The decreasing growth rate with increasing plant size produces a negative feed-back, since a reduction in growth rate yields smaller plants with a larger potential growth rate. Thus at prolonged periods of low root temperatures, the relative growth rate of these plants can be higher than that at an optimal root temperature.

Leaf expansion rate was reduced by root temperatures below 20°C. Besides that, relatively large variations from day to day of this growth parameter were observed.

Transpiration was markedly affected by root temperature and increased with increasing root temperature between 12 and 35°C. Since NAR was not affected, also the transpiration ratio increased with increasing root temperature.

Because of its sensitivity to root temperature the rate of leaf expansion under different conditions should be studied in more detail. Specific leaf area, which is closely related to leaf expansion is likely to be an important parameter in the study of the physiological background of root temperature effects.

4. EFFECT OF ROOT TEMPERATURE DURING RAISING ON SUBSEQUENT GROWTH, GENERATIVE DEVELOPMENT AND YIELD

4.1. INTRODUCTION

In the previous chapter the effect of root temperature on the growth of young tomato plants was discussed. It was demonstrated, that optimal conditions during raising were achieved with root temperatures between 20 and 30°C. Since in tomato growing earliness and fruit yield are important parameters, the effect of root temperature during raising on subsequent growth, generative development and yield has to be assessed.

In principle, two different pretreatments of root temperature can be distinguished. Plants can be raised for an equal period of time at different root temperatures, after which they are transplanted at the same time into a glasshouse. In this way transplants of different size and development are used, and MORGAN and CLARKE (1975) demonstrated that the ultimate yield can be affected by the stage of development at transplanting. The second possibility is varying the raising period for each root temperature in order to obtain plants of an equal size. Either different sowing or transplanting dates will be the consequence of the latter set-up. Although the advantage of plants with equal size is achieved, their age will vary. A drawback of the latter approach is the difficulty of planning such an experiment for which a large number of plants at each treatment is necessary. Therefore the former method was chosen.

Parallel to the root temperature pretreatments a number of plants was raised without root temperature control. Leaf pruning was applied during transplanting and also later on in order to assess the importance of leaf area on growth, development and yield.

The experiment was carried out three times, one sowing date being in autumn, one in winter and one in early spring.

4.2. MATERIALS AND METHODS

Seeds were sown in boxes at an air temperature of 25°C. One week after emergence the young plants were selected and transplanted into 5-litre pots as described in Section 3.2.1. Ninety pots were then placed into six Wisconsin tanks which were kept at 20°C for two days. Thereafter root temperatures of 12, 25 and 35°C were imposed (30 plants per treatment). At the same time ninety plants were raised in 5-litre pots which were placed on benches in a nearby glasshouse and left without root temperature control. The treatments are listed in Table 4.1.

The air temperature varied between 20 and 25°C during the day and between

TABLE 4.1. Treatments applied in the experiments on growth, generative development and yield.

Treatment	Conditions during raising			Removal of every second leaf	
	root temp. °C	air temp. day °C	night °C	at transplanting into the glasshouse	continuously after transplanting
A	35	20-25	15-18	no	no
B	25	20-25	15-18	no	no
C	12	20-25	15-18	no	no
D	15-20	20-22	15-16	no	no
E	15-20	20-22	15-16	yes	no
F	15-20	20-22	15-16	yes	yes

15 and 18°C during the night in the glasshouse with the controlled root temperatures. The glasshouse without root temperature control had an air temperature between 20 and 22°C during the day and between 15 and 16°C during the night.

Soil moisture was kept at a pF-value of about 1.5 by irrigation. The frequency and amount of irrigation was determined as described in Section 3.2.1.

When the plants at 25°C root temperature reached a height of approximately 35 cm, the height of all plants was measured and the leaf area estimated from the length of the leaves. Half of the leaf area was removed from the sixty plants which made up the treatments E and F (see Table 4.1.). Then all the plants were transplanted into a glasshouse where the air temperature was kept between 20 and 23°C during the day and at 17°C during the night. These day and night temperatures were increased to 22-25°C and 18-20°C, respectively by the end of February. On sunny days the air temperature sometimes rose to about 30°C. Soil temperature at a depth of 35 cm was approximately 17°C when the first experiment was started, and gradually rose to about 23°C at the end of the experiment in July.

The plants were grown in rows with an alternating distance of 50 and 75 cm and a planting distance in the row of 50 cm, according to normal practices. The treatments were not randomly distributed in the glasshouse, but blocks of six plants of the same treatment were systematically put at different locations within each double row. The whole plot of 180 plants of which each experiment consisted was surrounded on all sides by plants of the same age. These plants were not a part of the experiment.

The plants were treated as a commercial crop until a height of approximately 2 meter was reached. They were topped above the seventh truss and the experiment was continued until at least 90% of all fruits of each treatment were harvested.

As noted in Section 4.1. three sowing dates were applied. The time of sowing, transplanting into pots and into the glasshouse is given in Table 4.2.

TABLE 4.2. Dates of sowing and transplanting for the experiments I, II and III.

Exp.	Date of		
	Sowing	transplanting into pots	transplanting into glasshouse
I	Sept. 24 th	Oct. 5 th	Nov. 3 rd
II	Nov. 5 th	Nov. 16 th	Jan. 12 th
III	Jan. 14 th	Jan. 25 th	March 7 th

4.3. RESULTS AND DISCUSSION

4.3.1. General development

Data on plant height, leaf number and leaf area during transplanting into the glasshouse are listed in Table 4.3. for each treatment and for each experiment. The differences between treatment A and B, respectively raised at 35 and 25°C root temperature were negligible. This could be expected from the results reported in the previous chapter. The effect of the low root temperature treatment (C) on plant height and on leaf area at transplanting was larger for the early (I) and late sowing date (III) than for the intermediate one (II), which was also in accordance with results previously reported. Leaf number was only slightly affected by root temperature.

TABLE 4.3. Average plant height, leaf number and leaf area at transplanting into the glasshouse after different treatments during raising.

Exp.	treatment	plant height cm.	nr. of leaves	leaf area cm ²
I	A	32.8	11.4	1246
	B	31.9	11.5	1291
	C	12.8	8.8	420
	D	11.2	9.9	483
	E	11.9	5.0*	250*
	F	11.8	4.9*	252*
II	A	42.6	11.8	676
	B	41.8	11.5	646
	C	28.9	10.2	466
	D	22.5	11.2	465
	E	23.4	5.9*	236*
	F	22.4	5.8*	245*
III	A	39.2	12.0	1232
	B	38.6	11.1	1330
	C	21.6	9.6	562
	D	17.6	10.8	968
	E	18.5	5.7*	478*
	F	18.3	5.3*	484*

* after removal of every second leaf

The plants raised without root temperature control (D, E and F) were smaller than those from the 12°C root temperature treatment in all experiments as far as plant height is concerned. Leaf area was slightly higher in experiment I, the same in experiment II and substantially higher in experiment III as compared with C. The relatively small size of these plants was not caused by low root temperatures, since the average air temperature in the glasshouse during raising was approximately 17°C. Root temperature should have been the same, and a root temperature between 15 and 20°C has only a minor effect on growth. Obviously the lower air temperature at D, E and F reduced the growth rate of the plants. The effect of air temperature thus appears to be larger than that of root temperature.

The plants in the first experiment grew well, but flowering in the first truss occurred only in treatment A and B, where also some fruitset was observed. The buds in the second and third truss all aborted before flower opening. In the other treatments of this experiment no fruitset at all was observed before the end of January, when light conditions improved. Some fruitset occurred in the fourth to seventh trusses, but the total number of fruits per plant remained low in all treatments. The long period of vegetative growth obscured differences between the treatments and further data on fruiting were deleted.

In the second experiment the first truss failed in most plants of treatment A and B, and in all plants of the other treatments. The second and subsequent trusses showed a good development in all treatments except F, where also the second truss failed. Obviously leaf area limited a good development of flower buds.

In the third experiment normal flowering and fruitset was observed in all treatments. Dates of flowering are listed in Table 4.4. A low root temperature treatment during raising had no effect on the time of flowering in the first truss, but a delay of 3 to 4 days in the second and third truss was observed. The partial removal of leaf area appeared to hasten flowering with a few days. DE ZEEUW (1954) demonstrated, that the development of the inflorescences is inhibited by the young leaves of a tomato plant. Removal of these leaves decreases such an inhibition, as was observed in this experiment.

TABLE 4.4. Data on flowering of the first three trusses in experiment III.

Treatment	date of first flower opening		
	1 st truss	2 nd truss	3 rd truss
A	March 17 th	March 23 rd	April 1 st
B	March 18 th	March 24 th	April 1 st
C	March 18 th	March 27 th	April 5 th
D	March 24 th	April 2 nd	April 10 th
E	March 23 rd	April 1 st	April 8 th
F	March 20 th	March 29 th	April 6 th

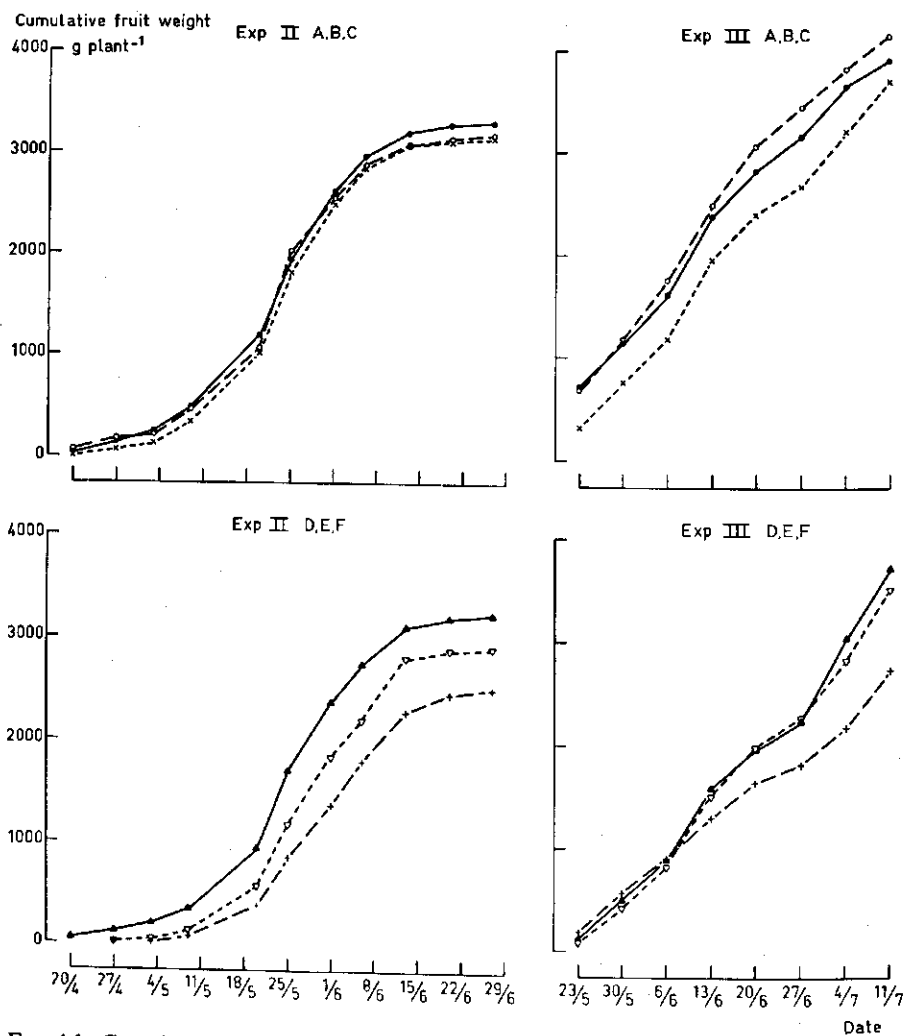


FIG. 4.1. Cumulative weight of fruits harvested after different pretreatments. (● treatment A; ○ treatment B; × treatment C; ▲ treatment D; ▽ treatment E; + treatment F).

4.3.2. Fruit production

The cumulative weight of fruits harvested in the second and third experiment is shown in Figure 4.1. S-shaped curves were obtained which indicates that three periods can be distinguished. First an exponential increase is observed, because successively more trusses are yielding fruits. Secondly a linear phase occurs, where an equilibrium exists between trusses finishing their production and new ones coming into production. Finally the phase of decreasing yield is reached, because no new trusses are available, which occurred after 7 trusses. The position of the exponential phase represents earliness, the slope of the

linear phase represents the production rate, which is determined by the number of fruits per truss, the weight per fruit and the rate of ripening. The position of the final phase represents the total production potential of the seven trusses.

As previously mentioned no data on fruiting will be presented for the first experiment.

In the second experiment (II) earliness was the same in treatments A and B and slightly less in C. Production rate was equal for each root temperature treatment and the total production potential was slightly higher in A than in B and C. Root temperature effects were very small, however. Partial removal of leaf area at transplanting decreased earliness in experiment II (E and F, compared with D). Production rate was not affected when leaves were partially removed only once (E), but decreased at continuous leaf pruning (F). The production potential was strongly decreased by continuous removal of leaves and less after removing leaves only once during transplanting.

In the third experiment the response was slightly different. Earliness was again decreased by a low root temperature during raising (C), but not by partial removal of leaves (E and F). Obviously leaf area was limiting fruit set during experiment II but not during experiment III, later in the season. Production rate was not clearly affected by root temperature and only decreased at continuous removal of leaves. This response is equal to that in experiment II. The production potential was clearly reduced by low root temperature during raising (C) and also by continuous removal of leaves (F). Partial defoliation at transplanting only (E) did not affect this parameter in experiment III.

TABLE 4.5. Cumulative number of fruits harvested and average fruit weight up to two dates in experiment II and III. Within each column different letters indicate statistically significant differences at $p < 5\%$ (DUNCAN, 1962).

Treatment	Exp. II		Exp. III	
	until May 25 th	until June 27 th	until June 20 th	until July 18 th
	fruits/plant		fruits/plant	
A	27.2 cd	45.4 b	41.1 c	60.1 c
B	28.9 d	44.7 ab	43.2 c	61.5 c
C	25.2 bc	42.1 ab	31.4 b	52.0 b
D	24.7 b	44.7 ab	27.0 a	53.1 b
E	17.0 a	39.5 a	29.2 ab	52.2 b
F	14.6 a	39.7 a	27.9 ab	44.8 a
	g/fruit		g/fruit	
A	71.0 b	71.8 b	69.0 b	66.2 ab
B	69.6 b	70.6 b	71.2 bc	68.0 b
C	71.4 b	74.2 b	76.4 c	71.6 b
D	68.9 b	72.1 b	73.4 bc	70.6 b
E	69.0 b	73.6 b	67.8 b	69.2 b
F	59.8 a	62.3 a	59.0 a	61.0 a

Fruit yield is the product of fruit number and average fruit weight. Therefore, separation of these two parameters may be useful in interpreting the results. Fruit number is determined by fruitset, which occurs 6-8 weeks before ripening and by the initiation of flower buds in the trusses, which takes place even earlier. The greater part of fruit weight increase occurs during the last few weeks before ripening. Cumulative values of fruit number per plant and average weight per fruit are listed in Table 4.5. at two dates for each run.

The negative effect of a low root temperature during raising which was small in experiment II and larger in experiment III was due mainly to a decrease in number of fruits. The average fruit weight was slightly higher but did not compensate the reduction in total yield as compared with optimal root temperatures. CHERMNIH (1971) reported that total yield was not affected when plants were raised at a root temperature of 17°C, compared with 25°C.

The effect of partial defoliation on fruit yield appeared to be more complex. In the second experiment the reduction of leaf area to one half during transplanting markedly reduced fruit number, whereas a continuous pruning had an insignificant effect on this parameter. Average fruit weight, on the other hand, was not affected by a single defoliation at the beginning, but largely decreased with a continuous removal of leaves. During the third experiment fruit number was not affected during the first half of the harvesting period, and reduced thereafter only by continuous partial removal of leaves. Fruit weight in this case was slightly but insignificantly reduced by leaf pruning once and clearly reduced by continuous removal of leaves. The results obtained in experiment III agree with the observation of COOPER (1964), that cutting of the lower leaves of tomato plants had no significant effect on yield, but that heavy defoliation clearly reduced yield.

4.4. CONCLUSIONS

Sowing of tomato seeds in September and transplanting of the plants into the glasshouse in November resulted in a slow, but regular vegetative development, but generative development was almost entirely suppressed until the end of January, irrespective of the treatment before or at transplanting. The ultimate yield was poor in all cases.

Sowing in November and January was more successful and the ultimate yield was approximately 3 kg/plant for the early and 4 kg/plant for the later sowing date.

A low root temperature during raising had an insignificant after effect on total yield for the early sowing, but reduced the final yield by about 10% in the case of the late sowing date. This reduction was caused by a decreased number of fruits per plant, which was not compensated by the slightly higher fruit weight. During the earlier part of the harvesting period the observed differences were at least partly due to a slight delay in the development of the trusses.

Leaf area at transplanting was found to be critical for fruitset under the poor

light conditions of January, but of no influence later in the season. The continuous removal of every second leaf initially caused an increase in the rate of development, but in the long run plants were less vigorous with a much lower fruit number and fruit weight.

Since these conclusions are based only on a one year's experience, they should be considered with great care. Small annual differences in weather conditions during sensitive periods may have a large effect on the subsequent development of flowering and fruiting and thus on the ultimate yield. The experiments reported in this chapter show, that root temperature during raising is of much less importance than air temperature. The yield of plants grown at a root temperature as low as 12°C appeared to be equal to or higher than that of plants, raised at a root temperature of 17 to 18°C, but at a slightly lower air temperature (17°C, compared with 20°C).

5. GROWTH AT VARIOUS COMBINATIONS OF CONTROLLED AIR AND ROOT TEMPERATURES

5.1. INTRODUCTION

Under the natural glasshouse conditions of the experiment described in Chapter 3 a rather close correlation between radiation and air temperature was observed, through which the separate effects of each climatic factor on growth was difficult to analyse. Although the correlation between growth and radiation was somewhat higher than that between growth and air temperature, the latter no doubt affects plant growth also, as was demonstrated in Chapter 4.

In this chapter the importance of air temperature relative to root temperature will be discussed. In order to avoid interrelationships with other environmental factors the experiments were conducted under the controlled conditions of a phytotron. The design of the experiment was different from that described in Chapter 3 for a number of reasons. The technique of periodic harvesting is useful, because growth in weight is determined directly. A serious disadvantage, however, is the fact, that each point on the growth curve represents different plants. In order to reduce the error caused by plant to plant differences, large samples should be harvested each time.

The rate of leaf expansion could be determined rapidly and accurately by repeated measurements of leaf length on the same plants (Section 3.2.2.). The variability of this parameter generally appeared to be less than 5%, for the mean of two replicates only. Moreover leaf expansion rate was found to be quite sensitive to root temperature. This non-destructive method for measuring growth was therefore used in the experiment described in this chapter, and a large number of air and root temperature combinations were feasible. Three series of experiments were carried out subsequently. In each of them a treatment with a continuous air and root temperature of 25°C was present as a reference. Throughout the experiment a uniform daylength of 12 hours was applied.

5.2. MATERIALS AND METHODS

Seeds were sown at 25°C and transplanted into 5-litre pots at the seventh day after emergence (*vide* 3.2.1). Until the sixth leaf had reached a length of approximately 1 cm, the plants were kept at 25°C in artificial light with an intensity at plant height of approximately 30 Watt m⁻² for 12 hours per day. Thereafter the temperature treatments were started. The experiment consisted of 3 series. In the first series air and root temperature combinations of 25/9°C were applied, in the second one combinations of 25/17° and in the third one combinations of 25/13°C. All 48 treatments are listed in Table 5.1. Three plants

per treatment were used and special care was devoted to the selection of uniform plants.

After an adaptation period of 24 hours at the experimental temperatures, stem length and the length of each leaf was measured at 6 P.M. Thereafter measurements of leaf length were done twice a day when the plants were transferred from light to darkness and vice versa. This transfer took place at 6 A.M. and 6 P.M. each day and by that time also the weight of pots with and without plants was determined in order to measure the rate of transpiration during day and night. The decline in weight of pots with plants, however, was only slightly higher than that of those without plants, so that large errors were introduced by the correction for evaporation. No data on transpiration are presented, therefore. Seven days after the beginning of the measurements, at the end of the light period, the plants were harvested. Stem length was measured again, while also fresh and dry weight of stems, petioles and leaf blades was determined. Leaf area was measured with an optical planimeter.

From the data of leaf length the leaf area at 12 hours' intervals was calculated as described in 3.2.2. The relative growth rate of the leaves (R_A) was then calculated for day, night and 24-hour-periods analogous to Eq. 3.4. (page 32).

The increase in stem length was determined from the measurements at the beginning and the end of the experimental period. Leaf weight ratio (LWR) and specific leaf area (SLA) were calculated from the measurements of weight and area at the end of each experiment.

TABLE 5.1. Treatment codes for each combination of air and root temperature by day (DA and DR, respectively) and night (NA and NR). Series I combinations of 25/9°C, series II 25/17 and series III 25/13°C.

Treatment code	Series I				Series II				Series III			
	DA	NA	DR	NR	DA	NA	DR	NR	DA	NA	DR	NR
Reference	25	25	25	25	25	25	25	25	25	25	25	25
DA	9	25	25	25	17	25	25	25	13	25	25	25
NA	25	9	25	25	25	17	25	25	25	13	25	25
DR	25	25	9	25	25	25	17	25	25	25	13	25
NR	25	25	25	9	25	25	25	17	25	25	25	13
DA, NA	9	9	25	25	17	17	25	25	13	13	25	25
DR, NR	25	25	9	9	25	25	17	17	25	25	13	13
DA, DR	9	25	9	25	17	25	17	25	13	25	13	25
NA, NR	25	9	25	9	25	17	25	17	25	13	25	13
DA, NR	9	25	25	9	17	25	25	17	13	25	25	13
NA, DR	25	9	9	25	25	17	17	25	25	13	13	25
DA, NA, DR	9	9	9	25	17	17	17	25	13	13	13	25
DA, NA, NR	9	9	25	9	17	17	25	17	13	13	25	13
DA, DR, NR	9	25	9	9	17	25	17	17	13	25	13	13
NA, DR, NR	25	9	9	9	25	17	17	17	25	13	13	13
DA, NA, DR, NR	9	9	9	9	17	17	17	17	13	13	13	13

5.3. RESULTS AND DISCUSSION

5.3.1. General

The variability between the three subsequent series was analysed by comparing the data of various plant parameters for each series at the reference treatment with a constant air and root temperature of 25°C (Table 5.2). Although each treatment consisted of three plants only, the values of LSD indicate, that accurate estimates of the plant parameters were obtained in this experiment.

Stem growth was slightly smaller and leaf growth slightly greater during the first series, while SLA was somewhat higher in the third one. However, the differences between the series were hardly significant. To ensure a proper comparison between the various imposed temperatures, each parameter was expressed as a percentage of its reference at 25°C. The results are presented in the Figures 5.1 to 5.6.

5.3.2. Stem growth

Stem growth depended strongly on the air temperature during the day (DA) (Figure 5.1). The effect of NA and DR was almost the same but much less than that of DA, while the effect of NR was negligible.

A decrease in air temperature during day and night (DA, NA) caused a more than additive reduction of stem growth. The effect of root temperature during day and night (DR, NR) was also slightly more than additive but less pronoun-

TABLE 5.2. Plant parameters at the reference treatment (25°C air and root temperature, by day and night) for the three subsequent series. Least Significant Differences (at $p < 0,05$) are also indicated; values in parentheses are Least Significant Differences expressed as a percentage of the average value.

Period	Series I Oct. 12-19	Series II Oct. 25-Nov. 1	Series III Dec. 12-19
Stem growth (mm in 7 days)	37	42	43
LSD	5.6 (15%)	4.3 (10%)	4.6 (11%)
Relative leaf growth rate - 24 hours (d^{-1})	0.214	0.195	0.196
LSD	0.019 (9%)	0.011 (6%)	0.012 (6%)
Relative leaf growth rate - day (d^{-1})	0.169	0.165	0.163
LSD	0.014 (8%)	0.010 (6%)	0.009 (6%)
Relative leaf growth rate - night (d^{-1})	0.259	0.226	0.229
LSD	0.023 (9%)	0.016 (7%)	0.014 (6%)
Leaf weight ratio	0.768	0.758	0.753
LSD	0.022 (3%)	0.017 (2%)	0.013 (2%)
Specific leaf area ($cm^2 g^{-1}$)	730	752	787
LSD	36 (5%)	45 (6%)	39 (5%)

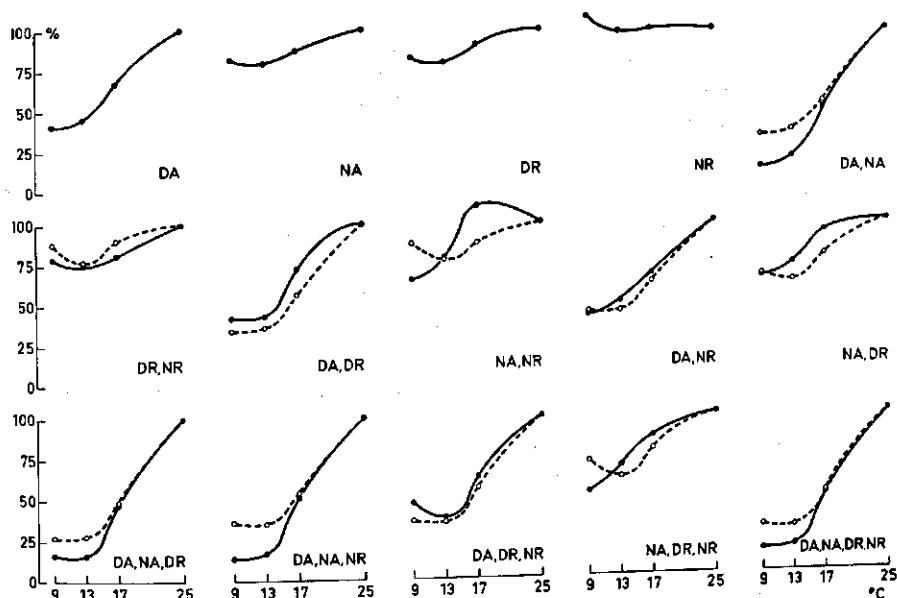


FIG. 5.1. Stem growth at various temperature regimes as a percentage of the reference at 25°C (see Table 5.2). Broken lines indicate the values obtained when the effects are assumed to be additive.

ced than in the case of air temperature. Combination of low air and root temperatures during the day (DA, DR) caused a less than additive effect on stem growth. At relatively low air and root temperatures during the night (NA, NR), however, an interesting interaction occurred: at 9°C the reduction of stem growth was more than additional, at 13°C just additional whereas at 17°C a significant increase in stem growth was observed. Whether this is just coincidental or a demonstration of a thermoperiodic response, cannot be concluded from this single observation. The latter would indicate, that thermoperiodicity of growth in the tomato only exists in the range between 25 and 17°C, when both air and root temperature are lowered by night. Thermoperiodicity has often been observed with larger plants, where plant height usually was represented as a growth parameter (WENT, 1945; VERKERK, 1955). When also DR was decreased (NA, DR, NR) no increase of stem growth at 17°C was observed, although growth reduction was less than additive. FRIEND and HELSON (1976) found no difference in growth of tomato plants at either 35°C (day)/15°C (night) or 25°C throughout.

In general the temperature effect on stem growth was relatively larger between 25 and 13°C than below 13°C. This indicates, that stem growth at 13°C is reduced so far, that a further reduction can hardly be achieved.

5.3.3. Relative leaf growth rate

The relative leaf growth rate at the reference treatment was approximately 20% per day (Table 5.2), which means a doubling of leaf area in $3\frac{1}{2}$ days, or a fourfold increase during the experimental week. Within a treatment an average standard deviation of only 2 to 3% of the mean value occurred.

Leaf growth rate was largely influenced by air temperature during daytime (Figure 5.2, DA); the effects of NA, DR or NR were almost the same and much smaller than that of DA. When both day and night air temperature (DA, NA) decreased, a slightly more than additive growth reduction occurred. When air temperature is low root temperature is of minor importance only. Reduction of root temperature during day and night (DR, NR) caused a more than additive growth reduction. A reasonable growth rate can be maintained in case root temperature is optimal during either day or night.

The combinations DA, DR and NA, NR demonstrated an additive decrease of leaf growth rate with declining temperatures, except at 17°C (NA, NR), where almost no growth reduction occurred.

The effect of temperature on leaf growth was in general slightly smaller between 25 and 17°C than between 17 and 9°C. Obviously the range of optimal temperatures for leaf growth is wider and the minimum temperature lower as compared with stem growth.

The rate of leaf growth during night was approximately 40 percent higher than that during the day at a constant air and root temperature of 25°C. In

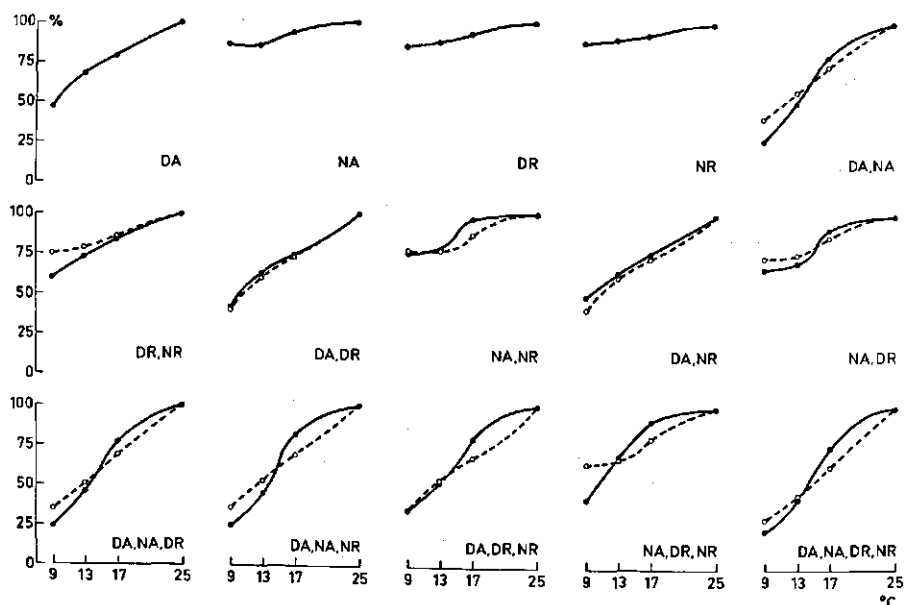


FIG. 5.2. Relative leaf growth rate at various temperature regimes as a percentage of the reference at 25°C (see Table 5.2). Broken lines indicate the values obtained when the effects are assumed to be additive.

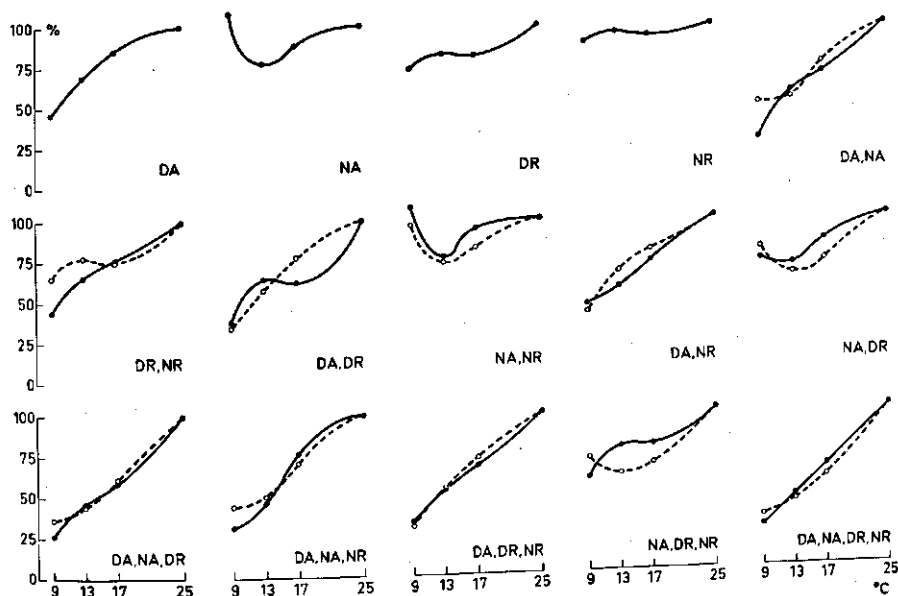


FIG. 5.3. Relative leaf growth rate during the light period at various temperature regimes as a percentage of the reference at 25°C (see Table 5.2). Broken lines indicate the values obtained when the effects are assumed to be additive.

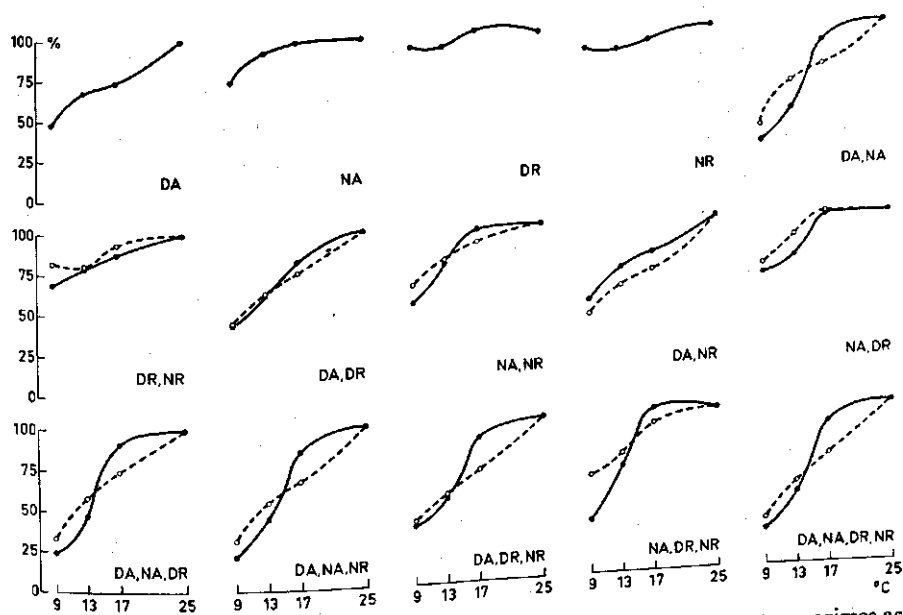


FIG. 5.4. Relative leaf growth rate during the dark period at various temperature regimes as a percentage of the reference at 25°C (see Table 5.2.) Broken lines indicate the values obtained when the effects are assumed to be additive.

Figure 5.3. and 5.4., therefore, leaf growth during day and night is presented separately.

It appears that the temperature regime during the day not only affected the growth rate during the day, but also that during the night and vice versa. A decrease of air temperature during the day (DA) reduced leaf growth during the day and that during the night. At 17°C the reduction of growth during the night was even more pronounced than that during the day. Air temperatures of 17 and 13°C during the night reduced leaf growth during the day more than that during the night; when air temperature during the night was 9°C, however, leaf growth during the day increased. In this case the growth reduction was thus partly compensated when more favourable conditions occurred.

Root temperature during the day did not affect growth rate by night significantly, but a decline of root temperature during the night equally affected leaf growth during day and night.

5.3.4. Leaf Weight Ratio and Specific Leaf Area

Leaf Weight Ratio and Specific Leaf Area were calculated from the data on plant weight and leaf area obtained at the end of each series. By this time large differences in plant size occurred between the various treatments, especially in the first series (25/9°C). Since leaf weight ratio strongly depends on plant size (Section 3.3.3.4.), the values had to be corrected for plant size in order to assess the actual temperature effect on this parameter. The relation between LWR and total dry weight of the plants at the reference treatments agreed with that obtained in Chapter 3.

Since LWR was found to be proportional to $W^{-0.1}$ (Eq. 3.2) all values of LWR were multiplied with a correction factor equal to $(W_{ref}/W_{tr})^{-0.1}$, in which W_{ref} is the dry weight at the reference treatment, and W_{tr} is the dry weight at the treatment considered. The correction factor ranged between 0.95 and 1.0 in all cases.

LWR appeared to be quite insensitive to temperature (Figure 5.5). When air temperature was continuously below 17°C there was a small but significant increase in the leaf weight ratio. This result was obtained irrespective of the root temperature. The small decrease of LWR at low root temperatures which was reported in Chapter 3 was confirmed by this experiment. It was only significant when root temperatures were low by day and night.

Specific Leaf Area was not corrected for the effect of plant size, although a significant negative correlation with plant size was demonstrated in Chapter 3 at optimum and high root temperatures. However, this correction would have been less than 1% in all cases.

The effect of day or night temperature (DA and NA) on SLA was relatively small, but when both were decreased (DA, NA) the reduction of SLA was much more pronounced. Between 25 and 13°C the effects were approximately additive but at 9°C a much sharper decline was observed with the combined treatment as compared with an air temperature of 9°C by day or night only. At a constant low air temperature, no effect of root temperature was observed.

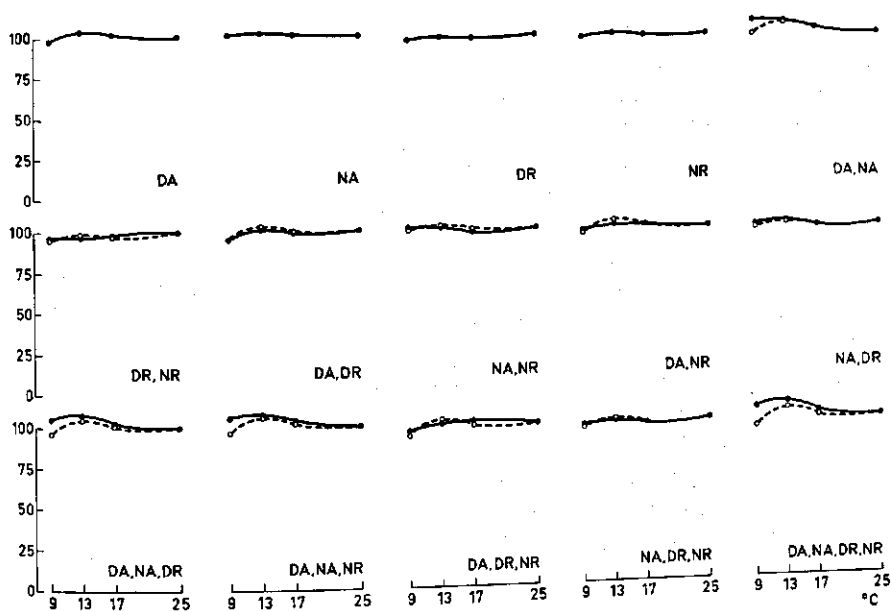


FIG. 5.5. Leaf Weight Ratio after one week at various temperature regimes as a percentage of the reference at 25°C (see Table 5.2). Broken lines indicate the values obtained when the effects are assumed to be additive.

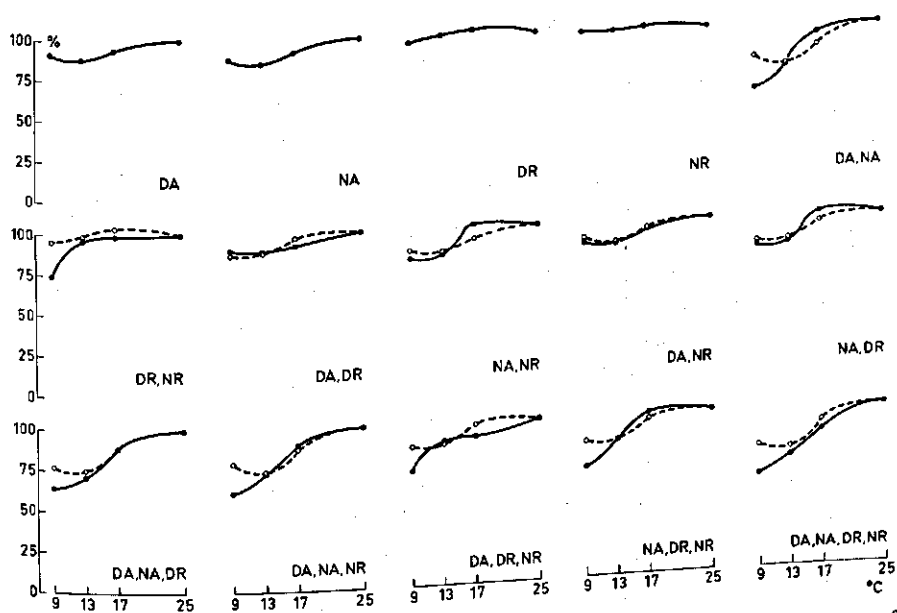


FIG. 5.6. Specific Leaf Area after one week at various temperature regimes as a percentage of the reference at 25°C (see Table 5.2). Broken lines indicate the values obtained when the effects are assumed to be additive.

Low root temperature during either day or night (DR and NR) did not affect SLA, but constant root temperatures below 13°C (DR, NR) reduced SLA markedly. The effect of equal air and root temperatures by day (DA, DR) was the same as that of air temperature by day alone (DA) and the same was true for those by night (NA, NR compared with NA).

5.3.5. General discussion

The observed effect of DA on growth of young tomato plants was large (Figures 5.1 and 5.2). Growth depended much more on DA than on NA, which is in accordance with results obtained by CALVERT (1962 and 1964). HUSSEY (1965) also reported a greater effect of day temperature on growth of young tomato plants compared with that of night temperature. He noticed, that the main effect of a higher night temperature was a stimulation of leaf growth during the night. In our experiment air temperatures by night affected leaf growth rate during the day more than that during the night, at least at 13 and 17°C. Whether this occurs also between 17 and 25°C, which range was used by HUSSEY (1965), cannot be concluded from the present experiment. Since Hussey did not control root temperature, another explanation of the apparent difference can be suggested. When both air and root temperature are varied, the relative effect of night temperature on leaf growth during the day is approximately equal to that during the night. Since the growth rate of leaves is generally larger during the night, the absolute effect of night temperature can be larger on growth by night than by day.

ABD EL RAHMAN, et. al. (1959a) reported a decrease of stem growth at temperatures below 15°C during the night, which is in agreement with the results presented in this paper. They also reported a slight increase of SLA at decreasing temperatures below 15°C, and this is in contrast with the results shown in Figure 5.6.

HORI, et. al. (1968) studied the effect of controlled air and root temperatures on growth of young tomato plants and reported a decreased growth rate at temperatures below 23°C. The effect of air temperature was greater than that of root temperature. The relative importance of day and night temperatures could not be assessed, since fixed combinations of DA/NA were used (28/23, 23/18 and 18/13°C, respectively).

Leaf growth proceeds at a higher rate during the night than during the day. BOLAS and MELVILLE (1933) reported, that growth of tomato leaves almost ceased during the day at high light intensities. CHEN, et al. (1968) reported an average ratio between leaf growth rate during the day and that during the night of 1 : 1.6 for tobacco. In our experiment the ratio was 1 : 1.5 (Table 5.2) for tomato.

In 3.3 it was shown, that the overall leaf growth rate is closely linked to three parameters, namely LWR, SLA and NAR. LWR appeared to be insensitive to temperature. SLA generally decreased at decreasing temperatures, and this decrease was always accompanied by a decrease in growth. However, the relatively large effect of DA on growth, compared with that of NA cannot be

ascribed to differences in SLA. It therefore seems likely, that NAR is affected by the air temperature during the day. This is in accordance with the conclusion of FRIEND and HELSON (1976).

5.4. CONCLUSIONS

Air temperature by day is by far the most important factor for growth of young tomato plants. The effect of root temperature is small, and completely obscured when air temperature is continuously low. A low root temperature during part of the day reduced the growth rate only slightly but at a continuous low root temperature the growth reduction is more pronounced.

Stem growth is slightly more sensitive to temperature in the range from 13 to 25°C than below 13°C, whereas leaf growth rate is affected relatively more between 13 and 9°C.

Leaf growth rate is higher during the dark period than in light, the ratio between both being approximately 1.5 at 25°C. The temperature regime during one part of the day often also affects leaf growth rate during the other part of the day.

Leaf weight ratio is rather independent of temperature. Only when air temperature is continuously lower than 17°C, there is a small but significant increase in this parameter.

Specific leaf area is decreased by declining air and root temperatures, but the effect is only small between 17 and 25°C. A low root temperature during part of the day has no effect on this parameter but a sharp decline is observed when root temperature is continuously below 13°C. Although the net assimilation rate was not determined, it was concluded from the results, that this parameter is reduced by low air temperatures during the day.

6. PHYSIOLOGICAL BACKGROUND OF THE GROWTH REDUCTION AT LOW ROOT TEMPERATURES

6.1. INTRODUCTION

The literature on the physiological background of the effect of suboptimal root temperatures on plant growth in general, and in particular on growth of young tomato plants has been briefly reviewed in Section 2.3. It was mentioned that a number of processes such as root growth, water uptake, mineral uptake and translocation, are affected by root temperature. Some processes may be affected without being the rate-limiting factor. It is thus not sufficient to know which processes are affected, but their relative importance should be considered as well.

In this Chapter some experiments will be reported with the ultimate aim to describe the mechanism of growth reduction in tomato plants at a suboptimal root temperature. It was shown in Chapter 3, that the decreasing growth rate at a low root temperature was accompanied by a systematic decline in specific leaf area. Leaf growth and specific leaf area were clearly reduced only when the root temperature was low during day and night (Chapter 5). When root temperature was low during part of the day only, growth was slightly reduced and SLA was unaffected. Specific leaf area and leaf growth rate seem to be linked in the response of young tomato plants to root temperature.

These parameters, therefore, will be discussed in relation to root temperature and water balance of the plants. Since phosphorus uptake has frequently been mentioned as an important factor in the response of tomato plants to root temperature, its role in the relation between root temperature and leaf growth rate will be discussed in a subsequent section. Finally the effect of phytohormones on growth of tomato plants will be discussed in relation to root temperature.

6.2. MATERIALS AND METHODS

Although the experiments described in this chapter were rather diverse, the design was generally the same. Therefore, in this section the main experimental technique will be described. Important deviations will be mentioned in subsequent sections.

Seeds of tomato were sown and the plants selected and transplanted into 5-litre plastic pots, as described in Section 3.2.1. The pots were put on benches in a glasshouse, where the temperature was kept at 20 to 22°C during the day, and at 15°C during the night. Since the air temperature could be controlled by heating and ventilation only, the temperature in midsummer sometimes rose to about 30°C by day and to 20°C by night. Successive sowings were done

between March and October in order to obtain an adequate number of plants of the right size at any moment. When the fifth leaf had a length of approximately 1 cm, the pots were placed into Wisconsin tanks and root temperature was controlled at 25°C for two or three days. By this time the sixth leaf was 1 cm long and the plants were selected for uniformity once more. Two root temperatures were generally applied, viz. 10 and 25°C, while at the same time the other treatments were imposed, which will be described in the following sections. Three plants per treatment were used throughout.

During the experimental period of seven days leaf length was measured daily at 9 A.M., while plant height was measured at the beginning and at the end of this period. The plants were harvested and fresh and dry weight of stems, petioles and leaf blades was determined. Leaf area was measured with an optical planimeter. Air temperature and relative humidity were recorded with a thermohygrograph and evaporation with a Piche evaporimeter.

6.3. RESULTS AND DISCUSSION

6.3.1. *Leaf expansion and specific leaf area in relation to root temperature and water balance*

6.3.1.1. Introduction

No direct evidence has been obtained, that the declining growth rate of young tomato plants at low root temperatures is primarily caused by an increased resistance in the water uptake pathway (Section 2.3.). In that case the effect of root temperature should be larger in summer than in winter, since the evaporative demand in summer is much greater. Such an effect was not observed in the experiments described in Chapter 3. Moreover, a low root temperature during the day should be more effective in limiting growth, than a low root temperature during the night, but in Chapter 5 it was shown that this was not the case. This suggests that a causal relationship between leaf expansion rate and a water deficit of the leaves at low root temperatures does not exist. More direct evidence on the absence of such a relationship however, is necessary. To achieve this aim experiments should be designed in which the water status of the leaves and root temperature are varied. Control of the water balance of the plant, without affecting other plant parameters, however, is almost impossible. In principle three methods could be applied to vary the water balance of a transpiring plant: by changing the evaporative conditions in the environment, by changing the ratio between the transpiring leaf area and the absorbing root surface of the plants, and finally by changing the availability of water in the rooting medium.

The first method can be achieved by controlling radiation intensity or relative humidity, but an accurate control of humidity was not available for these experiments. Variation of radiation would affect other growth determining processes such as photosynthesis as well. Changes in the ratio between the transpiring leaf surface and the absorbing root surface could be achieved either

by cutting part of the leaves or by growing plants on a double root system by approach-grafting. The latter method has been used by LONG (1943) in studies on salt-uptake and by JACKSON (1956) on flooding injury of tomatoes. It was tried, but had to be abandoned for practical reasons. In most cases the graft functioned only partly, which made the plant to plant differences in growth and development too large. Moreover the establishment of the graft took so much time, that the plants grew too large to be easily handled. No reproducible results could be obtained in this way. The remaining possibilities were then leaf pruning and changing the availability of water.

Two experiments will be reported, one in which part of the leaf area was removed and the other in which different soil moisture regimes were applied. In both experiments a root temperature of 25 and 10°C was used.

6.3.1.2. Partial defoliation

The treatments and the results of the experiment on leaf pruning are shown in Table 6.1. The lower three leaves were halved by cutting each second leaflet in the 40% leaf area reduction treatment, and the lower three leaves were fully removed in the 80% treatment. The length of leaves 4 to 6 was measured and at the final harvest the specific leaf area of these leaves was determined.

The partial removal of leaves not only reduced the transpirational demand of the plants, but inhibited the production of assimilates necessary for growth as well. Stem growth was reduced by approximately 50% after an 80% reduction of the leaf area at both root temperatures. Leaf growth rate decreased less at the optimal root temperature, whereas no significant reduction of leaf growth due to leaf pruning was observed at 10°C. Specific leaf area was not affected by the removal of leaves at the optimal root temperature but increased after an 80% removal of leaves at the low root temperature.

Although the pruning of leaves aimed at reducing the waterloss of the plants without affecting other processes, assimilation was reduced as well. Stem

TABLE 6.1. Effect of root temperature and pruning of leaves on stem growth, leaf growth and Specific Leaf Area.

treatment		results		
root temp. °C	leaf area reduction %	stem growth mm d ⁻¹	leaf growth mm d ⁻¹	specific leaf area cm ² g ⁻¹
25	0	7.3 ± 0.7	7.3 ± 0.3	737 ± 6
25	40	5.1 ± 0.4	5.9 ± 0.3	712 ± 21
25	80	3.4 ± 0.3	5.2 ± 0.2	740 ± 20
10	0	4.8 ± 0.4	4.0 ± 0.4	535 ± 14
10	40	3.8 ± 0.2	4.3 ± 0.2	566 ± 6
10	80	2.4 ± 0.2	3.7 ± 0.3	702 ± 12

growth was reduced by pruning at both root temperatures, whereas leaf growth was reduced at the optimum temperature only. This suggests, that assimilation was the rate-limiting factor for growth of stems and leaves at the optimum root temperature, and for stem growth only at 10°C root temperature. Whether the uptake of water at low root temperature was limiting leaf growth rate in the latter case, however, can not be deduced from the results.

6.3.1.3. Soil moisture

In a second experiment the moisture content of the soil was varied. Preliminary experiments had shown, that leaf growth was not affected in the moisture range between pF 1.2 and 2.5. A significant decrease in leaf growth rate occurs at pF 3.0, while growth is almost zero at pF 3.8.

A moderate water deficit was imposed in the present experiment. For this purpose a set of plants was left unirrigated until the soil reached a pF of 3.2. Thereafter soil moisture was kept between pF 3.0 and 3.2 by irrigation. Although no uniform soil moisture distribution in depth of the profile will be obtained in this way, it reduces the rooting zone where water is available for the plants. Another set of plants was kept at the normal soil moisture tension of approximately pF 1.5. When the experimental root temperatures (Table 6.2.) were imposed, differences in size were already present between the plants kept at the normal soil moisture tension and those of the dry series. The treatments were continued for one week and the lengths of the 4th till the 8th leaves were measured daily. At the end of the experiment fresh and dry weight and leaf area was determined and specific leaf area calculated.

TABLE 6.2. Effect of root temperature and soil moisture on leaf growth and Specific Leaf Area.

Treatment		Results	
root temp. °C	soil moisture pF	leaf growth mm d ⁻¹	specific leaf area cm ² g ⁻¹
25	1.5	14.4 ± 0.3	330 ± 14
25	3.0-3.2	7.7 ± 0.5	332 ± 9
10	1.5	8.3 ± 0.2	286 ± 19
10	3.0-3.2	4.5 ± 0.3	290 ± 3

Leaf growth was markedly reduced by the low water content of the soil (Table 6.2.). The percentual decline at both root temperatures was almost the same, which means that the effects are approximately additive.

Specific leaf area was not influenced by the water availability but was, as expected, reduced by low root temperature. This suggests, that the factor involved in the decline of leaf growth at a low root temperature is not the reduced availability of water.

6.3.1.4. Reversibility of root temperature effects

In order to obtain some idea of the reversibility of the root temperature effects, plants were raised as usual until the sixth leaf reached a length of 1 cm. Thereafter one set of plants was brought to 12°C root temperature for a period of 4½ days, after which root temperature was changed to 25°C for another 4½ days. Another set of plants was kept continuously at a temperature of 25°C. In both treatments leaf length of three plants was measured twice a day, at 6.00 A.M. and 6.00 P.M. At the same time three other plants were harvested to determine specific leaf area.

The relative leaf growth rates during day and night are shown in Figure 6.1. for both treatments. The values during the day were much lower than those at night, while day to day variations were large. The low temperature immediately reduced the rate of leaf growth, which remained more or less the same thereafter. After the 5th day, when root temperature was changed from 10°C to 25°C the growth rate recovered immediately and became higher than that of the control treatment. The growth rate during the day remained relatively low for two days and recovered thereafter, being slightly higher than the control.

Specific Leaf Area (Figure 6.2.) showed a significant diurnal fluctuation. SLA generally decreased by day and increased by night. During the low root temperature treatment of 4½ days SLA of these plants gradually declined relative to that of the control plants. After the change to the optimal temperature a gradual increase occurred until almost equal values were obtained at the end of the experiment. The decrease and increase of SLA was due mainly to changes during the night.

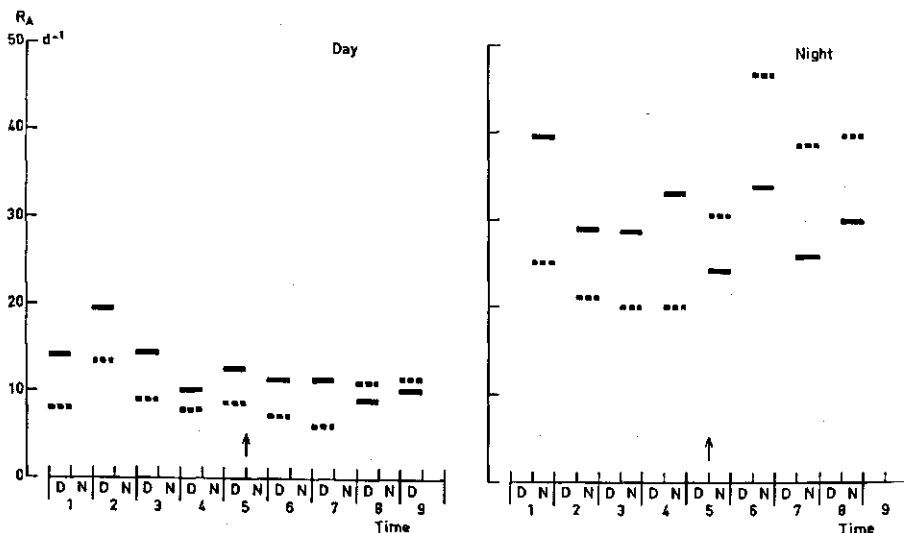


FIG. 6.1. Leaf growth rate (R_A) during day (left) and night (right). Full drawn lines: at 25°C root temperature throughout, broken lines: first 4½ days at 12°C, thereafter at 25°C root temperature.

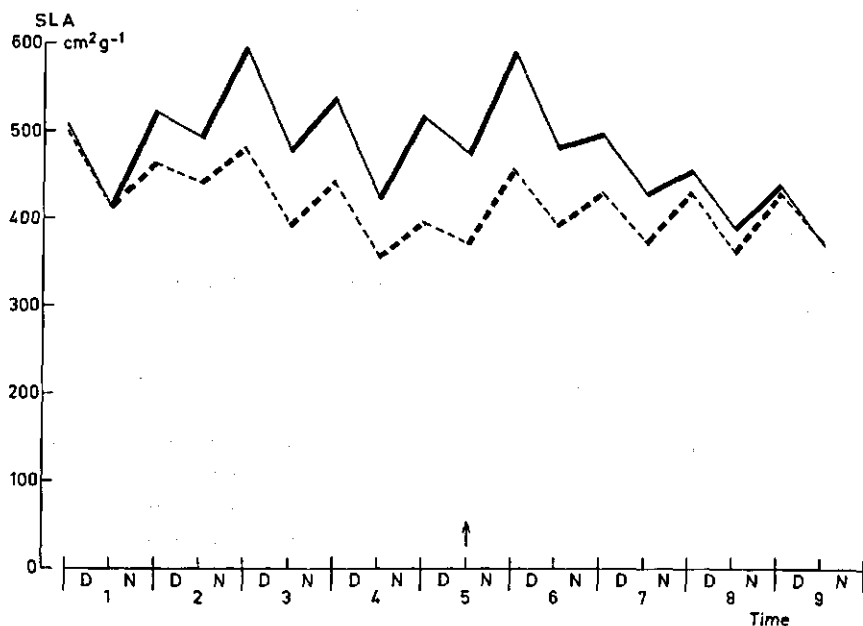


FIG. 6.2. Specific Leaf Area (SLA) at the beginning of the day (6.00 A.M.) and at the beginning of the night (6.00 P.M.). Full drawn lines: at 25°C root temperature throughout, broken lines: first 4½ days at 12°C, thereafter at 25°C root temperature.

Since SLA is the ratio between leaf area and dry weight a certain change of SLA with time will be the result of a change in either one of these parameters or in both. It should be kept in mind, that leaf dry weight increases mainly during the day and leaf area during the night.

In order to assess, whether the observed effect of root temperature on SLA was due to changes in leaf expansion, or in dry weight of the leaves, a balance was calculated for each day and each night from values of specific leaf area and relative leaf growth rate.

If for a given period, either day or night,

A_i is the initial leaf area (cm^2),

A_f is the final leaf area (cm^2),

S_i is the initial SLA ($\text{cm}^2 \text{g}^{-1}$),

S_f is the final SLA ($\text{cm}^2 \text{g}^{-1}$),

R_A is the relative leaf growth rate ($\text{cm}^2 \text{cm}^{-2} \text{d}^{-1}$),

t is the length of the period (d),

then the absolute increase in leaf dry weight (ΔD) during that period is given by:

$$\Delta D = \frac{A_f}{S_f} - \frac{A_i}{S_i} \quad (\text{g})$$

or, per unit leaf area initially present:

$$\frac{\Delta D}{A_i} = \frac{A_f}{A_i} \times \frac{1}{S_f} - \frac{1}{S_i} \quad (\text{g cm}^{-2})$$

Now, since

$$\frac{A_f}{A_i} = \exp \cdot (R_A \cdot \Delta t),$$

the increase in dry weight of the leaves per unit leaf area initially present is given by:

$$\frac{\Delta D}{A_i} = \frac{1}{S_f} \times \exp. (R_A \cdot \Delta t) - \frac{1}{S_i} \quad (\text{g cm}^{-2}) \quad (6.1)$$

The values thus obtained are listed in Table 6.3. Since these values were calculated from differences between various plants a rather large error in these estimates may be expected. Bearing this in mind it appears, that the root temperature treatments did not affect the dry matter balance of the leaves, since no systematic differences occur. During the day there was a positive gain in dry weight, which gain depends on radiation as is shown in Figure 6.3. For comparison, the curve from Figure 3.12. representing weekly averages of net assimilation rate is also shown in the figure. The results from the present experiment fairly well coincide with those reported in Chapter 3. It again confirms, that net assimilation rate is not affected by root temperature.

During the night the dry matter balance was almost zero (Table 6.3). In the second half of the experiment mainly positive values were obtained at both treatments, specially during the sixth night. No environmental factor could be found which was directly related to this phenomenon.

In summarizing the results, one may conclude that the effect of root tem-

TABLE 6.3. Increase in dry weight per unit leaf area initially present, for each 12-hours' period between 6.00 A.M. and 6.00 P.M., calculated with Eq. 6.1. Treatment I at 25°C root temperature continuously, treatment II for 4¹/₂ days at 12°C, thereafter at 25°C root temperature.

Period	Treatment		Period	Treatment	
DAY	I	II	NIGHT	I	II
1	0.65	0.54	1	- 0.09	+0.02
2	0.32	0.37	2	- 0.09	+0.04
3	0.57	0.59	3	+0.06	- 0.05
4	0.62	0.66	4	- 0.08	- 0.02
5	0.31	0.29	5	- 0.19	- 0.13
6	0.50	0.44	6	+0.31	+0.40
7	0.45	0.44	7	+0.17	+0.15
8	0.48	0.59	8	+0.09	+0.08
9	0.56	0.51			

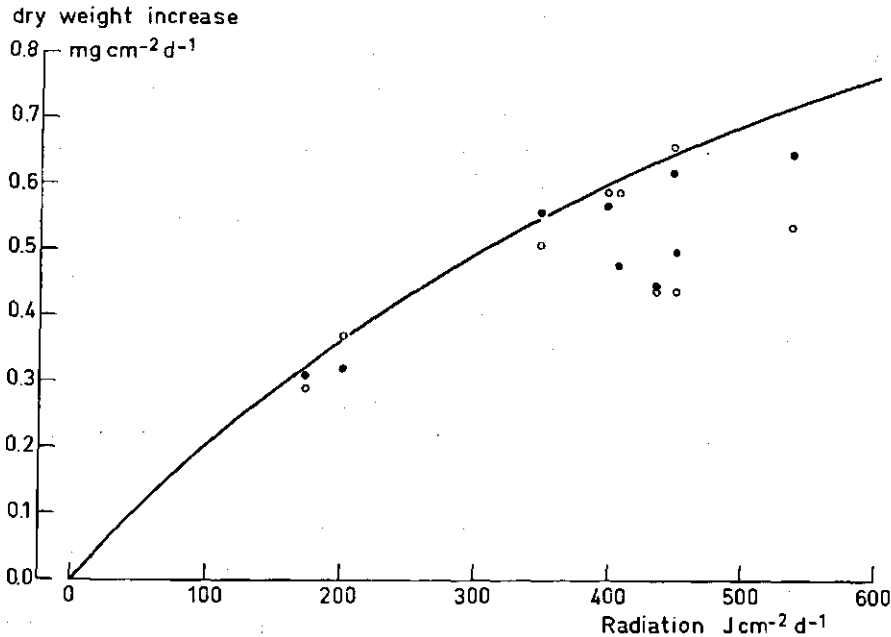


FIG. 6.3. Dry weight increase of leaves during the day per unit leaf area, vs. radiation. (● : at 25°C root temperature throughout; ○ : first 4½ days at 12°C, thereafter at 25°C root temperature). The curve gives the relationship between NAR and radiation, shown in Figure 3.12.

perature on Specific Leaf Area, and thus on growth, is reversible, at least within the experimental period of five days. This means, that a low root temperature during a short period can be compensated by optimal temperatures later on. It should be realized, however, that plant size will not reach the same value because the interception of radiation has been less for some time. Brouwer (1973) also mentioned, that effects of root temperature on growth of beans were, at least partly, reversible. After longer periods, however, also structural differences develop, which are irreversible.

The effect of root temperature on Specific Leaf Area is mainly due to the leaf expansion rate and not to the gain or loss in dry weight of the leaves.

6.3.2. Root temperature and the supply of minerals

The symptoms of tomato plants growing at a low root temperature fairly well resemble those at a low level of phosphorus nutrition. Therefore a reduced uptake of this element often has been proposed as one of the major causes of growth reduction at suboptimal root temperatures (Section 2.3.).

In the previous sections it has been shown that plant growth and especially leaf expansion rate declines rapidly after a decrease in root temperature. Such a fast response can hardly be ascribed to nutrient deficiency. In most cases plants, grown with an adequate supply of minerals demonstrate signs of

deficiency only after some days of decreased supply. In young plants, however, the growth rate is high and the storage small, so that a more rapid response may be expected. Therefore the role of phosphorus supply in relation to low root temperatures on growth was examined.

The experimental approach, proposed by Bonner and cited by KETELLAPPER (1963) was followed, according to the concept of chemical cure of climatic lesions. The assumption of this approach is, that a suboptimal climatic condition causes a shortage of one or more essential metabolites, which can be cured by supplying these substances externally. Since the application of a foliar spray of a monopotassiumphosphate solution can suppress phosphate deficiency in many plant species (VAN DIEST, personal communication), this technique was used in the present experiment.

Plants were raised as previously described until the sixth leaf was 1 cm long. Root temperatures of 10 and 25°C were then imposed for one week. On the first and fourth day the plants were sprayed with a 0, 2.5 or 5% solution of KH_2PO_4 , combined with 0.1% Tween-20 as a wetting agent. The length of the three higher leaves was measured daily and at the end of the experiment the Specific Leaf Area of these leaves was determined. The treatments and their results are listed in Table 6.4. It appears, that the application of phosphate solutions did not have any effect on the plant parameters determined at a root temperature of 25°C as well as 10°C.

The lack of response to phosphorus supply and the rapid decline of growth with a decrease in root temperature mentioned earlier, led to the conclusion, that phosphorus uptake is not likely to be the primary limiting factor in the growth of young tomato plants at low root temperatures. In Section 2.3 it was mentioned that on this subject the literature is contradictory. There is general agreement, however, that the phosphorus content of the plant decreases at low root temperatures (e.g. LOCASCIO and WARREN, 1960; JAWORSKI and VALLI, 1964). The phosphorus content is usually expressed on a dry weight basis. Dry weight increase is reduced relatively less than fresh weight at low root

TABLE 6.4. Effect of root temperature and phosphate application on leaf growth and Specific Leaf Area.

treatment		results	
root temp. °C	conc. KH_2PO_4 % (ww)	average growth of 4 th to 6 th leaves mm d^{-1}	average SLA of 4 th to 6 th leaves $\text{cm}^2 \text{g}^{-1}$
25	0	12.4 ± 0.3	356 ± 12
25	2.5	12.8 ± 0.5	361 ± 7
25	5.0	12.6 ± 0.3	358 ± 5
10	0	6.9 ± 0.2	255 ± 13
10	2.5	7.4 ± 0.4	225 ± 8
10	5.0	7.1 ± 0.3	251 ± 11

temperatures. The lower phosphorus content, therefore, may be partly caused by the increased dry matter content.

No further study on the relation between nutrient supply and root temperature was made, since this relation was not considered to be the most important one.

6.3.3. *Root temperature and phytohormones*

6.3.3.1. Introduction

In recent years increasing evidence is obtained, that phytohormones play a decisive role in the regulation of growth. Hormones are generally produced at specific sites in the plant and are then transported to other regions where certain processes in growth or development are regulated. Low temperatures in the rooting zone of plants may exert their influence on the aerial part by changing the hormonal balance.

The study of phytohormones, their production, transport, site and mode of action at present is a highly specialized field of research and a detailed analysis of the hormonal balances which regulate the growth of young tomato plants obviously was beyond the scope of the present work. A complete and detailed review of the literature on this subject therefore is not given and some references only will be mentioned, which discuss the possible relations between root temperature and phytohormones.

A review on root hormones and plant growth has been given by TORREY (1975). Three groups of phytohormones are distinguished, auxines, gibberellins and cytokinins. The latter two are known to be produced in the root system and transported to the shoot (CARR, et. al., 1964; SKENE & KERRIDGE, 1967, and JONES, 1973). Although gibberellins and cytokinins are expected to play a decisive role in the roots, important interactions have been observed between all three groups (BANERJI & LALORAYA, 1967; SCOTT, 1972, and RAILTON & REID, 1973).

In the present study experiments were done in which these substances were applied separately and in combination with each other at different root temperatures.

6.3.3.2. Materials and methods

Tomato plants were prepared as described in Section 6.2. The treatments were started when the plants had six to eight leaves. Root temperature was controlled at either 25 or 10°C and the plants were sprayed every other day with an aqueous solution with concentrations of phytohormones as listed in Table 6.5. Tween-20, at a concentration of 0.1% was added as a wetting agent. Gibberellic acid (GA_3) was used as a gibberellin, kinetin and benzyl-adenine as cytokinins and the sodiumsalt of Indolyl Acetic Acid as an auxin. The treatments were applied in three subsequent experiments. Each experiment had a reference treatment at 25°C root temperature, which was sprayed with water without phytohormones. Each experiment lasted seven days, during which leaf length

was measured daily. Stem length was measured at the beginning and the end of each experiment and fresh and dry weight and leaf area were determined at the end. Transpiration was determined by means of weighing the pots taking into account evaporative losses (see Section 3.2.).

6.3.3.3. Results

Data on stem growth, relative leaf growth rate, specific leaf area and transpiration are listed in Table 6.5. for each experiment. The plants were larger in the

TABLE 6.5. Effect of root temperature and spraying of gibberellic acid (GA_3), kinetin, benzyl adenine (BA) and indolyl acetic acid (IAA) on stem and leaf growth rate, Specific Leaf Area and transpiration rate. Absolute values are given for the control treatments at 25°C; the other figures are expressed as a percentage of this control.

Treatment			Result			
root temp. °C	substance	conc. ppm w/w	Stem growth	rel. leaf growth rate	SLA	transp. rate
25	control	0	13.2 ± 1.5 mm d ⁻¹ or 100%	0.196 ± 0.008 d ⁻¹ or 100%	503 ± 15 cm ² g ⁻¹ or 100%	121 ± 9 mg cm ⁻² d ⁻¹ or 100%
25	GA_3	25	283	103	108	109
25	GA_3	250	299	103	113	112
25	GA_3	2500	300	101	109	107
10	control	0	70	49	76	74
10	GA_3	25	289	62	93	98
10	GA_3	250	301	66	94	100
10	GA_3	2500	295	58	94	88
25	control	0	6.9 ± 0.2 mm d ⁻¹ or 100%	0.220 ± 0.005 d ⁻¹ or 100%	374 ± 4 cm ² g ⁻¹ or 100%	155 ± 5 mg cm ⁻² d ⁻¹ or 100%
25	kinetin	20	97	95	98	96
25	kinetin	200	93	90	96	101
25	B.A.	200	99	82	87	107
10	control	0	78	48	71	81
10	kinetin	20	81	53	71	85
10	kinetin	200	75	62	76	88
10	B.A.	200	78	59	74	94
25	control	0	6.3 ± 0.3 mm d ⁻¹ or 100%	0.210 ± 0.010 d ⁻¹ or 100%	481 ± 10 cm ² g ⁻¹ or 100%	104 ± 14 mg cm ⁻² d ⁻¹ or 100%
25	IAA	5	98	93	95	122
25	IAA	50	113	71	86	115
25	IAA	500	163	45	81	91
10	control	0	81	59	75	100
10	IAA	5	81	58	74	93
10	IAA	50	105	56	75	97
10	IAA	500	133	33	78	73

first experiment, which caused the relatively high stem growth rate and the low leaf growth rate (compare Section 3.3.2.2. and 3.3.5.). Daily radiation was rather high during the second experiment, which caused the lower SLA and the higher transpiration.

The effect of phytohormones is shown in the same table. All data were expressed as a percentage of that at the reference treatment during that experiment.

Gibberellic acid increased stem growth almost threefold at the optimal root temperature. A concentration of 25 ppm w/w already caused this effect, which was unaltered at concentrations up to 2500 ppm. Although stem growth was reduced by a low root temperature in the control treatment, spraying with GA₃ resulted in a more than threefold increase in stem growth, so that differences between root temperature treatments disappeared. Leaf growth rate was not affected by GA₃ at an optimum root temperature, but slightly increased at the low root temperature. SLA slightly increased by GA₃ at 25°C root temperature and more at 10°C. The same tendency was observed for transpiration.

The cytokinins kinetin (6-furfurylamino purine) and benzyl-adenine (BA) did not affect stem growth. Leaf growth, however, was reduced by the higher concentrations of either kinetin or BA at the optimal root temperature. At 10°C root temperature leaf growth was stimulated by these concentrations. SLA decreased slightly at the optimum root temperature by BA only. Transpiration was hardly affected by the application of cytokinins.

The higher concentrations of IAA enhanced stem growth at both root temperatures. Leaf growth rate declined by the application of IAA. At optimum root temperature this decline was clearly observed at a concentration of 50 ppm while at the low root temperature it occurred only at 500 ppm. SLA was reduced by IAA at the optimal but not at the suboptimal root temperature. Transpiration did not respond clearly; the observed differences are hardly significant since the standard deviation at the reference treatment was almost 14% for this experiment.

6.3.3.4. Discussion

An increase of stem growth after GA-application has been frequently reported, also for tomatoes (BROWN, et. al., 1968; MEHROTRA, et. al., 1970; MENHENNETT & WAREING, 1975). Stimulation of leaf growth in tomato by this hormone was reported by BRIANT (1974) and MENHENNETT & WAREING (1975). In our experiment it was only observed at a low root temperature. TOGNONI, et. al. (1967) reported an increase of the net assimilation rate of tomato plants after the application of gibberellins, but a decrease in the leaf area ratio (LAR), which is the product of SLA and LWR. Since SLA increased in our experiments by GA₃, it seems likely, that LWR is reduced by the application of gibberellins.

Cytokinins stimulated leaf growth at a low root temperature and slightly depressed it at an optimal root temperature in our experiments. Stimulation of growth in tomato by cytokinins was reported by PROTSKO & BOICHUK (1974) and AUNG & BYRNE (1976). The latter applied BA to the apical meristem, the

former kinetin to the leaves. Protsko and Boïchuk observed a growth reduction when kinetin was applied to the stem apex.

RAILTON & REID (1973) observed an increase in stem growth of water-logged tomato plants after foliar application of BA, but no response with non-water-logged plants.

TOGNONI, et. al. (1967), applied the auxin NAA to tomato plants, but did not observe a clear effect on growth. This is in contrast with our observation after the application of IAA. GRUNWALD & LOCKARD (1973), reported a synergism between gibberellins and auxins applied to tomato: IAA alone inhibited growth but a combined application of IAA and gibberellic acid stimulated growth more than GA₃ alone. This response, however, depended on age and cultivar.

The interactions between root temperature and hormone application described previously suggest, that there is a relation between root temperature, hormonal activity and growth. The reduction in stem growth, observed at low root temperatures is counteracted by the application of gibberellins or auxins, but stem growth is also stimulated at optimal root temperature by these substances, even at low concentrations.

Leaf growth rate is stimulated by GA₃ at a low root temperature only, suggesting that gibberellins are limiting leaf growth at this temperature. Cytokinins reduce leaf growth rate at an optimal root temperature and slightly stimulate it at a low root temperature. A higher concentration of IAA is necessary to reduce leaf growth rate at a low root temperature than at 25°C.

SLA is increased by GA₃ at both root temperatures, although the increase is more pronounced at the low root temperature. The decrease in SLA after the application of BA or IAA was only observed at an optimal root temperature.

Obviously the ultimate response of a plant depends on a delicate balance between these phytohormones. A number of experiments with combinations of various hormones were done in order to assess the interactions between them. No reproducible results could be obtained, however. Obviously the varying environmental conditions also affected the hormonal balance.

A fundamental investigation on the relation between environmental factors, hormonal balance and growth will be extremely useful in understanding the physiological background of a plants response to environmental variables. but was beyond the scope of this study.

6.4. CONCLUSIONS

Moderate water stress of tomato plants causes a reduced growth rate of the leaves, irrespective of the root temperature. This growth reduction due to water stress is not accompanied by a reduction of specific leaf area. Since specific leaf area is reduced at low root temperatures, it seems improbable that the decline of growth at a low root temperature is primarily caused by a reduced water uptake.

After a period of reduced growth rate at low root temperature, growth is

resumed at a much higher rate, when an optimal root temperature is applied. This increased growth rate is accompanied by a gradual increase of the specific leaf area to values which are normal at this root temperature. Root temperature affects specific leaf area by changes in leaf expansion; the dry matter balance of leaves is not affected.

The reduced growth rate of young tomato plants at low root temperatures is not primarily caused by a decreased uptake or availability of phosphorus.

There is some evidence that phytohormones are involved in the effect of root temperature on growth of young tomato plants. Gibberellins, cytokinins and auxins were found to interact with root temperature. Fundamental research on the relationship between environmental factors, hormonal balances and plant growth is necessary for a better understanding of the effect of root temperature on the growth of young tomato plants.

SUMMARY

During recent years sophisticated techniques are applied in the glasshouse industry for the control of the glasshouse climate. Along with that development, extensive research programs were carried out to establish optimum conditions for growth. Air temperature, radiation, CO₂-concentration and humidity of the air were the most important factors studied. Relatively little is known about optimum conditions in the root environment. Although some reports are available on the effect of root temperature on growth of tomato plants, the results have only limited applicability and were often contradictory. Therefore, the effect of root temperature on growth of young tomato plants was studied, with two objectives:

- a. to quantify the effect of root temperature on growth of young tomato plants in order to establish the profitability of root temperature control techniques in practice, and
- b. to understand the physiological background of the observed effects.

Tomato plants were raised at root temperatures of 12, 15, 20, 25, 30 and 35°C in a glasshouse under natural radiation conditions throughout the year. Air temperature ranged from 17°C in winter to 30°C in summer by day and from 15°C in winter to 20°C in summer by night. Data on plant height, number of leaves, fresh and dry weight of leaves, petioles and stems and on leaf area were recorded periodically during each experiment.

The effect of season on growth was much larger than the effect of root temperature. At root temperatures below 20°C growth was reduced irrespective of the season; above 30°C growth was reduced during the summer only. An apparent interaction between season and low root temperature could be ascribed to the fact that plants, although of the same age, were at different stages of growth after some time of treatment.

Growth analysis showed, that the reduced growth rate at low root temperature was mainly caused by a decrease of the Specific Leaf Area (SLA). Net Assimilation Rate (NAR) was not affected by root temperature. Daily measurements of leaf length revealed, that especially leaf expansion rate was reduced by low root temperatures; this reduction was not correlated with incoming radiation or evaporation in the glasshouse.

The after-effect of root temperature during raising on subsequent growth, development and yield was studied in three experiments in which plants were raised at either 12, 25 or 35°C root temperature until flowering. After transplanting the plants into a glasshouse normal cultural practices were applied. The first experiment started in very early winter (sowing in September), the second one was a normal early crop (sowing in November) while the third one was a rather late crop (sowing in January). Besides the after-effect of root temperature, the influence of the leaf area per plant was studied by partial defoliation.

The first experiment was too early for normal fruit set and almost no fruits were produced in any of the treatments. Raising the plants at a low root temperature did not adversely affect the yield in the second experiment, but reduced total yield by approximately 10% in the third one. This reduction of yield was caused by a decrease in the number of fruits. Halving the leaf area at transplanting reduced fruit set in January but was without effect later on in the season. Continuous removal of every second leaf accelerated the development during the first weeks but later on weak plants with a much smaller yield were obtained.

The relative effect on air and root temperature was studied under controlled conditions. Leaf growth rate by day and night was measured separately with various combinations of air and root temperatures by day or by night. After 7 days of treatment, Leaf Weight Ratio (LWR) and SLA were determined as well. Air temperature by day was by far the most important factor, followed by air temperature during the night. Leaf growth rate was slightly reduced when root temperature was low during part of the day only. No difference between the effect of root temperature by day and that by night was observed. Growth was reduced more than additional at continuously low root temperatures.

Since the effect of root temperature on growth was independent of season and of time-of-day, the most common hypothesis, that the growth reduction at low root temperatures is due to a reduced rate of water uptake, was doubted. Therefore, some experiments were done in which the relation between water balance, root temperature and leaf growth were studied. One of the results was, that both water stress and a low root temperature decreased leaf growth rate, but this decrease was not accompanied by a decrease in SLA at drought, whereas it was reduced at a low root temperature. These doubts on the primary rôle of the water balance in the root temperature response of tomato plants was a reason for an investigation into the possible involvement of phytohormones.

Application of phytohormones in foliar sprays on plants at low or optimum root temperatures showed, that complicated interactions exist between these factors. In some cases the growth reduction due to a low root temperature could be partly compensated by addition of gibberellines and cytokinins, but the results were too variable for definite conclusions.

Finally, it may be concluded, that root temperature is not an important factor in the practice of glasshouse tomato growing in the Netherlands. A detailed study into the hormonal balance of tomato plants will be useful for a better understanding of the growth process.

SAMENVATTING

Gedurende de laatste jaren worden in de glastuinbouw in toenemende mate verfijnde technieken voor de regeling van het kasklimaat toegepast. In verband hiermee is uitgebreid onderzoek uitgevoerd naar de optimale luchttemperatuur, belichting, CO₂-concentratie en luchtvochtigheid voor groei en ontwikkeling van de belangrijkste gewassen. In tegenstelling daarmee is de beschikbare informatie over de optimale wortelomstandigheden vrij beperkt. Hoewel in het verleden wel onderzoek naar het effect van de worteltemperatuur op de groei van tomaten is uitgevoerd, zijn de resultaten slechts beperkt bruikbaar en vaak tegenstrijdig. Daarom werd een onderzoek ingesteld naar het effect van de worteltemperatuur op de groei van jonge tomatplanten, met als doelstellingen:

- a. kwantificeren van het effect van de worteltemperatuur op de groei van jonge tomatplanten teneinde na te gaan, onder welke omstandigheden toepassing van bodemverwarming rendabel zou kunnen zijn in de praktijk, en
- b. verkrijgen van inzicht in de fysiologische achtergronden van de reactie van tomatplanten op verschillende worteltemperaturen, teneinde de verkregen resultaten te kunnen generaliseren.

In een zevental experimenten, verspreid over een heel jaar, werden tomatplanten opgekweekt bij worteltemperaturen van 12, 15, 20, 25, 30 en 35°C, vanaf het kiemplantstadium tot aan de bloei. De proeven werden uitgevoerd in een kas onder natuurlijke lichtomstandigheden, en bij luchttemperaturen tussen 17°C in de winter en 30°C in de zomer (overdag) en tussen 15°C in de winter en 20°C in de zomer ('s nachts). Plantgrootte, bladaantal, vers en drooggewicht van bladeren, bladstelen en stengel en het bladoppervlak werden periodiek bepaald.

Seizoeninvloeden op de groei waren veel groter dan de invloed van de worteltemperatuur. Bij worteltemperaturen beneden 20°C trad een groeireductie op, ongeacht het seizoen; boven 30°C werd de groei alleen gedurende de zomer geremd. Een ogenschijnlijke interactie tussen seizoen en lage worteltemperaturen bleek toegeschreven te kunnen worden aan de verschillende groeistadia waarin de planten zich bij een bepaalde leeftijd bevonden.

Een groeianalyse toonde aan, dat de groeivermindering bij lage worteltemperatuur vooral werd veroorzaakt door een daling van de Specific Leaf Area (SLA, het bladoppervlak per gram bladgewicht). De Net Assimilation Rate (NAR, de drooggewichttoename van de plant per cm² bladoppervlak) werd niet door de worteltemperatuur beïnvloed. Dagelijkse bladlengte metingen gaven aan, dat vooral de bladstrekking door een lage worteltemperatuur wordt geremd; deze remming was niet gecorreleerd met de inkomende straling of met de evaporatie in de kas.

Teneinde na te gaan wat het gevolg van opkweek bij verschillende worteltemperaturen zou zijn op de verdere ontwikkeling en productie van de tomaat,

werden in drie achtereenvolgende proeven planten opgekweekt bij zowel 12, 25 als 35°C worteltemperatuur tot aan het bloeistadium, en vervolgens in een kas uitgeplant en als een commercieel gewas behandeld. De eerste proef werd extreem vroeg in de winter uitgevoerd (gezaaid in september), de tweede op een normale tijd voor een vroege teelt (gezaaid in november) en de derde betrekkelijk laat in de winter (gezaaid in januari). Naast een eventueel na-effect van de worteltemperatuur tijdens de opkweek, werd de invloed nagegaan van het aanwezige bladoppervlak, door middel van gedeeltelijke bladsnoei.

De eerste proef was te vroeg in het seizoen om tot een redelijke productie te komen. Opkweek bij een lage worteltemperatuur had geen effect op de productie in de tweede proef, maar veroorzaakte een reductie van ongeveer 10% in de derde proef. Deze reductie was een gevolg van een verminderd aantal vruchten. Halvering van het bladoppervlak bij het uitplanten in de kas beperkte de vruchtzetting in januari, maar had geen gevolg later in het seizoen. Het continu verwijderen van elk tweede blad versnelde de ontwikkeling aanvankelijk, maar leidde op de duur tot verzwakte planten met een veel lagere opbrengst.

In een volgende serie proeven onder geconditioneerde omstandigheden werd de relatieve invloed van lucht- en worteltemperatuur overdag en 's nachts op de bladgroeisnelheid nagegaan. Tevens werden de Leaf Weight Ratio (LWR, het drooggewicht van het blad per gram totaalgewicht) en de SLA na een behandeling gedurende 7 dagen bepaald. De luchttemperatuur overdag bleek veruit de grootste invloed op deze parameters te hebben, gevolgd door de luchttemperatuur 's nachts. De bladgroei werd licht geremd wanneer de worteltemperatuur slechts gedurende een deel van het etmaal laag is, waarbij geen verschil werd gevonden tussen het effect van een lage worteltemperatuur alleen overdag en alleen 's nachts. Een meer dan additionele groeireductie trad op bij continu lage worteltemperaturen.

Het feit, dat het effect van lage worteltemperaturen niet afhankelijk bleek van het jaargetijde of de tijd van de dag, deed twijfel ontstaan aan de meest gangbare opvatting, dat de hogere weerstand tegen wateropname door de wortel de belangrijkste oorzaak zou zijn van de verminderde groei bij lage worteltemperatuur. Daarom werden een aantal aanvullende proeven uitgevoerd teneinde de relatie tussen waterhuishouding, worteltemperatuur en bladgroei nader te bestuderen. Er bleek ondermeer, dat zowel watergebrek als lage worteltemperatuur een daling van de bladgroeisnelheid veroorzaakten, maar dat deze daling bij lage worteltemperatuur gepaard ging met een daling van de SLA, terwijl dat niet het geval was bij droogte. De twijfels omtrent de primaire rol van de waterbalans bij de effecten van lage worteltemperaturen waren aanleiding voor een nader onderzoek naar de mogelijke rol van phytohormonen.

Toediening van phytohormonen door middel van bladbespuitingen aan planten bij optimale en lage worteltemperatuur toonde aan, dat er gecompliceerde interacties bestaan tussen deze factoren. In sommige gevallen kon het effect van een lage worteltemperatuur gedeeltelijk teniet worden gedaan door toediening van combinaties van gibberellinen en cytokininen, maar de resultaten

waren onvoldoende reproduceerbaar voor definitieve conclusies.

Tenslotte kan geconcludeerd worden, dat de worteltemperatuur in de praktijk van de Nederlandse glastuinbouw voor tomaat althans geen erg belangrijke factor is. Een gedetailleerd onderzoek naar de hormoonhuishouding van tomatplanten is van groot belang voor een goed begrip van het groeiproces.

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De auteur werd op 3 augustus 1944 te Noorddijk (Gr.) geboren. Na Mulo-B en H.B.S.-B doorlopen te hebben, studeerde hij aan de Landbouwhogeschool te Wageningen, waar hij in 1970 het ingenieursdiploma in de studierichting Tuinbouwplantenteelt behaalde.

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