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RESPONSES OF YOUNG MAIZE PLANTS
TO ROOT TEMPERATURES

W. P. GROBBELAAR

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RESPONSES OF YOUNG MAIZE PLANTS TO ROOT TEMPERATURES

(MET EEN SAMENVATTING IN HET NEDERLANDS)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWKUNDE
OP GEZAG VAN DE RECTOR MAGNIFICUS IR. W. F. EJSVOOGEL,
HOGLERAAR IN DE HYDRAULICA, DE BEVLOEIING,
DE WEG- EN WATERBOUWKUNDE EN DE BOSBOUWARCHITECTUUR,
TE VERDEDIGEN TEGEN DE BEDENKINGEN
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VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP VRIJDAG 5 JULI 1963 TE 16 UUR

DOOR

W. P. GROBBELAAR



H. VEENMAN EN ZONEN N.V. - WAGENINGEN - 1963

STELLINGEN

I

Het is zeer gewenst het gebruik van het woord groei bij planten te reserveren voor de volumetoename waarvoor als maat de versgewichtstoename kan gelden.

Dit proefschrift.

II

Een laag suikergehalte in de bladeren van aardnootplanten bij hoge temperaturen kan niet beschouwd worden als een aanduiding dat het transport van koolhydraten naar het wortelstelsel onder die omstandigheden groter is dan bij lage temperaturen.

J. F. DE BEER, Influences of temperature on *Arachis hypogaea* L. with special reference to its pollen viability. Versl. Landbouwk. Onderz. nr. 69.2 (1963) p. 69.

III

Aangenomen moet worden dat bij suboptimale temperaturen de geremde groei leidt tot een verhoogd droge-stofgehalte en dat niet omgekeerd het verhoogde droge-stofgehalte de oorzaak is van de groeivertraging zoals VAN DOBBEN veronderstelt.

W. H. VAN DOBBEN, Influence of temperature and light conditions on dry matter distribution, development rate and yield in arable crops. Neth. J. Agric. Sci. 10 (1962) p. 378.

IV

Het begrip warmtesom is in vele gevallen niet bruikbaar bij het voorspellen van het intreden van een bepaald ontwikkelingsstadium.

F. J. DIJKHUIS, Computation of heat unit accumulations in maize for practical application. Euphytica 5 (1956) 267-275.

V

Bij de uitzaai van wintertarwe onder droge omstandigheden, zoals die voorkomen in het Zuid-Afrikaanse gebied met zomerregenval, is het korrelgewicht van belang.

VI

Bij de veredeling van maïs op droogteresistentie wordt te weinig gelet op de mogelijke vorming van bijwortels aan het mesocotyl.

VII

Bestudering van de waterbesparing en het verlies aan koolhydraatreserves bij beweiding van wintertarwe in Zuid-Afrika kan de sterk uiteenlopende standpunten over het nut van deze beweiding nader tot elkaar brengen.

VIII

In verband met het gevaar van nadelige veranderingen in de botanische samenstelling van het natuurlijke grasland in de Hoëveldstreek van Zuid-Afrika ten gevolge van bemesting, verdient aanwending van kunstmest op dit grasland voorlopig geen aanbeveling.

IX

Vele planten die als tredplanten worden beschouwd zijn in wezen soorten die hoge eisen aan de vruchtbaarheid van de grond stellen.

WOORD VOORAF

Het afsluiten van dit proefschrift biedt een goede gelegenheid om al diegenen, die op enigerlei wijze hebben bijgedragen dit te bereiken, mijn dank te betuigen.

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MEDEDELINGEN VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN,
NEDERLAND 63 (5) 1-71 (1963)

RESPONSES OF YOUNG MAIZE PLANTS TO ROOT TEMPERATURES

(met een samenvatting in het Nederlands)

by

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relatively long duration (24 days) cylindric plastic containers of 700 cc capacity were used, as described by BROUWER and VAN VLIET (1960). One seedling only was mounted in the plastic lid of each container. For the short term experiments where plants were subjected to the different root temperatures for five to eight days, large 5 l containers were used, each containing eight plants.

Aeration of the culture solution, in addition to supplying oxygen to the root system, also ensured a thorough circulation of the solution which maintained a uniform temperature throughout the container.

The plants were allowed to develop at an air and root temperature of 20 °C for ten days before being used for studies at the different root temperatures. During this period the containers with plants were arranged on rotating tables in order to eliminate as far as possible any effect of variations due to environmental conditions.

2.3. NUTRIENT SOLUTION

The nutrient solution used was based on the No. 1 formulation of HOAGLAND and ARNON (1950). Unless otherwise stated, all plants were grown in a "half strength" solution similar to that used for maize by HAGEMAN et al. (1961). The composition of the solution is given in table 1.

TABLE 1. Composition of nutrient solution

Macro-elements		Micro-elements	
Salt	Concentration	Salt	Concentration
KH ₂ PO ₄	0.0005 M	H ₃ BO ₃	1.0 p.p.m. B
KNO ₃	0.0025 M	MnO ₂ · 4 H ₂ O	1.0 p.p.m. Mn
Ca(NO ₃) ₂ · 4 H ₂ O	0.0025 M	ZnSO ₄ · 7 H ₂ O	0.1 p.p.m. Zn
MgSO ₄ · 7 H ₂ O	0.001 M	CuSO ₄ · 5 H ₂ O	0.04 p.p.m. Cu
		H ₂ MoO ₄ · H ₂ O	0.02 p.p.m. Mo

Ferrous sulphate was used as iron source and periodically supplied as described by HAGEMAN et al. (1961). Applications of 3.5 p.p.m. Fe were given per litre of culture solution at the commencement of an experiment or after renewal of the solution. Additional applications of 1.75 p.p.m. were made every third day.

The carboxyl cation exchange resin IRC-50 was used as pH buffer according to the technique of HAGEMAN et al. (1961). The nutrient solution was made with tap water and adjusted with sulphuric acid to approximately pH 4.5. Ion exchange resin was, however, excluded during those periods when the ion uptake of the plants was studied by measuring the amount of ion depletion of the nutrient solution.

A periodical chemical analysis of the solution for N, P and K, as well as a daily check on pH was carried out. In general the solution was changed every 7 days during the early growth stages but ultimately it had to be

changed twice daily to ensure a continued supply of macro-elements in the optimum temperature range.

2.4. TEMPERATURE CONTROL AND LIGHT INTENSITY

The required root temperatures were applied by immersing the containers in which the plants were growing in temperature controlled water baths. Two units, each subdivided into isolated water baths $26 \times 26 \times 30$ cm, were installed in a temperature controlled room. By means of thermoregulators it was possible to maintain a constant temperature of 20°C above room temperature with one unit, and 20°C below room temperature with the other unit.

Eight constant temperatures controlled at intervals of 5°C , from 5° to 40°C were used throughout. The desired temperature in each water bath was maintained within a range of $\pm 1^{\circ}\text{C}$.

The relative humidity was maintained at approximately 65 percent.

High pressure mercury lamps (Philips HPL 400 W) were mounted above the plants at such a distance that an average light intensity of 10.2×10^4 ergs $\text{sec}^{-1} \text{cm}^{-2}$ was supplied at a height of 9 cm above the lids in which the plants were mounted.

A photoperiod of sixteen hours and a constant air temperature of 20°C was maintained during the course of the experiments.

2.5. PLANT WEIGHT AND LENGTH MEASUREMENTS

Leaf lengths were recorded daily by measuring each leaf from the surface of the lid to the tip of the leaf.

The fresh weight of shoots was obtained by harvesting the plants constantly at a fixed time during the photoperiod. The roots were placed between two double sheets of filter paper and a slight pressure applied to remove excess moisture.

The dry weights were determined after drying in an oven for 24 hours at 105°C .

2.6. TRANSPIRATION

Water loss was measured by the decrease in weight of the culture solution in the containers in which the plants were growing.

Losses due to evaporation were obtained by measuring the decrease in weight of the solution in the containers without plants but with aeration.

2.7. CHEMICAL ANALYSIS

2.7.1. Culture solution

Phosphate as well as nitrate was determined colorimetrically with a Vitatron colorimeter. The procedure of SCHUFFELEN et al. (1961) for plant samples was used for phosphate determination, the phenoldisulfonic acid method of SNELL and SNELL (1949) for nitrate determination and potassium was determined with a Dr. B. Lange flame photometer.

2.7.2. Plant material

The plants were analysed by the chemical laboratory of the Institute for Biological and Chemical Research on Field Crops and Herbage. The different elements were determined as follows:

Nitrogen : by the Kjeldahl method with a selenium containing catalyst.

Phosphate : colorimetrically as molybdenum blue.

Potassium : by means of a Kipp flame photometer.

Calcium : as oxalate by titration with potassium permanganate.

Magnesium: colorimetrically using titan yellow.

Water soluble carbohydrates: these were determined according to the method of VAN DER PLANK (1936). Sulphuric acid was used to hydrolise sucrose to glucose and fructose.

2.8. EXPERIMENT WITH RADIO-ACTIVE RUBIDIUM

Plants which had been exposed to 20 °C for 10 days were transferred to the different root temperatures and 1 μ C of Rb⁸⁶ added, as 0.01 ml of 0.001 M rubidium chloride, per litre of nutrient solution.

Eight plants were used per temperature with the roots suspended in 5 litre of nutrient solution without ion exchange resin. Four plants were harvested successively after 24 and 72 hours. The fresh weight of the shoots and roots was determined separately. The roots were rinsed with 200 ml of distilled water after harvesting. The fresh shoots as well as the roots were digested with sulphuric acid according to the method described by SCHUFFELEN et al. (1961) with some modifications. The clear solution was transferred to 100 ml flasks and made up to 100 ml with distilled water. Aliquots of 5 ml were used for counting.

A Philips – decade scaling unit (PW 4032, PW 4062 and PW 4022) and a G.M. – end window counter (type 18505) was employed.

The β -emission of all aliquots were counted to a minimum of 1000 counts. The random error did not exceed 3.2 per cent. All samples were corrected for background only.

3. RESULTS

3.1. GROWTH PHENOMENA

3.1.1. Introduction

The development of the maize plant can be divided into five reasonably distinct stages (SHAW and LOOMIS, 1950). These are:

- a. early vegetative growth from planting to flower differentiation. This stage includes germination, the seedling stage and early leaf growth during three to four weeks of independent development of the plant. At the end of this period the above ground parts are limited to leaf sheaths and blades, the tassel is microscopically visible at or below ground level, culm development is largely embryonic but the maximum number of ovules on the embryonic ear shoots are already determined. The theoretical potentialities of the plant are therefore, established;

- b. rapid vegetative growth up to silking;
- c. pollination and fertilization;
- d. grain production from fertilization to maximum dry weight of grain;
- e. maturation or drying of grain and silk.

The present study was limited to the effect of soil temperature on the growth of the maize plant in this early vegetative phase. The term growth will serve to designate the over-all process whereby new organs and their constituent tissues develop, which therefore, include the processes of cell division and elongation as well as differentiation which precedes, accompanies and follows cell division.

According to MEYER et al. (1960) the principal indices which have been employed to measure growth quantitatively are:

- a. increase in length of stem, root or other organ of the plant;
- b. increase in area of the leaves;
- c. increase in diameter of the stem or other organ;
- d. dry weight increment;
- e. fresh weight increment.

Each of the indices, however, measure only certain quantitative phases of growth. The most generally used were increase in height and fresh weight (MEYER et al., 1960). Soil temperature effects on growth, have generally been studied by using length or dry weight, or both, as criteria for growth (RICHARDS et al., 1952). The data of DAVIS and LINGLE (1961) on tomatoes, however, reveal that in the absence of differences between dry weights produced by various root temperatures, significant differences were obtained in fresh weights. This is not surprising since internal water deficits which seemingly check cell enlargement more than cell division, terminate cell enlargement earlier and result in structural differentiation of the cells ensuing sooner (MEYER et al., 1960). LOOMIS (1953) also states that any factor such as a deficient supply of water or nitrogen, which checks growth without correspondingly reducing photosynthesis, will tend to increase any differentiation response of which the plant is capable. Thus plants in which development is shifted to differentiation will produce more cuticle, thicker cell walls and more resistant protoplasm. Alterations in the growth pattern (shoot-root ratio) of the maize plant, produced by periodically withholding or supplying nitrogen, also affected the dry matter percentage of the shoot whenever nitrogen was withheld (BROUWER et al., 1961). According to these authors shoot growth is more sensitive to nitrogen shortage than the process of carbon dioxide-assimilation. The increased dry matter percentage of the shoots therefore, mainly consists of carbohydrates. WENT (1957) also found that at high and low night temperatures very little growth of the tomato plant took place, and that consequently only a small amount of photosynthates was utilized, which resulted in a higher concentration in the leaves of the plants.

The fresh weight production is, therefore, an essential indice when studying soil temperature effects on growth. In addition, it provides data to calculate the dry matter percentage, which seems to be a useful measurement for determining qualitative changes. Care should, however, be exercised when in-

terpreting differences in dry matter percentage. An increase usually occurs during or after the initiation of flower primordia (VAN DE SANDE BAKHUYZEN, 1937; VAN DOBBEN, 1959).

SINNOTT (1960) states that in higher plants a close relation exists between the growth of the shoots and roots. Its value differs in different plants, at different stages of development and in different environments. In most cases the root is relatively large in the seedling but growth is relatively slower than in the shoot. The shoot increases at a rate which maintains a constant proportion to that of the root.

ROBERTS and STRUCKMEYER (1946) presented data on 29 species and varieties which indicated that neither photoperiod nor temperature was consistently related to top-root ratio. Flower or fruit formation, however, was found to be associated with a higher top-root ratio. They concluded that these observations point to the possibility that internal conditions, e.g. developmental stage, rather than purely external factors, would be the real determinants of root production.

The data discussed by WASSINK (1955) further revealed a pronounced correlation between root growth and photosynthesis in *Acer Pseudoplatanus* and *Acer saccharinum*. MEYER et al. (1960) also state that a diminution in the rate of photosynthesis or a decrease in the supply of carbohydrates within the plant, influences the shoot-root ratio. A diminution of carbohydrates available in the tops, results in an increased shoot-root ratio and *vice versa*.

Air temperature has also been noted to affect the shoot-root ratio. KHALIL (1956) established that in wheat, the higher the temperature the higher the shoot-root ratio. In almost all cases examined the roots of the plants which were grown at relatively high temperatures (30°C) were proportionately weak when compared with the roots produced at the lower temperature.

Data presented by MEYER et al. (1960) further indicate that the nutritional environment of the root also affects the shoot-root ratio. The effect of an increased nitrate concentration in the root environment resulted in a relatively larger increase in shoot weight. This effect is interpreted in terms of the influence on the internal food relations of the plant, a relatively larger proportion of the nitrogen being translocated to the shoot. With a low nitrate concentration in the substratum in which the plant is rooted, most of the nitrates are utilized in the roots. The tops are therefore relatively deficient in proteins, and hence the growth rate of the tops is relatively slow and the shoot-root ratio relatively low. BROUWER et al. (1961) demonstrated that with maize the relative growth of shoots and roots did not respond immediately to the presence or absence of nitrogen in the root medium. They noted a delayed response of the root after withholding nitrogen and concluded that the presence of nitrates in the plant was the determining factor. This was later confirmed by BROUWER and LOEN (1962) with maize, where it was found that the presence of nitrogen in the root medium had no effect on the growth of the root if the total supply in the plant was sufficient.

SINNOTT (1960) mentions that the effect of the shoot on the roots is not always nutritional but may result from the action of auxin, vitamins or other regulating substances. WASSINK (1955) concluded that in addition to the direct effect of photosynthesis on root growth of *Acer* species it was evident that leaf produced substances, probably hormones, also influenced root growth.

The shoot-root ratio, in addition to the dry matter percentage, can there-

fore be useful in indicating qualitative changes occurring in the internal food relations of plants.

3.1.2. Increase in fresh weight

3.1.2.1. Plants subjected to various root temperatures at the age of ten days

The fresh weight accumulation of the plants previously held at 20°C for ten days and then exposed to various root temperatures for fourteen days, is given in fig. 1. An immediate effect of root temperature on the fresh weight

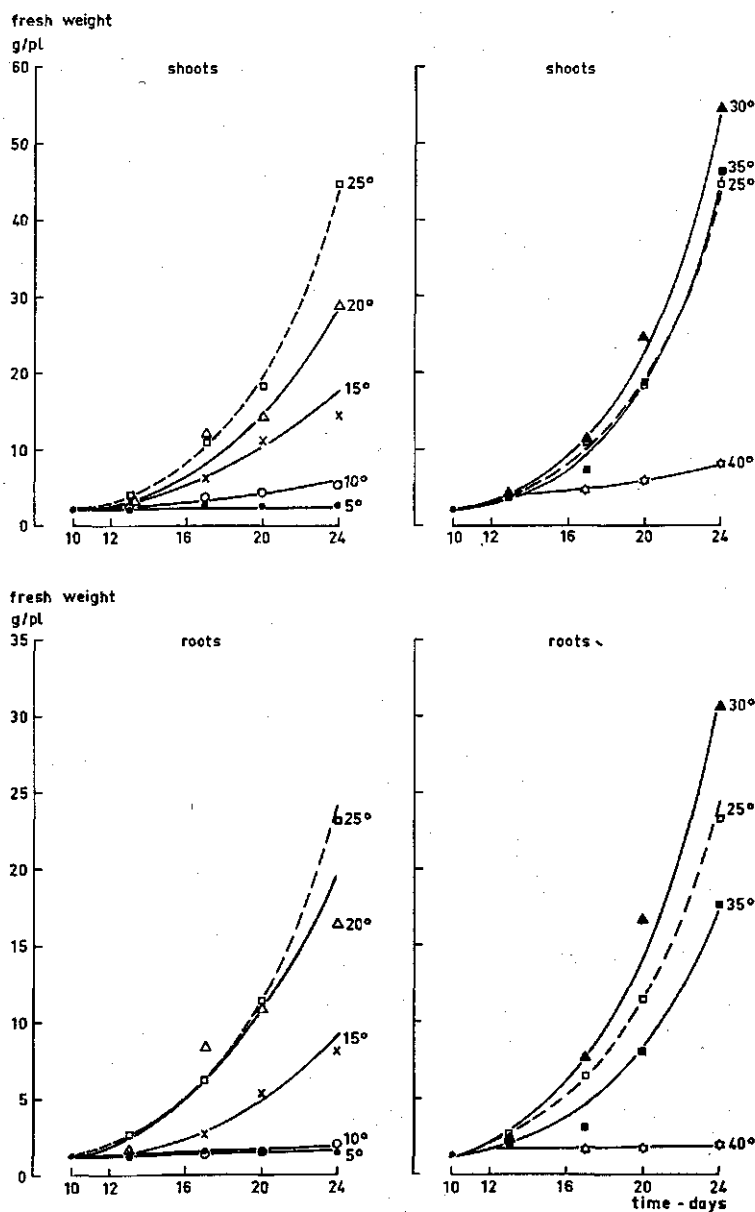


FIG. 1. Influence of root temperature on increase in fresh weight of shoots and roots of plants previously exposed to 20°C for 10 days

production is evident, becoming more pronounced as the period of exposure advances (fig. 1). The data also indicate that the temperature range chosen was sufficient to include the minimum and maximum temperature range. If the minimum temperature is considered as the lowest temperature at which plants will continue to grow without injury after a specified period of exposure (RICHARDS et al., 1952), the data in fig. 1 illustrate that this appears to be in the range 5° – 10° C for the shoots and roots. The maximum temperature after fourteen days is probably between 35° and 40° C for the shoots and roots. The increase in weight of the shoot at 40° C indicates continued growth but desiccation of the three oldest leaves and wilting of the other leaves was evident, which indicates that the plants were injured.

The most rapid growth was found at 30° C, indicating that the optimum temperature occurs in the temperature range 25° – 35° C for the shoots and at 20° – 30° C for the roots (fig. 1). No decrease in optimum temperature was evident as the period of exposure advanced.

The increase in leaf length of the plants when exposed to different root temperatures exhibited similar differences (fig. 2). The optimum temperature again occurring in the range 25° – 35° C.

A marked effect of root temperature on the rate of leaf initiation (fig. 2)

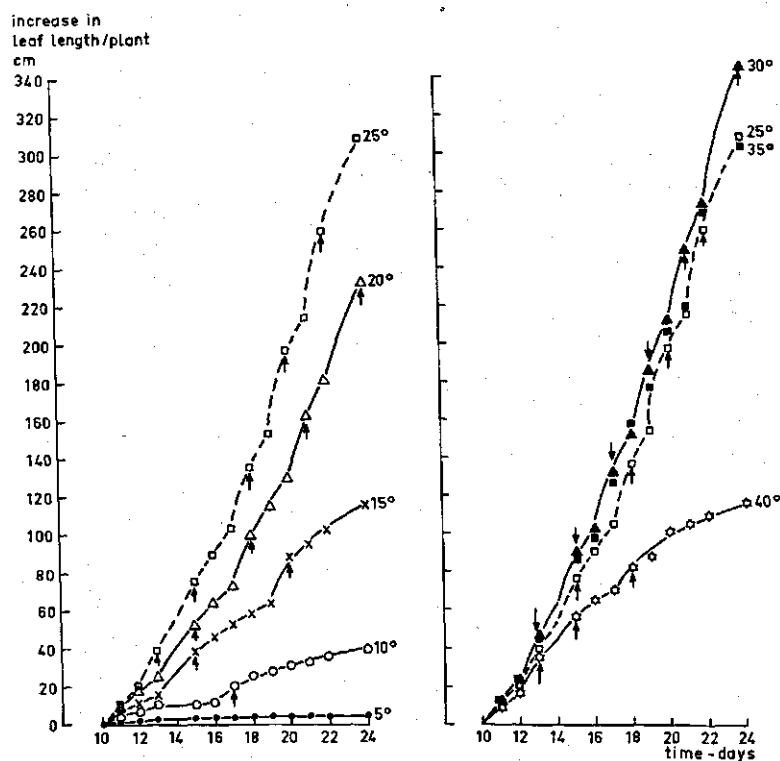


FIG. 2. Increase in total leaf length per plant after exposure to the root temperatures indicated for 14 days. The plants were kept at 20° C for 10 days prior to transference. \uparrow denotes appearance of a new leaf

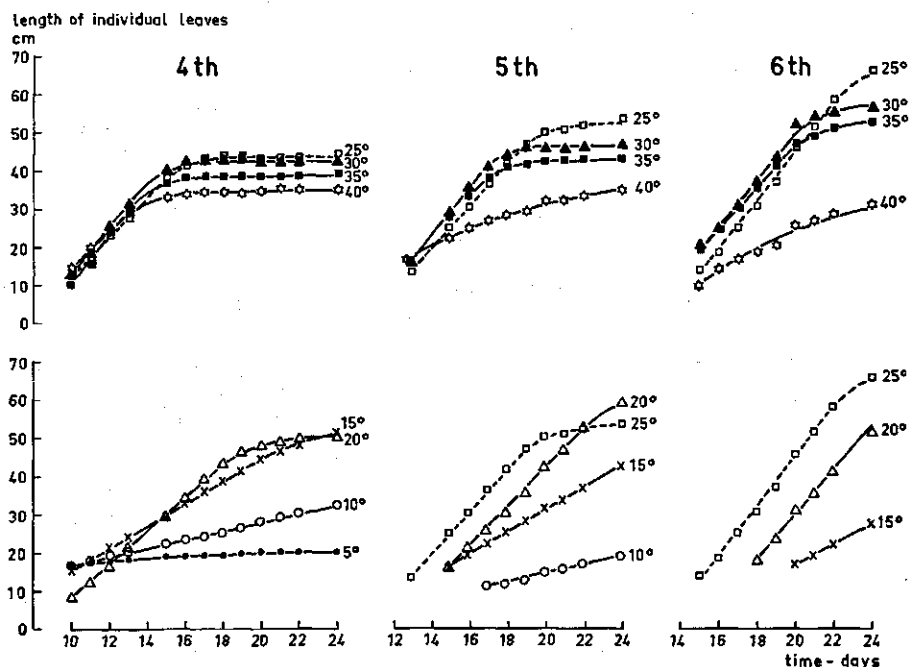


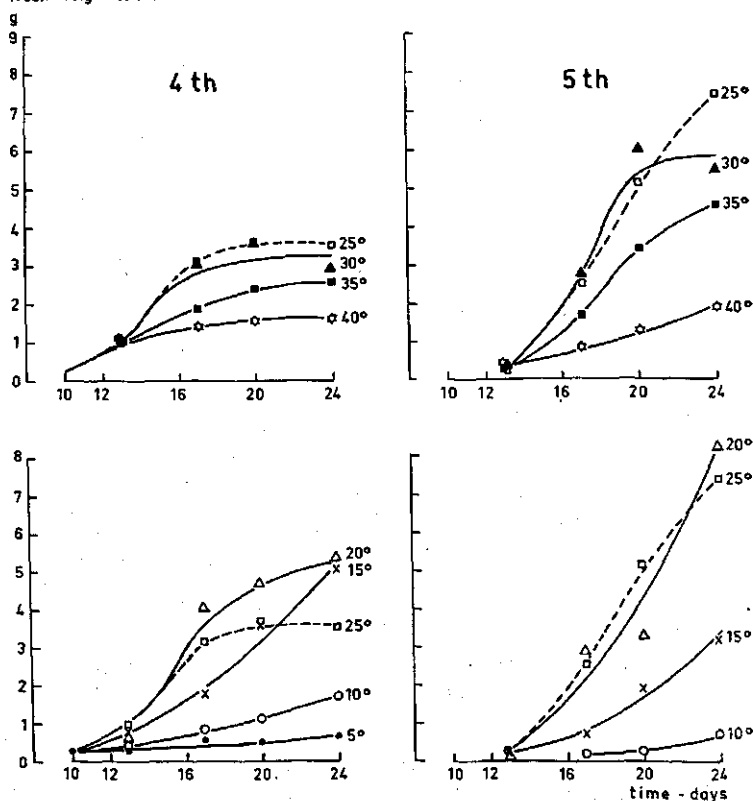
FIG. 3. Elongation of the 4th, 5th and 6th leaf of plants, previously exposed to 20°C for 10 days, at the root temperatures indicated

as indicated by the emergence of new leaves, is evident. Leaf initiation proceeded most rapidly at 25°, 30° and 35°C, which may account for the greater increase in total leaf length at these temperatures.

Marked differences in elongation of individual leaves, however, are noticeable (fig. 3). The fourth leaf, the youngest visible leaf when the plants were transferred to the different temperatures, elongated the most rapidly at 25°, 30°, 35° and 40°C. It was retarded to a marked extent at 5°, 10° and 15°C; the increase in length being less than at 20°C. The effect is most marked at 5°C decreasing with increase in temperature up to 25°C. The data in fig. 3 also indicate that root temperature has a pronounced effect on leaf maturation and consequently ultimate leaf length. Leaf maturation proceeded most rapidly at 40°C decreasing progressively as the temperature is lowered to 15°C. Elongation at 5° and 10°C had not yet ceased in the exposure period applied. An estimate of the ultimate length could therefore, not be obtained.

Elongation of the fifth leaf (fig. 3) exhibited similar differences except that a conspicuous decrease is evident at 40°C, elongation proceeding less rapidly than at 15°C. In addition inconspicuous differences are noticeable between 20°, 25°, 30° and 35°C. The order of differences in ultimate leaf length, however, was similar to those previously encountered with the fourth leaf except that elongation at 40°C was retarded with no indication that it had ceased. No alteration in relative differences is evident when comparing the elongation data of the sixth leaf (fig. 3). No measurements at 5° and 10°C were possible since the sixth leaf had not yet emerged.

fresh weight of individual leaves



The less rapid increase in leaf length per plant after exposure to 5°, 10° and 15°C is, therefore, the result of a retarded rate of leaf initiation and a decreased rate of leaf elongation (fig. 2 and 3). The marked increase in total leaf length per plant at 25°, 30° and 35°C, compared with 20°C, is mainly caused by a larger increase in rate of leaf initiation and to a minor extent by leaf elongation.

Leaf elongation and initiation do not explain the larger fresh weight accumulation of the shoot obtained at 30°C in comparison with 25° and 35°C. The increase in fresh weight of the individual leaves after exposure to these temperatures is given in fig. 4. The data indicate that the greater increase of the fifth, sixth and seventh leaf is one factor which contributed to a larger fresh weight per plant at 30°C. The weight of the fourth and fifth leaf at 30° and 25°C, however, also exceeded that of 35°C. The greater length of the leaves and weight of the fourth and fifth leaf at 25°C does not result in any difference in total fresh weight when compared with 35°C. The rate of emergence of new leaves at 35°C does exceed that of 25°C (fig. 2). This probably offsets the advantage gained by 25°C resulting in similar fresh weights per plant. The data in fig. 4 also demonstrate that the weight of the sixth and succeeding leaves at 35°C was similar to that of 25°C which is an additional

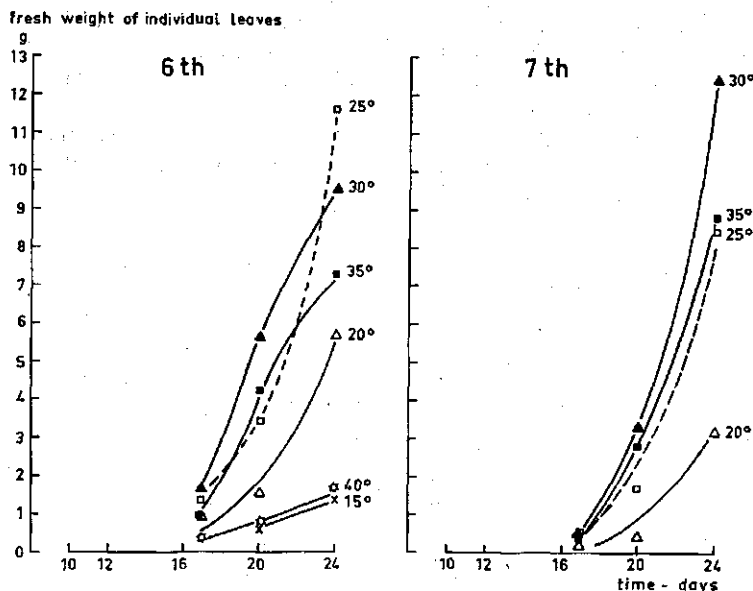


FIG. 4. Increase in fresh weight of individual leaves during an exposure period of 14 days to the different root temperatures (4th and 5th leaf, see page 12)

factor contributing to the elimination of differences in weight per plant between 25°C and 35°C.

Fig. 4 furthermore illustrates that the leaves continued to increase in weight after leaf elongation has ceased (fig. 3). The leaf weights (fig. 4) also indicate that the effect of root temperature on the weight of corresponding leaves was quite similar to that encountered in leaf length. The ultimate weight and length decreasing with an increase in root temperature (fig. 3 and 4).

The increase in stem length is presented in fig. 5. This was determined by measuring the length of the stem from the first whorl of crown roots to the tip of the shoot apex – the apex being determined microscopically. These data indicate that the order of differences corresponds to that produced by the fresh weights (fig. 1). No differentiation of flower primordia could be detected after fourteen days at the various temperatures.

The root system of maize consists of two sets of roots viz. seminal roots whose initials are present in the embryo and adventitious roots which arise from stem tissue after germination (KIESSELBACH, 1949). The seminal roots include the primary root and a variable number of lateral roots which arise adventitiously at the base of the first internode of the stem. Roots which may form adventitiously elsewhere in the first internode of the stem (mesocotyl)

are commonly also included. Such roots, however, very seldom occurred on the single cross studied. The seminal roots, therefore, consisted of the primary root and the adventitious lateral roots arising at the base of the stem. The number of seminal roots present after ten days at 20°C and fourteen days at the various root temperatures is given in table 2. It seems that the number varied from four to six and that exposure to the different root temperatures after ten days at 20°C had no significant effect on the ultimate number.

TABLE 2. The number of seminal roots after ten days at 20°C and fourteen days at the root temperatures indicated

Time-days	Temperature -°C							
	5°	10°	15°	20°	25°	30°	35°	40°
10	—	—	—	5.2	—	—	—	—
13	4.5	4.5	4.5	4.0	4.0	5.5	4.0	5.5
17	5.5	5.0	4.0	6.0	5.5	5.0	4.0	4.0
20	4.0	4.5	5.0	3.5	4.5	4.0	6.0	4.5
24	4.5	4.5	4.0	5.5	6.0	5.0	4.5	5.5
Mean	4.6	4.6	4.4	4.8	5.0	4.9	4.6	4.9

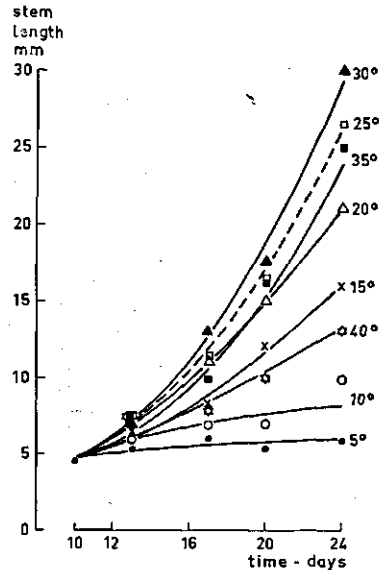
The first whorl of adventitious or crown roots appears at the base of the second internode (KIESSELBACH, 1949). The increase in number of crown roots per plant during fourteen days at the different root temperatures is given in table 3.

TABLE 3. The number of crown roots per plant after exposure to 20°C for ten days, followed by fourteen days at the different root temperatures

Time-days	Temperature -°C							
	5°	10°	15°	20°	25°	30°	35°	40°
10	—	—	—	5.4	—	—	—	—
13	4.0	5.5	4.5	6.5	7.0	7.0	6.5	7.0
17	4.0	4.5	9.0	10.5	9.5	9.0	10.0	7.0
20	5.0	7.5	11.0	9.0	12.0	12.5	13.0	8.0
24	5.0	8.0	9.5	13.0	18.0	18.0	16.0	7.5

From table 3 it is evident that the most rapid increase in crown root number occurred at 25°, 30° and 35°C. The fresh weight accumulation of the crown roots, presented in fig. 6, reveals pronounced differences between 25°, 30° and 35°C. The increase at 30°C exceeding that of 25° and 35°C. The data in fig. 6 also indicate that crown root production at 20°C exceeded that at 15°C. Corresponding differences in crown root number were less conspicuous (table 3). PLATE I showing the plants after being exposed to the different temperatures for fourteen days, clearly demonstrates that the roots at 20°C were more profusely branched and greater in length. The additional crown roots which developed at 10°C and 40°C during exposure to these temperatures, attained maximum lengths of only 1–2 cm (PLATE I). Thickening of the root tips was evident at both temperatures while the root apex at 40°C turned dark brown. These roots contributed very little to the fresh weights at

FIG. 5. Stem elongation of plants exposed to the root temperatures indicated. Plants were transferred to the different root temperatures at the age of 10 days



these temperatures and probably account for the inconspicuous increase in weight (fig. 6).

The effect of root temperature on the growth of the seminal roots, as measured by the increase in fresh weight, is shown in fig. 6. The data demonstrate a marked effect of root temperature on fresh weight production after being transferred from 20°C. Since root temperature had no effect on seminal root number it follows that the differences in weight are most probably the result of temperature on root elongation and branching (see PLATE I). The largest increase in weight occurred in the temperature range 20°–30°C (fig. 6). The root temperature of 35°C retarded the growth of the seminal roots, the weights being similar to that produced at 15°C.

The analysis of the increase in weight of the seminal and crown roots separately (fig. 6), reveals that the differences in total weight (seminal plus crown roots) presented in fig. 1, in the temperature range 20°–35°C, is primarily caused by the effect of root temperature on crown root production *viz.* growth and crown root number. The influence on seminal or crown root production of 5°, 10° and 40°C proves to be similar, both sets of roots being affected to the same extent (fig. 6). Crown root production at 15°C, however, seems to have been favoured to a relatively greater extent than that of the seminal roots.

3.1.2.2. Plants exposed to the various root temperatures at the age of 20 days

The cardinal temperatures for plant growth are not precise but extend over ranges of several degrees at least (RICHARDS *et al.*, 1952). They depend on several factors, one of which is the stage of development of the plant. Plants were, therefore, allowed to grow at 20°C for twenty days before being sub-

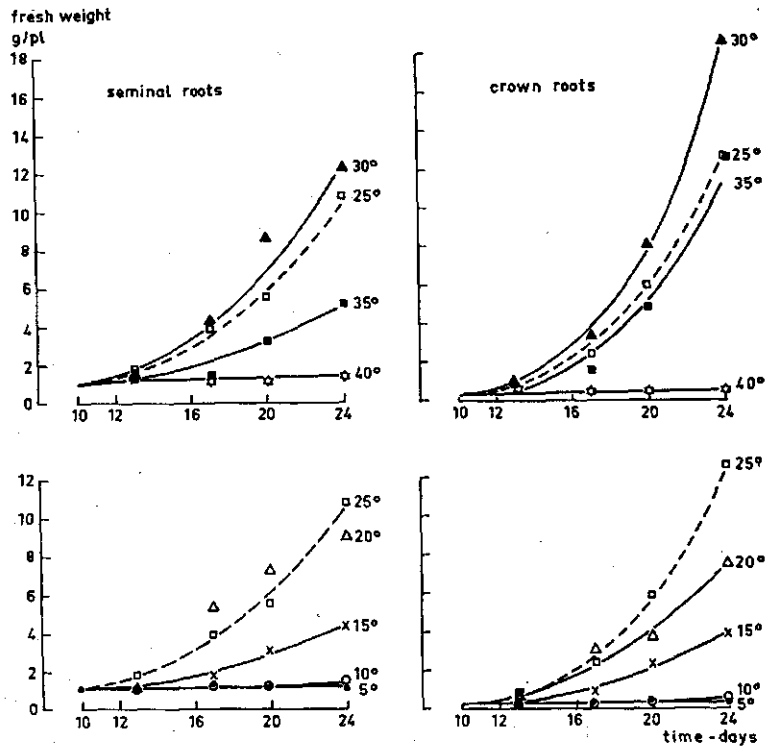


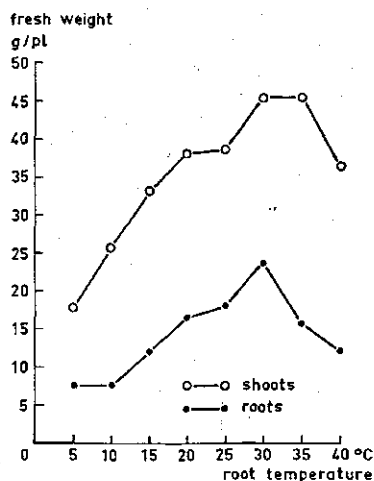
FIG. 6. Increase in fresh weight of seminal roots and crown roots during 14 days at the different root temperatures

jected to the different root temperatures. At this stage the seventh leaf had just emerged. The fresh weights of the shoots and roots after five days at the different root temperatures are presented in fig. 7. Since no increase in fresh weight of the shoots and roots was evident after five days at 5°C (fig. 1) it can be assumed that a similar inhibition of growth occurred in the plants of which the data are given in fig. 7. The weights of both organs at 5°C can, therefore, be regarded as an indication of the original weight when the plants were subjected to the different root temperatures. The relative order of differences in the temperature range 5°–20°C (fig. 7) is similar to that observed in younger plants (fig. 1). The optimum temperature range occurs between 20° and 35°C for the shoots and 20°–30°C for the roots. The effect of 40°C on the shoots and roots was less than that obtained with younger plants.

3.1.2.3. Growth in relation to increased concentration of nutrients

Several authors have studied the effect of levels of fertilizer application at various root temperatures. KETCHESON (1957) found that the relative increase in yield by phosphate treatment was significantly better when eight-week-old

FIG. 7. Fresh weights of shoots and roots of plants exposed for 5 days to the root temperatures indicated. The plants were grown at 20°C for 20 days before transference to the different root temperatures



maize plants were exposed to a soil temperature of 13°C than when kept at 20°C. Decreased root activity at the low temperature was partially overcome by phosphate fertilizing. NIELSEN et al. (1961) using soil temperatures of 5°, 12°, 19° and 27°C stated that the addition of N, P and K did not offset the effect of the unfavourable temperature. Similar results were obtained by DAVIS and LINGLE (1961) with tomato plants exposed to soil temperatures of 18° and 24°C in sand culture. The plants at 18°C did not respond to increased nutrient levels. Data obtained with water culture, however, revealed a depressing effect by increasing the nutrient concentration.

Since these results were mainly obtained with sand or soil culture under a limited temperature range, further experimentation with water culture seemed justified.

The fresh weights obtained with plants after twelve days at 20°C followed

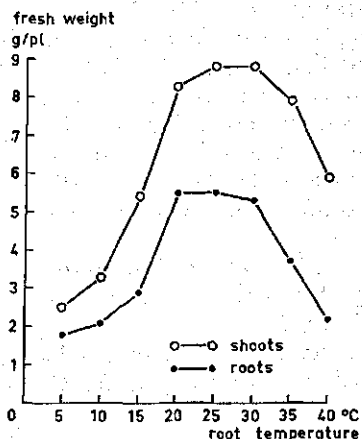


FIG. 8. Fresh weights of shoots and roots after 6 days at the different root temperatures. A nutrient solution with double the concentration of macro-elements was used throughout

by six days at the different root temperatures are given in fig. 8. The nutrient solution used contained double the concentration of macro-elements during the whole growth period viz. twelve days at 20°C and six days at the various root temperatures.

The data in fig. 8 indicate that the retarded growth at the low temperatures could not be eliminated by doubling the concentration of macro-elements. In the optimum temperature range the growth rate was reduced similarly to that presented by DAVIS and LINGLE (1961).

The fresh weight production of plants previously kept at 20°C for 22 days and thereafter exposed to the various root temperatures for five days, is given in table 4.

TABLE 4. Shoot and root fresh weights after five days at the temperatures indicated

	Temperature - °C							
	5°	10°	15°	20°	25°	30°	35°	40°
	g	g	g	g	g	g	g	g
Shoots	19.1	26.3	31.1	41.0	37.5	43.6	44.0	31.6
Roots	8.3	8.4	11.2	18.8	18.7	25.5	18.2	10.1

It is evident that the relative differences in the shoots and roots (table 4) closely resemble those obtained on a half strength solution (fig. 7). Indications that the detrimental effect of the lower temperature range could be eliminated or altered by doubling the concentration of macro-elements were not detectable.

3.1.3. Dry weight production

3.1.3.1. Plants exposed to various root temperatures after 10 days at 20°C

The dry weight production of the plants subjected to the various root temperatures for fourteen days is presented in fig. 9. The optimum temperature range for shoot production is 25°–35°C and for the roots 20°–35°C (fig. 9). The relative differences in the optimum range, however, decreased. The difference in shoot weight between 30° and 35°C being relatively less than that obtained with the fresh weights (fig. 1). A similar diminution in relative differences between 40°C and the optimum temperature range (fig. 9) is evident when compared with the fresh weight data of the shoots (fig. 1). It also appears that a relatively larger increase in dry weight of the shoot at 5°, 10° and 15°C occurred in comparison to 25°, 30° and 35°C than was obtained with the fresh weights.

The roots also exhibited alterations in relative differences – no difference being evident between 20°, 25° and 35°C (fig. 9) whereas the fresh weight at 35°C was distinctly less than that of 20° and 25°C.

The temperatures 10°, 15° and 40°C influenced the dry weight production relatively less than the fresh weights when compared with that of 30°C. The differences being relatively less for the dry weights (fig. 9).

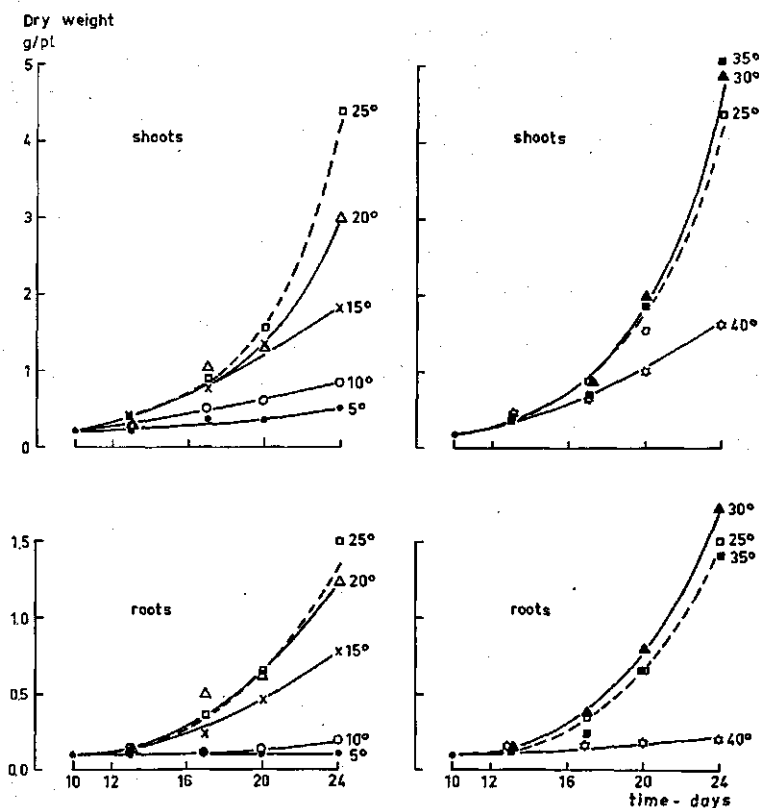


FIG. 9. Increase in dry weight of shoots and roots at the root temperatures indicated. The plants were grown at 20°C for 10 days prior to transference

3.1.3.2. Effects of root temperature on twenty-day-old plants

The weight per plant (eight plants per temperature treatment) after being exposed to the various root temperatures for five days is given in table 5.

TABLE 5. Dry weight per plant after five days at the temperatures indicated

	Temperature - °C							
	5°	10°	15°	20°	25°	30°	35°	40°
	g	g	g	g	g	g	g	g
Shoots	2.11	3.08	2.93	3.21	3.00	3.45	3.72	3.03
Roots	0.61	0.62	0.85	1.12	1.08	1.20	1.04	0.89

From table 5 it is evident that a marked increase of the shoot occurred at 30° and 35°C. A notable response to the temperatures 10°, 15°, 20°, 25° and 40°C is indicated by table 5, heavier shoots being produced than at 5°C. No differences, however, were evident between these temperatures.

A remarkable increase in the weight of the roots is evident at 20°, 25°, 30° and 35°C (table 5). The weights at these temperatures are quite similar. Root growth was inhibited at 5° and 10°C corresponding to the effect of these temperatures on younger plants (fig. 9). Root temperatures of 15° and 40°C produced root systems of intermediate weight.

3.1.3.3. Dry weight production with an increased concentration of macro-elements

The dry weights obtained with plants held at 20°C for twelve days and thereafter exposed to the various root temperatures for six days is given in fig. 10. The concentration of macro-elements in the nutrient solution was doubled and applied during the whole experimental period.

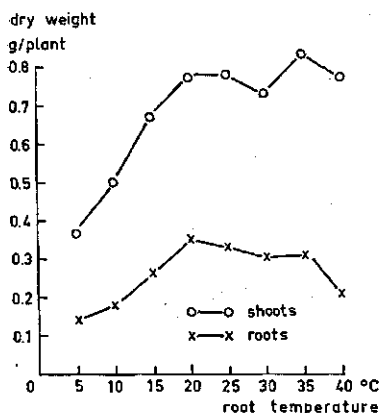


FIG. 10. Dry weights of shoots and roots after 6 days at the different root temperatures. The plants were previously exposed to 20°C for 12 days. A double strength nutrient solution was used throughout

Fig. 10 indicates that the relative differences of the shoot corresponds to that obtained with a half strength solution (fig. 9). No pronounced differences are evident in shoot weight at 20°, 25°, 30°, 35° and 40°C. The poorest growth occurred at 5°C followed by 10° and 15°C. The shoot weight at 40°C (fig. 10) seems to have been affected relatively less than with the half strength solution (fig. 9). The plants used for the data in fig. 10 were probably somewhat larger when transferred to the various root temperatures, resulting in relatively higher yields.

The relative response of the roots to the increased nutrient concentration (fig. 10) was similar to that encountered with half the concentration in macro-elements (fig. 9). No difference being evident between 15°, 20°, 25°, 30° and 35°C after six days, while a pronounced retarding effect on dry weight production occurred at 5°, 10° and 40°C.

3.1.4. Dry matter content

3.1.4.1. Root temperature effects on ten-day-old plants

The dry matter percentage of the shoots and roots after fourteen days at the various root temperatures is presented in fig. 11. It is evident that root

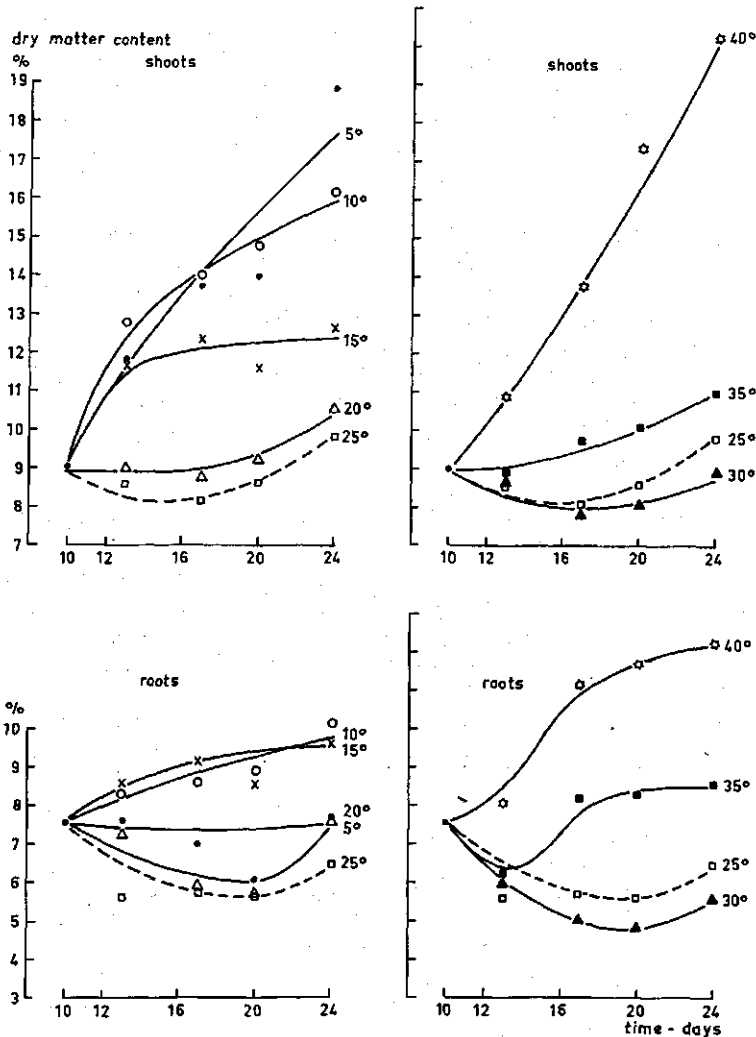


FIG. 11. Dry matter percentage (fresh weight basis) of shoots and roots of plants previously exposed to 20°C for 10 days and thereafter to the different root temperatures for 14 days

temperature had a pronounced effect on the dry matter content of the shoots and roots.

The change in the content of the shoots in the temperature range 20°–35°C was relatively less than at the temperatures beyond these limits viz. 5°, 10°, 15° and 40°C. Exposure to 25° and 30°C resulted in a rapid decrease in dry matter percentage followed by an increase during the latter half of the experimental period. No immediate reaction occurred at 20° and 35°C, the dry matter content remained unchanged for approximately seven and three days respectively (fig. 11). A gradual increase, however, is evident after this period, at both temperatures.

A factor which may have contributed to this increased dry matter content in the optimum temperature range, is plant density. Mutual shading of plants in this temperature range increased to a relatively greater extent with age in comparison to those beyond these temperatures. This effect was lessened during the course of the experiment since two plants were harvested successively. The intercepted radiation per plant consequently increased in the favourable temperature range, which probably increased the dry matter percentage. Shading effects at 5°, 10°, 15° and 40°C during the latter part of the exposure period probably did not occur. The growth of these plants was retarded and removal of plants by harvesting, maintained a spacing between the plants which eliminated mutual shading, which was not the case with the larger plants in the optimum temperature range.

Fig. 11 also demonstrates that the dry matter content increased conspicuously at 5°, 10°, 15° and 40°C; the shoots after containing 9.0 per cent had increased to 11.6, 12.5, 11.5 and 11.0 per cent respectively within three days after transference to these temperatures. The values continued to increase at 5°, 10° and 40°C ultimately exceeding that of 15°C which remained practically unchanged during the last nine days. The ultimate value at 10°C being less than that of 5° and 40°C (fig. 11).

The dry matter content of the roots in the temperature range 20°–35°C shows a conspicuous decrease immediately after exposure to these temperatures (fig. 11). The effect is only temporary since a rapid increase took place at all these temperatures, rising sooner at 35°C than at 20°, 25° and 30°C (fig. 11).

The values in fig. 11 furthermore illustrate that the increase at 10°, 15° and 40°C was relatively less than that obtained with the shoots. The content at 5°C remained unchanged once subjected to this temperature.

Wilting of the leaves was evident at 5°C, commencing during the photoperiod, once the plants were subjected to this temperature. This condition continued to exist during the first five days of exposure. Anthocyanin pigmentation was noticeable on the leaves at this stage. Some recovery in turgescence of the leaves occurred after this period and the shoots continued to increase in dry weight (fig. 9). Desiccation of the first, second and third leaves was evident during the last few days, commencing from the leaf tip. The progressive increase in dry matter percentage (fig. 11), however, was primarily a result of a greater dry weight production (fig. 9) than of water loss.

Anthocyanin pigmentation was also noticed on the three lowest leaves at 10°C, followed by desiccation of the first and partial yellowing and necroses of the second leaf when the experiment terminated. Only the leaf sheaths of the first three leaves at 15°C showed anthocyanin pigmentation; while the leaf blades of these and the rest of the leaves were dark green in colour in comparison with the plants at 20°, 25°, 30° and 35°C. Anthocyanin pigmentation also appeared in the older leaves at 40°C within three days after exposure to this temperature. Wilting and necroses of the first leaf was noticeable four days later, followed by necroses of the second and third leaves as well as wilting of the other visible leaves when the experiment was discontinued. The progressive increase in dry matter percentage, however, seems to have been caused mainly by a relatively larger increase in the amount of dry matter (fig. 9); desiccation of the older and smaller leaves contributing less.

The increase in dry matter content of the shoots and roots which ultimately occurred in the temperature range 20°–35°C (fig. 11) seems extraordinary since no transition to the reproductive phase was evident, judged by the initiation of flower primordia. The plants were all in the vegetative phase.

Examination of the seminal and crown roots indicates that notable differences in dry matter content existed between these two sets of roots (table 6). The dry matter percentage of the roots during fourteen days at the various root temperatures is given in table 6.

TABLE 6. The dry matter percentage of seminal and crown roots after fourteen days at the temperatures indicated

Temp.-°C	Time - days							
	13		17		20		24	
	Seminal	Crown	Seminal	Crown	Seminal	Crown	Seminal	Crown
	%	%	%	%	%	%	%	%
15°	8.5	9.1	9.3	9.2	8.4	8.7	9.5	9.8
20°	7.4	6.8	5.5	6.7	5.0	7.2	6.6	8.8
25°	5.6	5.7	5.3	6.3	5.0	6.4	5.6	7.3
30°	5.9	6.0	4.8	5.4	4.3	5.4	4.6	6.1
35°	6.2	6.3	7.4	9.1	7.9	8.7	7.7	9.0

It is evident that no differences in dry matter content occurred between the two sets of roots on the thirteenth day (3 days after transference). After this date a progressive increase is noticeable in the crown roots at 20°, 25°, 30° and 35°C which is absent at 15°C. The plants contained only one whorl of crown roots on the thirteenth day while some of the second whorl had also appeared. On the twentieth day the plants at 25°, 30° and 35°C had three whorls of crown roots, those of the third being much thicker than those of the first and second whorl. During the last four days (20–24 days) the fourth whorl of crown roots appeared measuring 3–4 mm in diameter. The roots of the third and fourth whorl probably contributed the most to the increased dry matter content. The data in table 6 also demonstrate that no conspicuous increase occurred in the seminal roots at all the temperatures.

An analyses of the dry matter percentage of the individual leaves also revealed that notable differences existed between individual leaves. Furthermore that the upper leaves, but not the youngest visible, contained a higher dry matter content than the lower leaves. A stage is, however, reached where the dry matter content of the oldest (lower) leaves exceeds that of the upper more xeromorph leaves. This is probably the result of desiccation of the lower leaves, the sheaths of which are ripped apart by the thick emerging crown roots. The dry matter content of the whole shoot, given in fig. 11, therefore, is only the average of a large variation between individual leaves.

According to LOOMIS (1937) starch is not formed in the vegetative parts of maize and its nearest equivalent an. amyloextrin is only a minor constituent. Sucrose is the characteristic carbohydrate of the vegetative plant. LOOMIS (1945) also found that the overnight losses from the stalk in maize are nearly pure sucrose and that sucrose is the only carbohydrate which shows losses in darkness along the translocation pathways of leaves to sheaths

to stalks. The soluble carbohydrate content of maize plants will, therefore, mainly consist of sucrose.

Soluble carbohydrate determinations, in addition to dry matter content, can be used as a valuable criterion to indicate qualitative changes which may occur in the growth of the plant.

The soluble carbohydrate percentage (dry weight basis) as well as the dry matter percentage of plants, subjected to the various root temperatures for eight days at the age of twelve days is given in fig. 12. It is evident that the relative order of differences corresponds closely to the dry matter values. Since the dry matter content of the shoot remained unchanged during this experimental period at 20°C (fig. 11) it can be assumed that the soluble carbohydrate content behaved similarly. The data in fig. 12, therefore, indicate that the soluble carbohydrates accumulated at 5°, 10°, 15° and 40°C, but decreased at 25° and 30°C.

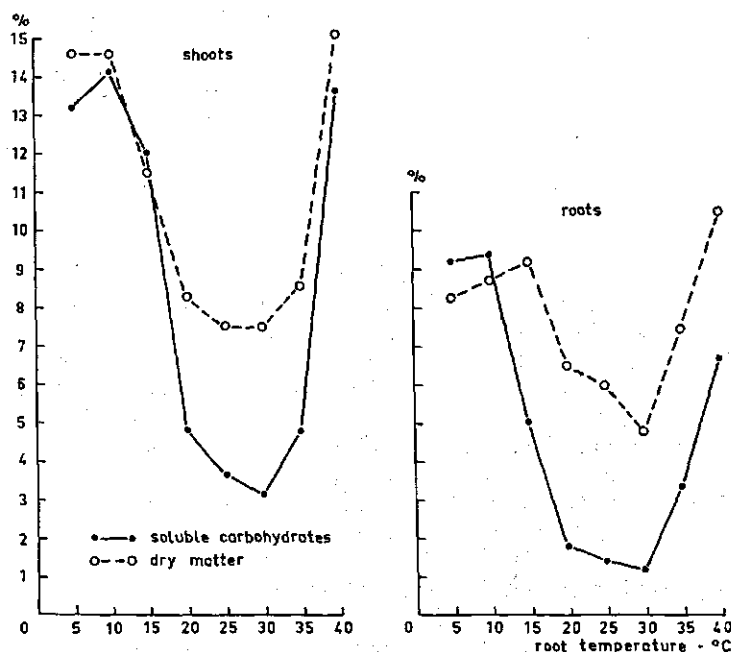


FIG. 12. Dry matter percentage (fresh weight basis) and water soluble carbohydrate content (dry weight basis) of shoots and roots after 8 days at the root temperatures indicated

The relative effect of temperature on the soluble carbohydrate percentage of the roots was similar to that found for the shoots (fig. 12). The general trend of the dry matter percentage was in close agreement with that of the soluble carbohydrate content except for a discrepancy at 15°C.

3.1.5. Shoot-root ratio

The shoot-root ratio per plant of the fresh weights is presented in fig. 13. These plants were grown at 20°C for ten days and thereafter exposed to the various root temperatures.

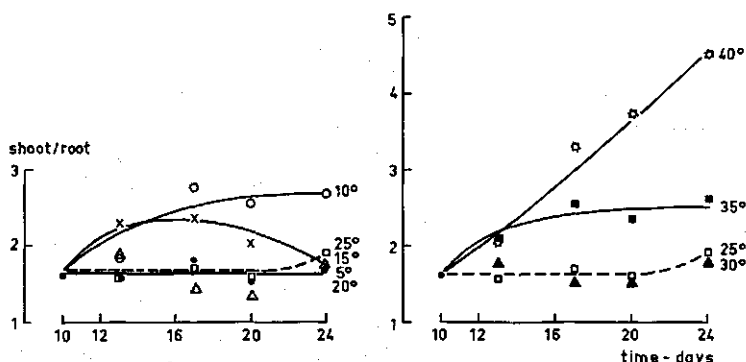


FIG. 13. Shoot-root ratio, based on the fresh weights, during 14 days at the different root temperatures

A pronounced effect of the root temperature on the shoot-root ratio is evident (fig. 13). A marked increase occurred at temperatures beyond the range 20°–30°C, with the exception of 5°C which remained unchanged. In the temperature range 20°–30°C it remained constant during the first ten days after transference. A notable increase in ratio is evident during the period 20–24 days at 25° and 30°C (fig. 13). These data seem to indicate that the relative increase in weight of the shoots and roots remained unchanged during the first 10 days after transfer. The condition, however, changes during the last four days when root growth is relatively retarded to a greater extent, resulting in an increased shoot-root ratio.

The ratio at 10°C and 35°C increased from 1.6 to values of 2.6 and 2.5 respectively as a result of a relatively greater increase in shoot weight (fig. 1) and then remained unchanged. A transition period of approximately 7–8 days was required before an equilibrium between shoot and root growth was established.

The root temperature of 15°C retarded root growth to a relatively greater extent than shoot growth, causing an increase in shoot-root ratio (fig. 13). This effect was only temporary since the ratio decreased progressively after the seventeenth day with no indication that an equilibrium is reached within the following seven days (17–24 days). This seems to indicate that the growth of the root system, although relatively less than that of the shoot, is sufficient to maintain shoot growth for approximately three days (10–13 days). After this stage root growth increases relatively more to maintain shoot growth, resulting in a diminishing of the shoot-root ratio (fig. 13).

A pronounced increase is evident at 40°C (fig. 13) since root growth practically ceased while that of the shoot continued.

If the shoot-root ratio of the dry weights, presented in fig. 14, are examined, further changes are detectable which were not observed with the fresh weights.

In the temperature range 20°–35°C the plants reacted quite similarly. An immediate increase in shoot-root ratio is evident within three days after exposure to these root temperatures (fig. 14). The most pronounced increase was obtained at 35°C, the effect being relatively less with a decrease in temperature up to 20°C. This is followed by a period of approximately seven

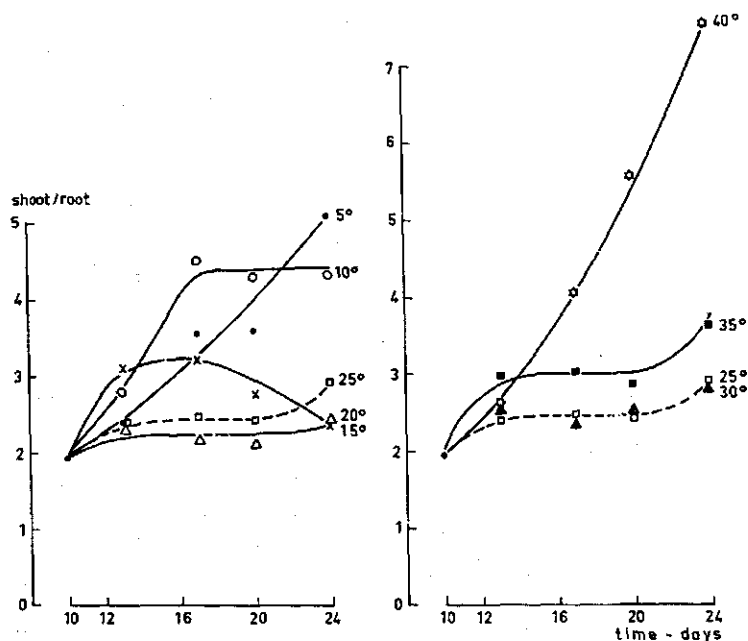


FIG. 14. Shoot-root ratio of the dry weights during an exposure period of 14 days to the root temperatures indicated

days in which the relative increase in weight of the shoots and roots remains in equilibrium (fig. 14). During the last four days the ratio again increases except at 20°C. This coincides with the remarkable rise in dry matter percentage of the shoots and roots (fig. 11). The relatively larger increase in dry matter content which occurred in the shoot at 35°C may have contributed to the higher shoot-root ratio at this temperature. This, however, seems to be negligible since a relatively greater increase in dry matter percentage is also evident in the roots at 20°, 25° and 30°C (fig. 11). The higher shoot-root ratio is primarily a result of a relatively larger increase in dry weight of the shoot during the period 20–24 days (fig. 9) at 20°, 25°, 30° and 35°C.

Fig. 14 demonstrates that the trends at 10°, 15° and 40°C are similar to those found for the fresh weights (fig. 13). The ratios obtained with the dry weights, however, were higher than those calculated for the fresh weights.

The shoot-root ratio based on the dry weight increased progressively at 5°C (fig. 14). Such an effect was undetectable in the fresh weights (fig. 13). The relatively larger increase in dry weight of the shoot and practically no increase in root weight seems to be the primary cause. The increase in dry weight of the shoot probably just compensated for the loss of moisture due to desiccation, resulting in a constant fresh weight of the shoot (fig. 1). Since the fresh weight of the root remained unchanged (fig. 1) this had no effect on the shoot-root ratio based on the fresh weight (fig. 13).

3.1.6. Relative growth rate

$$\text{The formula: } R = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

where $t_2 - t_1$ is the time between initial weight W_1 and any weight W_2 at time t_2 and R the growth constant or relative growth rate, has been employed by numerous investigators (BALLARD and PETRIE, 1936; VAN DE SANDE BAKHUYZEN, 1937; WILLIAMS, 1946; HAMMOND and KIRKHAM, 1949) to reveal interesting features of growth.

The relative growth rate is a convenient measure for comparing rate of increase in weight at different times and in different plants (BALLARD and PETRIE, 1936). It may therefore, be of value to evaluate growth effects of soil temperature which are difficult to detect, by comparing absolute weight determinations only.

Data on maize were used by VAN DE SANDE BAKHUYZEN (1937) to calculate the relative growth rate of weekly periods up to the age of fifteen weeks. These data indicate that the relative growth rate was highest during the period preceeding the appearance of the male inflorescence with a marked decrease already noticeable three weeks before this stage. The period from the appearance of the male inflorescence was characterised by a further diminishing in relative growth rate. HAMMOND and KIRKHAM (1949) in analysing growth data on field maize demonstrated a similar decrease in relative growth rate when the tassel appeared and again at silking. No decrease in relative growth rate, however, was evident before the appearance of the tassel.

These data indicate that erroneous conclusions may be drawn if plants are compared when they are not in the same growth stages.

The relative growth rate of the shoots and roots, calculated from the fresh weights, is given in table 7. The data were obtained from two experiments in which the plants were exposed to the different root temperatures for eight days (10–18 days) and an additional six days (18–24 days). In the first experiment the values have been calculated by interpolating in the smoothed curves (fig. 1) where two plants were harvested successively. In the second experiment the calculation is based on the increase in weight of eight plants harvested per temperature after eight days.

The data in table 7 indicate that in general the relative growth rate of the shoot in the first period (10–18 days) for the two experiments was in close agreement with the exception of 15° and 35°C which showed a larger variation. Higher relative growth rates of the roots, are evident in experiment one, in which two plants were harvested successively. This seems to indicate that where eight plants are grown in the same space previously allocated to four plants, the relative growth rate of the roots decreases. The data nevertheless demonstrate that the relative effect of root temperature was quite similar to that obtained in experiment one.

From table 7 it is evident that the relative growth rate of the shoot at 25°, 30° and 35°C exceeded that of the other temperatures. Temperatures of 20°, 25° and 30°C, however, seem to have been the most favourable for root growth. The data clearly demonstrate that in the second growth period (18–24 days) the relative growth rate of the shoot remained unchanged at all temperatures except at 40°C where it showed a marked decreased rate compared to the first period. The relative growth rate of the roots was maintained at 5°, 20°, 25°, 30°, 35° and 40°C and increased 4.0 and 1.5 times respectively at 10° and 15°C.

The relative growth rates calculated from the dry weights are given in table 8.

TABLE 7. The relative growth rate in gram/gram/day of the shoots and roots (fresh weight) at the different root temperatures for two periods

Temp.-°C	Exp. no.	Relative growth rate g/g/day			
		10-18 days		18-24 days	
		Shoots	Roots	Shoots	Roots
5°	1	0.017	0.004	0.013	0.006
	2	0.015	—	—	—
10°	1	0.071	0.013	0.063	0.054
	2	0.065	0.005	—	—
15°	1	0.156	0.119	0.146	0.170
	2	0.128	0.057	—	—
20°	1	0.187	0.192	0.187	0.192
	2	0.191	0.145	—	—
25°	1	0.220	0.213	0.218	0.212
	2	0.225	0.150	—	—
30°	1	0.240	0.238	0.235	0.238
	2	0.215	0.165	—	—
35°	1	0.218	0.177	0.222	0.196
	2	0.186	0.100	—	—
40°	1	0.120	0.025	0.062	0.017
	2	0.105	0.018	—	—

TABLE 8. The relative growth rate in gram/gram/day, based on the dry weight of the shoots and roots, at the different root temperatures for two periods

Temp.-°C	Exp. no.	Relative growth rate g/g/day			
		10-18 days		18-24 days	
		Shoots	Roots	Shoots	Roots
5°	1	0.070	—	0.069	0.003
	2	0.104	0.036	—	—
10°	1	0.124	0.024	0.094	0.083
	2	0.154	0.056	—	—
15°	1	0.183	0.143	0.126	0.162
	2	0.187	0.116	—	—
20°	1	0.192	0.181	0.195	0.178
	2	0.210	0.162	—	—
25°	1	0.214	0.189	0.218	0.197
	2	0.231	0.153	—	—
30°	1	0.224	0.200	0.226	0.200
	2	0.221	0.143	—	—
35°	1	0.214	0.189	0.218	0.197
	2	0.210	0.132	—	—
40°	1	0.165	0.075	0.139	0.033
	2	0.198	0.095	—	—

The relative growth rate of the shoot at 5°, 10°, 15° and 40°C during the 10-18 day period is remarkably greater than that obtained on a fresh weight basis, whereas no differences are evident for the temperatures 20°, 25°, 30° and 35°C (table 8). A similar increase in relative growth rate of the roots is also noticeable. In the period 18-24 days the relative growth rate of the shoot remained unaltered at all temperatures except at 10°, 15° and 40°C where it

was less than in the previous period (10–18 days). The greater increase in relative rate compared with the fresh weights, however, was maintained at 5°, 10° and 40°C. The relative growth rate of the roots increased at 10° and 15°C but decreased at 40°C (table 8). Those of the other temperatures remained constant.

3.1.7. Discussion

The results presented in the previous chapter confirm those published by DICKSON (1923); WILLIS et al. (1957); and NIELSEN et al. (1961) which have been obtained on soil culture with maize. Pronounced differences in shoot and root growth were evident where the shoots were exposed to a uniform temperature and the roots subjected to various root temperatures.

The present study with water culture demonstrates that shoot growth of the single cross K_{64r} × E₁₈₄ as measured by increase in fresh and dry weight as well as leaf elongation, has an optimum in the temperature range 25°–35°C.

KIESSELBACH (1949 and SHAW and LOOMIS (1950) discussing the development of maize, stated that within two to three weeks after seedling emergence the entire stem surmounted by the differentiated tassel is visible at or below the soil surface. According to KIESSELBACH (1949) the stem from the base of the crown to the tassel initials is only about 2.5 cm long at this stage. This signifies that in experiments with maize in soil culture the shoot apex is also exposed to the ambient soil temperature. The effect of increased temperatures of the shoot and root environment within the physiological range, on the growth of plants has been well established (WENT, 1953). In studies with young plants soil temperature effects on shoot growth are therefore, bound to occur because of the direct influence on the shoot apex (BROUWER, 1959; VAN DOBBEN, 1963).

In the present experiments on water culture the shoot apex of young plants (10 days) has also been exposed to the ambient root temperature up to the age of 20 days. A marked effect of root temperature, however, was also evident when older plants (20 days) were subjected to the different root temperatures being quite similar to that encountered in the younger plants. An effect of the ambient temperature of the root system on shoot growth therefore, seems to have been established. In addition, experiments with species of which the shoot apex is well above the soil surface, have demonstrated marked growth effects of soil temperature (RICHARDS et al., 1952; BROUWER and VAN VLIET, 1960; DAVIS and LINGLE, 1961; BROUWER, 1962).

The exposure of the roots, shoot apex and the leaf base of the plant to the ambient soil temperature does, however, complicate the unravelling of the results. The plants were nevertheless exposed to the various root temperatures as it usually occurs in the field.

In studies thus far conducted with maize the effect of soil temperature on the overall growth process has mainly received attention. No evidence has been furnished of the effect on the growth and development of individual parts which seems to be necessary to provide a better insight into the actual cause of root temperature induced differences.

The present data indicate that an excellent rate of leaf initiation at the temperatures 25°, 30° and 35°C was one factor which accounted for the greater

overall growth rate at these temperatures. Leaf initiation in maize has also been noted to be speeded up by temperature with a Q_{10} of 1.3 when the whole plant was exposed to the temperatures tested (WENT, 1957). KHALIL (1956) also found that in wheat the time required for the emergence of successive leaves is decreased significantly by increasing the temperature within the range 10° to 30°C. These results are in agreement with that of GREGORY (1956) and BLACKMAN (1956) who concluded that the effect of temperature is to hasten development of the leaf primordium and thus hasten time of unfolding.

Evidence that the excelled rate of leaf initiation was not only caused by the effect of soil temperature on the shoot apex but also by effects on the roots is furnished by the data of TAKAMURA et al. (1961). By subjecting the sheath, base and roots in various combinations, to soil temperatures of 20° or 30°C they established that the rate of leaf initiation of rice plants was greater when the base and roots were exposed to the higher temperature than exposure of base and sheath to the higher temperatures. This indicates that the root temperature of the root system also contributed to the excelled rate of leaf initiation.

The present results on leaf initiation and those previously presented (GROBELAAR, 1962) do not reveal any break in time between the embryo leaves (no.'s 1-6) and the post embryo leaves as suggested by WHALEY et al. (1950).

The results of the present study furthermore indicate that root temperature influenced leaf elongation which proceeded the most rapidly in the optimum range (25°-35°C). Data furnished by BROUWER (1962) indicate that for *Vicia* plants differences in leaf size were mainly caused by the effect of root temperature on cell extension of the leaves. Cell extension decreasing at temperatures beyond the optimum temperatures range. Cell division, however, seems to have been retarded only at 5°C. The differences in elongation of the leaves at 10°, 15° and 20°C may therefore, most probably, be the result of reduced cell extension. The conspicuous decrease in leaf elongation at 5°C, however, may have been caused by a reduced rate of cell division and extension.

The fresh weight of individual leaves exhibited differences quite similar to those obtained with leaf length. Increase in weight at 5°, 10° and 15°C being retarded. A similar effect was obtained by BROUWER (1962) with *Vicia* plants; the rate and ultimate size of leaf decreasing progressively at temperatures beyond the optimum temperature range. Indications that the ultimate leaf size is larger in a certain temperature range (15° and 20°C) below the optimum was evident. The influence of root and base temperature on leaf length and weight in a temperature range below the optimum is therefore, just the opposite to that presented by BROUWER (1962) for *Vicia* and *Phaseolus* plants where leaf size was greatly reduced at temperatures below the optimum temperature range. A factor which possibly contributed to these differences was the location of the shoot apex, which remained exposed to the root temperature in the case of maize.

The data on leaf length and weight indicate that although the rate of increase was less at 15°C the duration of elongation continued over a longer period of time. This is substantiated by data on cell elongation presented by BURSTRÖM (1961) where the rate of elongation increases with increasing temperature, but the duration of elongation is shortened.

The leaf growth data illustrate that elongation measurements alone are insufficient as criterion for growth. Leaves of which elongation had ceased still increased in fresh weight. This indicates that lateral growth or increase in leaf thickness did not cease simultaneously with leaf elongation. In addition differentiation of cell walls ensues at about the time that cell enlargement ceases (MEYER et al., 1960).

The application of individual leaf weights to explain differences in growth of the shoot in maize is complicated by the effect of temperature on leaf initiation. This is clearly demonstrated by the individual leaves at 35°C. The fourth and fifth leaves were distinctly smaller than those at 25° and 30°C. No differences, however, occurred in weight of the sixth and seventh leaf at 25° and 35°C. Since leaf initiation was excelled at 35°C these leaves were actually compared at different stages of development; those at 35°C being further developed. Using the length measurements in addition to weights, it is evident that the sixth leaf at 35°C was further advanced which partially eliminated differences in comparison with 25°C. Indications nevertheless seem to exist that a relatively greater increase in weight of the sixth and seventh leaf at 35°C also occurred. At the time these leaves elongate the shoot apex has probably emerged from the high root temperature. As a consequence the initiation of new leaf primordia has been retarded (compared with the time that the shoot apex was at the ambient root temperature of 35°C) and with it the inhibition of growing leaves by these primordia.

The effect of soil temperature on root growth judged by fresh weight production, did not correspond to that found for the shoot. The temperature range 20°–30°C seemed to be the optimum, fresh weight accumulation at 35°C being distinctly less. DICKSON (1923) reported similar effects on maize where it was found that the largest root system, irrespective of age, developed at 20°C whereas that for the shoot was 24°–28°C. Maize grown in soil culture, with sufficient nitrogen, phosphorus and potassium at soil temperatures of 5°, 12°, 19° and 27°C, by NIELSEN et al. (1961) exhibited a similar effect. Root weights were similar at 19° and 27°C whereas the heaviest tops were produced at 27°C.

Root growth practically ceased at 5° and 10°C with indications that some increase occurred during the latter half of the exposure period. This can be interpreted as a shock effect since the plants were transferred from 20°C to a temperature as low as 5°C. The effect of sudden temperature changes on root elongation was measured by BARNEY (1951) on loblolly pine seedlings. He determined that an immediate increase in elongation within 60 minutes after transference from 20° to 35°C occurred, followed by a decrease in elongation. Within 30 hours after transfer a final constant rate was, however, maintained. GELLERMAN et al. (1958) also noted that root elongation of peas, maize, oats and tomatoes ceased when the temperature was increased from 20° to 30°C. This initial disturbance was followed by increased growth of the root at higher temperature as compared with the lower temperature. RICHARDS et al. (1952) mention that sudden temperature shifts may temporarily retard root growth but the rate characteristic of the new temperature is usually resumed soon after the change has been made.

Corresponding measurements on the reaction of the above ground parts were not carried out by BARNEY (1951) or GELLERMAN et al. (1958).

In the present study no shock effect was noticeable on the shoots as mea-

sured by leaf length or weight increase. At both the upper and lower temperatures a constant or gradually decreasing rate was observed during the fourteen days of exposure.

Since no effect of the sudden change in temperature on shoot growth was noted, it can be assumed that the less rapid increase in rate of root elongation, which possibly occurred, did not influence shoot growth. It can also be argued that the root system present was sufficient to supply the necessary essentials to maintain shoot growth at a constant rate and that root growth only increased when it was no longer sufficient to maintain the growth of the shoot which had increased at a relatively higher rate. A similar effect is described by GROBBELAAR (1962) for maize which had been transferred from 5° and 10°C to 20°C without any shock effect being shown by the shoot.

The poorer root growth at 35°C in comparison to that of 20°, 25° and 30°C does not therefore seem to have been the result of a shock effect.

When considering the seminal and crown root growth at 35°C it is clear that the seminal roots increased relatively less in comparison to those at 20°, 25° and 30°C. Crown root growth, however, was quite similar to that of 25°C with no remarkable difference in fresh weight between these two temperatures. Indications of a stimulatory and/or compensatory correlation seems to exist; crown root initiation being stimulated to a relatively greater extent under conditions of retarded seminal root growth.

At the temperature of 20°C the relative effect on seminal and crown root growth seems to have been reversed. The increase of the seminal roots was favoured to a greater extent. This, however, seems to have been caused by the retarded crown root initiation.

The fact that the optimum temperature range for shoot growth did not correspond to that for root growth indicates that the relative effect of temperature on the shoot and root was not the same. In this optimum temperature range shoot growth proceeded at a relatively higher rate than root growth. Root growth at 35°C was relatively less, resulting in a pronounced increase in shoot-root ratio. This seems to indicate that at 35°C, relative to the shoot, less roots by weight, were able to produce shoot growth similar to that obtained at the temperature of 25°C.

A similar effect was noticed with tomato plants in the experiments of ABD EL RAHMAN et al. (1959). Practically no differences in shoot growth occurred at soil temperatures of 25.3° and 29.9°C whereas an increase in shoot-root ratio was evident at 29.9°C.

RICHARDS et al. (1952) reviewing the effect of temperature on root morphology concluded that in general, roots mature sooner at high temperatures with more frequent branching. A greater number of active root tips relative to weight should therefore occur at the higher temperature and may have contributed to the more efficient shoot production per unit root weight at 35°C.

A striking fact is that the shoot-root ratio in the case of maize diminishes with rising root temperatures from 5°C up to 30°C and increases again with a further rise in temperature up to 40°C. NIELSEN et al. (1961) established with maize plants that the shoot-root ratio diminished by increasing the root temperature from 5° to 19°C with some indication that it increased again at 29°C. ABD EL RAHMAN et al. (1959), however, have noted an increase in ratio with soil temperatures of 16.8°C up to 29.9°C for tomato plants.

The temperature range studied by these authors does seem to have been too small to reveal the whole effect of soil temperature on this ratio. This effect seems to be complicated.

The high ratio at the lowest and highest root temperature is the result of a fully inhibited root growth and steady but notably retarded increase in shoot weight. In the remaining temperature range of 10°–35°C, the ratio seems to be determined by the influence of temperature on activity per gram of root and on the morphology of the roots. Although a proper understanding of this relationship requires further experimentation there seems to be no need to assume that a luxury root production existed here, as was indicated in other cases by GOEDEWAAGEN and PEERLKAMP (1951) and WENT (1943).

The air temperature of 20°C applied throughout, does not seem to have been suboptimal for shoot growth and probably was no limiting factor which may have depressed the reaction of the shoot to root temperature in the range 25°–35°C. The ultimate shoot weight at 30°C exceeded that of 25° and 35°C.

If the dry matter percentage is considered, it is evident that the content of the shoot and root at 35°C exceeded that obtained at 25° and 30°C. A corresponding increase in sucrose percentage was also found, indicating that the high dry matter content was partly a result of accumulated sucrose and not only caused by a more rapid maturation of tissues consisting of inactive carbohydrates. The roots at 25°C exhibited a higher growth rate, utilizing the photosynthates to a greater extent than at 35°C where root growth was relatively limited. Photosynthates therefore, accumulated in the roots at 35°C since photosynthesis and translocation of these products do not seem to have been limited in comparison to 25°C. Unfortunately these experiments were not continued long enough to determine whether the growth rate of the shoot will be maintained under conditions of such a high concentration of photosynthates. The decreased utilization of sucrose by the roots eventually resulted in an accumulation of carbohydrates in the shoot as well. It therefore, seems plausible to assume that the higher sucrose content of the plants at 35°C was mainly caused by a more restricted root growth.

The shoots of the plants continually held at 20°C exhibited a constant dry matter percentage up to the age of 20 days when a marked increase was evident. In previous experiments it was established that in the period prior to the date of transfer, the dry matter percentage remained constant. VAN DOBBEN (1959) established that in wheat, grown under controlled environmental conditions, a similar relation existed between the dry weight and fresh weight production up to the ear initiation stage. In the following generative phase the relation changed, the increase in fresh weight being relatively less. A constant ratio is, however, again maintained. BROUWER (1959) analysing the growth and development of peas in artificial temperature, light and air conditioned rooms, noted a similar relation between dry and fresh weight increase. He distinguished two phases up to the flowering stage.

The present results with maize reveal a marked decrease in dry matter percentage of the shoots and roots after exposure to 25° and 30°C. A similar effect was also noted with the sucrose content. An acceptable assumption seems to be that the relative increased growth which occurred at these temperatures resulted in a corresponding utilization of photosynthates, thereby reducing the sucrose and dry matter content. The absence of such an effect at 35°C has already been discussed (*cf.* par. 4). The decrease in dry matter

percentage, however, was only temporary, a rapid increase occurring during the latter part of the experimental period which coincided with the trend exhibited by the plants at 20°C. Indications that a constant relation between dry weight and fresh weight production existed during this period does not seem to have occurred.

According to LOOMIS (1953) any reduction in growth which does not correspondingly reduce the supply in photosynthate, results in an accumulation of carbohydrates previously used in growth. This then becomes the stimulus and supplies the raw material for increased differentiation. Experimental data, confirming this view have been furnished by WENT (1957); BROUWER and VAN VLIET (1960); BROUWER et al. (1961) and VAN DOBBEN (1961).

Since sufficient nutrients were available throughout the experimental period and no initiation of flower primordia was detectable, the rapid rise in dry matter percentage seems to be a disturbing factor. KAMEL (1959), however, established that the degree of shading had a pronounced effect on the dry matter percentage of barley plants; the dry matter percentage of the shoots being higher with increased light intensities. Furthermore, plant density also influenced the dry matter percentage of the shoot. During the early vegetative stage thinly spaced plants contained a higher dry matter content.

The rapid increase in dry matter content of the shoots in the present experiments during the latter part of the exposure period, in the temperature range 20°–35°C, may to some extent have been caused by radiation effects. Mutual shading of the plants in this temperature range probably decreased the intercepted radiation per plant. Since two plants were harvested successively, shading effects became less, due to the wider spacing as a consequence of harvesting. This increased the intercepted radiation per plant and consequently the dry matter content.

This however, may not have been the only cause of the increase in dry matter percentage. SINNOTT (1960) discussing differentiation during ontogeny mentions that the life history of a plant, particularly up to the time of flowering, consists of a series of successive phases, each a necessary precursor of the next, but independent of the amount of growth attained. In such phasic development the major change is the onset of the reproductive period after one of purely vegetative development. This apparently begins with a physiological change the 'ripeness to flower' as KLEBS called it. Only after this has begun do the floral primordia appear at the meristem.

According to SINNOTT (1960) it has been shown by ROBERTS and STRUCKMEYER that the induction of the flowering phase is very early indicated by a number of anatomical changes. Root growth is much reduced, cambial activity almost ceases and the vascular tissues tend rapidly to complete their full differentiation. Indications that root growth was reduced to a relatively greater extent during the last four days in the present study is revealed by the increase in shoot-root ratio. A corresponding decrease in relative growth rate is not demonstrable since the values were calculated over the latter half of the experimental period. Furthermore it was established that the increase in dry matter percentage occurred in the crown roots, where it became more conspicuous by the addition of successive whorls.

HEIMSCH et al. (1950) studying vascular development in maize, established that the diameter of the stele increases in successive sets of adventitious roots to a maximum and then decreases. This was correlated with the number and

size of xylem vessels. This seems to suggest that the increase in dry matter percentage of the roots may have been due to structural differences between the successive whorls of crown roots.

BROUWER et al. (1961) and VAN DOBBEN (1961) with maize and wheat respectively, noted no increase in dry matter percentage of the roots of these plants when nitrogen was withheld or a nitrogen shortage existed. The possibility that the increased dry matter percentage of the roots may have been caused by a limited supply of nutrients therefore, seems to be eliminated.

The results previously presented on the dry matter percentage of the leaves, revealed a more xeromorphic characteristic with progressively higher leaf insertion. SINNOTT (1960) discusses numerous results where a similar relation has been established. Such xeromorphic leaves were characterised by relatively small cells, smaller stomata and more of them per unit of area. He states that small cell size grows out of the difficulty with which water is obtained by the higher leaves since they have to lift it further and against competition from the lower ones. Thus at the critical period of rapid leaf growth, which results primarily from cell expansion through the absorption of water, the cells of the upper leaves cannot attain the size of the cells of the lower ones.

In the present study a marked increase in dry matter percentage of the older leaves, also contributed to the higher dry matter content of the whole shoot.

It can therefore, be assumed that an increase in dry matter percentage of the shoot in maize, apart from increased radiation effects, may not necessarily be related to a limited supply of nutrients or water in the root environment. The internal supply and translocation of these constituents may also be of importance. It is, however, possible that in maize these transformations coincided with an early physiological change prior to the initiation of flower primordia.

Considering the temperatures beyond the range 20°–35°C it is evident that the retarded growth of the shoot, as a result of the reduced activity of the root system, resulted in an increase in dry matter content, primarily as a result of sucrose accumulation. This is clearly demonstrated at 5° and 10°C where shoot growth was at a minimum, as measured by leaf elongation and fresh weight, immediately after transference to these temperatures. A remarkable increase in dry weight however, occurred, clearly indicating that photosynthesis was relatively less influenced than growth, resulting in an accumulation of carbohydrates, presumably mostly sucrose. A similar reaction has also been described by BROUWER and VAN VLIET (1960) for peas exposed to various root temperatures.

Root growth at 5°C was inhibited with no indication of an increase in dry matter percentage (*cf.* fig. 11). The relatively high sucrose content still found in the roots after eight days of exposure seems to represent the portion present when the plants were transferred. This implies that none or little translocation of the accumulated photosynthates in the leaves had occurred, which is substantiated by the results of numerous investigators as reported by CRAFTS (1961). The pronounced increase in shoot-root ratio obtained with the dry weights therefore, does not seem to be a result of relative differences in growth since a constant ratio was obtained with the fresh weights, but merely

due to the fact that photosynthesis was retarded relatively less or not at all.

Some increase in dry matter content of the roots was evident at 10°C. Measurable growth of the root also occurred thus utilizing some of the photosynthates. An increase in dry weight was therefore evident without a marked corresponding rise in sucrose content. The increase in shoot-root ratio during the early periods of exposure is, therefore, a result of a relatively retarded root growth and sucrose accumulation in the shoot. Root growth, however, was retarded relatively less during the last seven days, resulting in a constant shoot-root ratio. This seems to have been caused by numerous factors. The increase in crown root number was one factor which contributed to the increased relative growth rate. These roots were initiated above the nutrient solution in the transition temperature zone where temperatures exceeded 10°C. Their elongation however, was practically inhibited once the nutrient solution had been penetrated. Furthermore, a relatively greater increase in seminal root weight occurred during the last four days. Evidence of a compensatory correlation seems to exist even at 10°C once the root system becomes limiting to maintain shoot growth. Some increase in dry matter percentage and sucrose content was evident in the roots at 10°C suggesting that translocation was not limiting at this temperature.

The marked increase in dry matter content of the shoot at 15°C and a similar rise in sucrose percentage in conjunction with a retarded growth rate, indicate that relatively less photosynthates were used for growth than produced by photosynthesis. A relatively larger increase in shoot growth occurred once the roots were exposed to 15°C. The shoot-root ratio and relative growth rates, however, show that this was only temporary. Root growth eventually increased with indications that shoot growth diminished, resulting in a progressive decrease in shoot-root ratio. The relative growth rates indicate that the weight gained by the roots at 15°C in relation to their weight when transferred, was nine times greater than that of the roots at 10°C. Root growth was, therefore, considerable as compared to 10°C, with a corresponding utilization of sucrose and therefore, a lower sucrose content. The root system however, showed a marked increase in dry matter content which indicates that incorporation of carbohydrates in the plant body as inactive material (cellulose and hemicellulose), occurred at a relatively greater extent than sucrose accumulation. At higher root temperatures the dry matter percentage and its sucrose content follows the same trend.

The increase in root growth and decreased shoot growth suggests some nutritional correlation where the root system becomes limiting to supply the nutritional requirements for the shoot to maintain its growth rate. The appearance of the second whorl of crown roots coincided with the stage when the shoot-root ratio was reduced (13-17 day period). In addition, these roots revealed a relatively greater increase in growth (fresh weight) than the seminal roots. The increased relative growth rate of the whole root system was therefore, mainly due to the crown roots. These roots were much thicker than the first whorl of crown roots which may have been a factor contributing to the greater increase in weight.

The detrimental effect of 40°C while exposing the shoot to 20°C has clearly been demonstrated. WENT (1953), however, has stated that most physiological processes proceed normally in plants from approximately 0°-40°C. The data obtained in the present study seem to indicate that a

constant temperature of 40°C for the roots is decidedly too high for the exposure period applied; the detrimental effect, judged by fresh and dry weight accumulation, only becoming evident after three days of exposure.

The pronounced increase in dry matter percentage was more the result of a relatively greater increase in dry weight than loss of moisture caused by desiccation. A considerable portion of the dry matter increase still consisted of soluble carbohydrates, mostly sucrose. Furthermore, the limited growth of the shoot is partly due to the fact that crown roots developed at the nodi above the nutrient solution where the temperature was decidedly less than 40°C. These roots probably absorbed water and nutrients which contributed to the maintenance of the limited growth.

Differentiation and suberization of the seminal and crown roots present, when the plants were transferred to 40°C, as well as translocation of photosynthates to these and the newly developed roots, probably resulted in the rapid increase in dry matter percentage within the first seven days after exposure. Once differentiation of these tissues had been completed the dry matter percentage increased very little.

No shift in optimum temperature occurred in these experiments in the period following the first three days after transference. The plants at 40°C still seemed to maintain a growth rate similar to those in the optimum temperature range during the first three days of exposure. The data on total leaf elongation, however, indicate that root activity had already diminished within the second day after exposure. Root activity was probably reduced as a result of increased suberization of the roots.

The effect of soil temperature on growth was not generally altered when older plants (22 days) were also subjected to the various temperatures. Indications that the shift in optimum with time is a function of size and not of age, as interpreted by WENT (1957) was unnoticeable. In fact, it was noted that the effect of a root temperature of 40°C was less severe than on younger plants (10 days old). The leaves of the older plants maintained photosynthesis for a longer period than was the case with younger plants. The length of the exposure period therefore, seems to be a determining factor as concluded by RICHARDS et al. (1952) and BROUWER and VAN VLIET (1960) and this effect depends on the age of the plants.

3.2. SHOOT AND ROOT ACTIVITIES

3.2.1. Introduction

In the previous chapter it has been shown that the temperature to which the root system is exposed has a marked effect on the relative growth rate of the shoot. BRIGGS et al. (1920) used the relative growth rate as primary measure of the rate of change in weight and resolved it into two components, the net assimilation rate and leaf-area ratio. According to BALLARD and PETRIE (1936) the leaf-area ratio constitutes the fraction of the plant that is producing new material. The new material is produced mainly by the leaves and the fraction of the plant that they represent can be measured as leaf-weight or leaf-area ratio. The second component, the rate of increase in dry weight per unit of leaf results from a number of metabolic processes, the rates of all of which, except carbon assimilation, are generally relatively small.

WATSON (1952) discussing the best basis on which to express net assimilation rate mentioned that ideally it should be a precise measure of the capacity of the system responsible for dry matter accumulation, that is, of the 'internal factor' or 'growing material' of the plant. However, as photosynthesis occurs mainly in the leaves, whereas respiration proceeds throughout the whole plant, it seems to be impossible for any one attribute to be a precise measure of the 'internal factor' for both processes. The best course according to WATSON (1952) seems to be to use a basis of reference appropriate for photosynthesis, since this must be the dominant process whenever increase in dry weight is taking place. WILLIAMS (1946), after reviewing the literature on net assimilation rate, concluded that the crudity of leaf area, leaf weight and leaf protein as measures of the 'internal factor' for growth does not destroy the value of these rates, provided they are interpreted with caution.

The determination of the net assimilation rate and leaf-weight ratio may therefore, be of advantage in clarifying the growth responses, discussed in the previous chapter, to some extent.

The efficiency of water use by plants expressed as the ratio of water used per unit increase in dry matter, has been shown to vary with climate, plant species, fertilization and other cultural practices (KRAMER, 1959a; BURTON, 1959).

No consistent effect of soil temperature on the transpiration ratio was found with maize (NIELSEN et al., 1961). Marked effects, however, were noted with oats and lucern, the efficiency of water use decreasing with increasing soil temperature. A similar decrease in water use efficiency with rising solution culture temperatures has also been determined by BROUWER and VAN VLIET (1960) for peas.

These results seem to indicate that increase in dry matter was influenced relatively less than water uptake.

Additional information on the effect of soil temperature on water use efficiency by maize under controlled conditions seems necessary.

The most important phase of plant-water relations with respect to plant growth is the degree of turgidity maintained in the tissues, since loss of turgidity interferes with plant growth in various ways (KRAMER, 1949). Rapid transpiration, however, is not harmful in itself if it is accompanied by absorption sufficiently rapid to prevent a serious internal water deficit resulting in a loss of turgidity.

One of the first effects of a water deficit is a decrease in or cessation of elongation of stems and enlargement of leaves and fruits because these processes are dependant on a turgid condition of the cells (KRAMER, 1959a; BROUWER, 1963).

KRAMER (1959b) has demonstrated experimentally that the rate of water absorption is usually closely correlated with the rate of water loss. Transpiration rate may therefore, be considered a fair indication of rate of water absorption.

Soil temperature has also been noted to affect rate of water absorption by plants (KRAMER, 1949; RICHARDS et al., 1952). Low soil temperature usually reduced absorption of water but according to KRAMER (1949) species differences occur. The reduction in species native to cooler climates being less than for warm-weather crops.

The rate of water absorption by plants appears to increase with increasing root temperature up to a point above which absorption is depressed by a further rise in temperature (RICHARDS et al., 1952).

KRAMER (1949) concluded that the principal cause of reduced intake of water by transpiring plants in cold soil, results from the combined effects of the decreased permeability and increased viscosity of the protoplasm of the living cells in the roots and the increased viscosity and decreased diffusion pressure of the water intake.

Retarded growth of plants at low soil temperatures has accordingly been ascribed to a reduced water uptake (RICHARDS et al., 1952).

Recent experiments with tomatoes by ABD EL RAHMAN et al. (1959) confirmed previous results, demonstrating that water supply was a limiting factor at low soil temperature. A similar conclusion was reached by BROWER and VAN VLIET (1960) in the growth of pea plants at low root temperatures in solution culture.

DAVIS and LINGLE (1961) presented data where the shoot growth depression of tomatoes, generally found at low root temperatures, could not be eliminated by increasing moisture supply to the shoot. LUNT et al. (1960) observed with red kidney beans that growth was consistently better at a higher humidity than at a lower humidity. At the lowest root temperature (13°C) the differences in fresh weight due to relative humidity was approximately 30 per cent. At more favourable root temperatures (21° and 29°C) a relatively small effect of relative humidity was found, averaging about 14 per cent.

Data on water uptake by maize as influenced by soil or root temperature appear to be limited. Furthermore, since growth of the plant is dependant on water supply, which is influenced by the roots, transpiration measurements are essential if growth responses to root temperature are to be clarified.

The uptake of mineral nutrients by plants has also been shown to be affected by temperature (BROYER, 1951; RICHARDS et al., 1952; STEWARD and SUTCLIFFE, 1959; SUTCLIFFE, 1962). The rate of absorption tends to increase with increasing temperature until a maximum rate is reached and then to decrease again at still higher temperatures. According to SUTCLIFFE (1962) absorption is progressively reduced in many plants at temperatures above 40°C presumably because of the inactivation of enzyme systems involved. Furthermore, the cytoplasm becomes more permeable to passive leakage of salts through it at high temperatures so that if a concentration gradient exists net absorption is reduced as the temperature is raised. At the lower temperatures absorption is decreased both by diminution in the rate of chemical reactions involved in active transport and by increased viscosity and hence higher resistance of the cell membranes.

According to KRAMER (1949) and RICHARDS et al. (1952) many investigators have indicated that the absorption of salts by intact plants is reduced by low temperature. They emphasize, however, that it is difficult to separate the effects of low temperature on the absorption process from its effects on translocation and on utilization of the nutrients in the plant.

It is also conceivable that the absorption of nutrients by plants, exposed to different root temperatures, may be altered when compared with data obtained by subjecting the shoot and root to the same temperature.

Numerous data have recently been published where the effect of soil temperature has been studied in soil culture (KETCHESON, 1957; PARKS and FISHER, 1958; LINGLE and DAVIS, 1959; LOCASCIO and WARREN, 1960; NIELSEN et al., 1961). Many secondary effects of soil temperature are liable to influence growth and nutrient uptake in such experiments. The microbial activity and consequently availability of nitrogen and other mineral elements is altered by soil temperature (RICHARDS et al., 1952). Soil temperature affects the water supplying power of the soil, being one-third to one-half as great at freezing as at 25°C (KRAMER, 1949).

Variations in soil temperature may also influence nutrient uptake through changes in amount of root extension (KETCHESON, 1957).

If the direct effect of root temperature on the uptake of nutrient elements is to be clarified the solution culture technique seems to be the most appropriate.

ZHURBITZKY and SHTRAUSBERG (1958) recently established in solution culture that the initial absorption of phosphorus by the root system of oats, with the shoots exposed to 20°C, is very little affected by root temperature but assimilation and transport to above ground organs are favoured by the higher root temperature. If the absorption period is extended (3–4 hours) the lower root temperature also reduced uptake judged by a lower P^{32} content of the roots.

McEvoy (1960) measured the P^{32} content of tobacco leaves after the root systems had been exposed to temperatures ranging from 10°–40°C for eight hours. He stated that this exposure period was so brief that development of significant variation in root growth among temperature treatments was improbable. An increase in P^{32} uptake with increasing temperature occurred, whereas no significant difference in fresh weight per plant was observed. With increased periods of exposure a marked time effect was noticed. The uptake of P^{32} being decreased at 40°C when the exposure period was extended beyond four days.

GUKOVA (1962) determined the effect of increased root temperatures on the uptake of P^{32} by lupins. He found that during short periods (3–4 hours) of absorption, at root temperatures of 20° and 32°C, the accumulation of phosphorus in the shoot increased at 32°C while its total absorption by the roots was less than at 20°C. After fourteen hours, however, the content of leaves and roots at 32°C was less than at 20°C. Here it was established that an overall loss to the ambient root environment had occurred. With an increased exposure period (20 days) a similar relation was found between root temperature and P^{32} uptake; the content being higher in the shoot and roots at 20°C. Additional experimentation with peas, beans and lupins revealed that fresh weight production seemed to be greater at 32°C. A similar trend was noted in nitrogen content whereas the opposite occurred in phosphate content.

In young tomato plants DAVIS and LINGLE (1961) detected no differences in potassium or soluble phosphorus content of the shoots within 24 hours after exposure to solution culture temperatures of 13° and 25°C. The nitrate nitrogen content, however, was less at the lower temperature. From additional results with longer exposure periods they concluded that rate of nutrient supply was not the factor which limited shoot growth at cool temperatures.

It is evident that different results have been obtained in regard to nutrient uptake as influenced by root temperature. This may to some extent be due to the fact that different species have been used.

Data on maize are limited and are mainly based on soil culture experiments (KETCHESON, 1957; DORMAAR and KETCHESON, 1960; NIELSEN et al., 1961). Additional information seems necessary under conditions where secondary effects of the root medium have been minimized.

3.2.2. Net assimilation rate and leaf-weight ratio

The net assimilation rate or unit leaf rate has been calculated on a basis of leaf fresh weight. The leaf fresh weight was obtained by separating the various portions of the plant at harvest and determining the weight of the individual leaves viz. sheath and blade, of all the leaves visible. The values are therefore, slightly in error on account of the inclusion of all the leaf sheaths since they overlap and only a small part performs a certain amount of carbon assimilation.

The net assimilation rate (E) has been calculated from the equation

$$E = \frac{w_2 - w_1}{L_2 - L_1} \times \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1},$$

where W denotes the total dry weight (shoots and roots) of the plants and L the leaf fresh weight. The subscripts 1 and 2 refer to the periods between which the average value of the quantity is being calculated.

WILLIAMS (1946) demonstrated that the direct application of this equation, when the Lw - W relation is not linear, may give values of E which are erroneous.

This relation was practically linear for the data obtained with young plants (10 days old) during an exposure period of fourteen days to the different root temperatures. E -values were nevertheless calculated for each two-day interval; the values of W and L being obtained by interpolation after plotting leaf fresh weight against total dry weight as advocated by WILLIAMS (1946). The E -values for the period 10–24 days, presented in fig. 15, are means of seven values calculated per temperature for each two-day interval.

Fig. 15 illustrates that the average net assimilation rate (NAR) in the

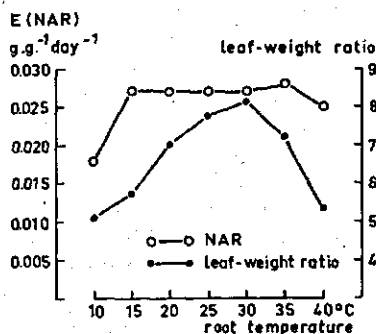


FIG. 15. Mean net assimilation rate (NAR) and mean leaf-weight ratio of plants grown during 14 days at the root temperatures indicated

range 15°–35°C exceeded that at 10° and 40°C. A decline in NAR was, however, found at 15°C during the course of the experiment, which did not occur at the temperatures 20°, 25°, 30° and 35°C. This seems to indicate that a root temperature of 15°C also has an adverse effect on NAR, becoming more pronounced with a prolonged exposure period.

The leaf-weight ratio, presented in fig. 15 was calculated from the total leaf fresh weight and total dry weight (shoots and roots) per plant. It is evident that the largest proportion of leaves in relation to the total plant dry weight occurred at 30°C. This ratio decreased rapidly with a further rise or lowering of the root temperature.

3.2.3. Transpiration

The effect of root temperature on the transpiration ratio *viz.* grams water used per gram of dry matter produced, is demonstrated by fig. 16.

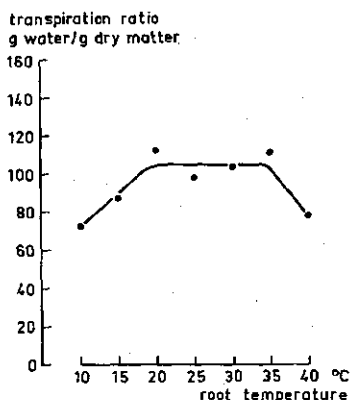


FIG. 16. Transpiration ratio of plants during the latter 10 days of an exposure period of 14 days to the root temperatures indicated

The transpiration of the plants, exposed to the different root temperatures, for a period of fourteen days (after growing at 20°C for ten days), was determined during the latter ten days of the experiment. The ratios presented in fig. 16 being the average for this period. It is evident that less water was transpired at 10°, 15° and 40°C per gram of dry matter produced than in the temperature range 20°–35°C. The effect of the root temperature in the range 20°–35°C seems to be similar judged by the transpiration ratios (fig. 16). A conspicuous time effect, however, was noticed at 40°C. Within the first four days after transference the transpiration ratio was approximately similar to that obtained in the temperature range 20°–35°C. After this period it gradually diminished to a value of 41.7 during the last two days of the experiment. This seems to indicate that injury and ultimate death of the root system, when exposed to 40°C, was responsible for a progressive decrease in the water absorption capacity of the root system.

To determine whether the differences in water requirement were the result of differences in rate of transpiration, data obtained by four separate experiments were used. The transpiration values, obtained during the last day before harvest, of the following experiments were used:

- plants exposed to the various root temperatures at the age of twelve days for a period of eight days;
- plants exposed to the various root temperatures at the age of twenty days for five days;
- plants exposed to the different root temperatures at the age of twelve days for six days; a 'double strength' nutrient solution being used throughout;
- plants exposed to the different root temperatures for five days at the age of twenty-two days. The nutrient solution used throughout contained double the concentration of macro-elements used in experiments 1 and 2.

Unfortunately no leaf area determinations were made to calculate the transpiration rate on a leaf area basis. Leaf fresh weight data, however, had been determined, which was regarded as a fair indication of leaf area. The transpiration rate in gram per day per gram leaf fresh weight is given in fig. 17.

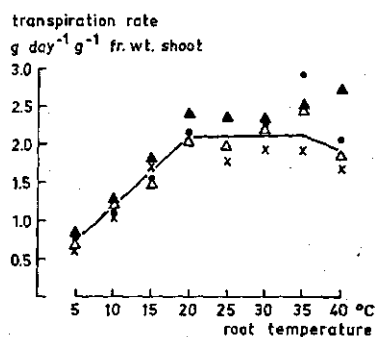


FIG. 17. Effect of root temperature on the transpiration rate per gram fresh weight of the shoot

• 12 days at 20°C, 8 days at 5°-40°C
 x 20 " " 20°C, 5 " " 5°-40°C
 ▲ 12 " " 20°C, 6 " " 5°-40°C
 △ 22 " " 20°C, 5 " " 5°-40°C

A linear relation is evident between temperature and transpiration rate in the temperature range 5°-20°C (fig. 17). The transpiration rates in the range 20°-35°C seem to be similar, notwithstanding the larger differences between experiments. Indications that the rate decreases if the temperature is increased to 40°C was evident in three of the four experiments. A more pronounced depression will probably occur if the exposure periods are extended.

No depressing effect of an increased osmotic pressure from 0.3-0.6 atmospheres of the nutrient solution on transpiration rate is evident. HEWITT (1952) in his review on the effect of osmotic pressure on plant growth presented data which indicated that values of 0.32-0.78 atmospheres were optimum in water culture.

DE WIT and ALBERDA (1961) mention that plants growing faster also grow into a different climatic environment since light intensity increases without corresponding changes in other factors viz. wind velocity, temper-

ature and humidity. Since notable differences in growth rate have been established at the various root temperatures it is possible that the plants at the favourable temperatures may ultimately grow into an environment of especially a higher light intensity. According to DE WIT and ALBERDA (1961) transpiration rate is approximately proportional to the intercepted radiation, consequently a higher rate may be obtained purely as a result of an increased light intensity. PLATE II shows the relative sizes of the plants harvested after exposure to the root temperatures for eight days. It is evident that the differences in transpiration rate between 5°, 10° and 40°C cannot be ascribed to differences in height and therefore, light intensity. Furthermore, the plants at 20° and 25°C appeared taller than those at 30° and 35°C, but no differences in transpiration rate apparently existed between these temperatures. If transpiration rate was influenced by intercepted radiation, PLATE II indicates that the more erect leaves at 5° and 10°C may have resulted in less interception, thereby decreasing the transpiration rate.

The data in fig. 17 indicate that the decreased transpiration ratios at 10°, 15° and 40°C (fig. 16) were mainly the result of a relatively greater decrease in transpiration rate as compared with the net assimilation rate.

3.2.4. Ion uptake

The plants used in these experiments were grown at 20°C for ten days and then subjected to the different root temperatures for fourteen days. To eliminate any possible effect of a low internal nutrient status of the plants on absorption during the succeeding absorption period at the different root temperatures, the nutrient solution was renewed regularly as well as 24 hours prior to transference. The plants were transferred to a renewed nutrient solution when subjected to the different root temperatures.

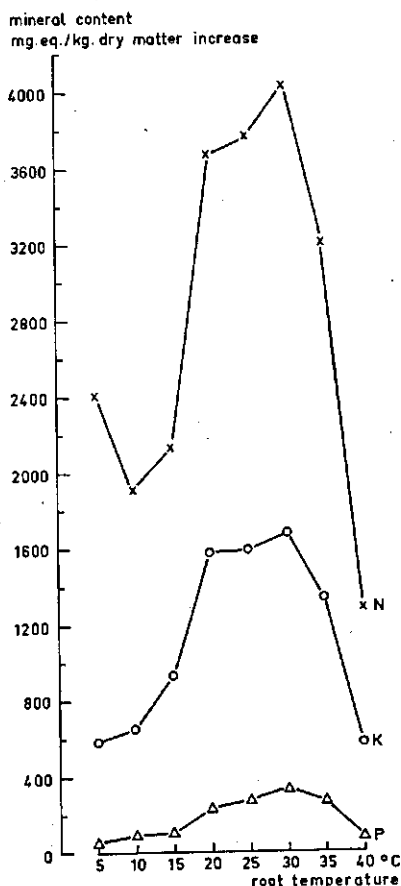
The absorption of nitrate, phosphorus and potassium (N, P and K) was determined by measuring the amount of depletion of these nutrients in the solution during four successive periods. Two separate plants were used per temperature for each successive period and harvested immediately there-after. The increase in weight and corresponding nutrient uptake during the exposure period could, therefore, be determined.

The uptake of N, P and K per unit increase in total dry weight is given in fig. 18. The values are expressed in milligram equivalent per kilogram dry matter, phosphate and nitrogen being calculated as monovalent ions.

The trends in fig. 18 indicate that accumulation of N, P and K was most rapid in the temperature range 20°–35°C; uptake of N and K being relatively less at 35°C. The uptake of N at 40°C seems to have been relatively less than K and P in comparison to 5° and 10°C. A higher content of N occurred at 5°C exceeding that of 10° and 15°C. The increase in total dry weight at 5°C was decidedly less than at 10°C (fig. 9) probably resulting in less dilution per unit increase in weight.

BIDDULPH (1951) stated that in a general sense two basic phenomena influence the direction of movement of minerals within a plant. These are metabolic use and transpiration. The intensity of these factors in any tissue will determine the net movement to the tissue. SUTCLIFFE (1962) also states that the rate at which salts are delivered to the leaves is determined by the rate at which they are supplied to the conducting elements in the roots. The

FIG. 18. Uptake of nitrate (N), phosphate (P) and potassium (K) per unit increase in total dry weight (shoots plus roots) during an exposure period of 14 days to the root temperatures indicated (analysis of nutrient solution)



transport into the stele from the cortex of the root, however, is also influenced by the concentration of salts in the xylem sap. An increased concentration in the stele reduces transport into the stele. In this way transpiration rate exerts an indirect influence on salt absorption into the root.

Since large differences in growth and transpiration rate occurred at the various root temperatures studied, it seemed probable that the distribution of the nutrients between shoots and roots may not necessarily be similar at the various temperatures. The nutrient uptake by the whole plant may, therefore, be insufficient as an aid in clarifying growth responses of the shoot. Additional information on the mineral content of the shoot seems necessary.

An experiment was therefore, conducted using plants which had been growing at 20°C for twelve days and subjecting these to the different root temperatures for eight days.

The N, P, K, Ca and Mg content of the shoots are presented in fig. 19. No data on the Ca content at 5°C is presented since insufficient plant material was available for a chemical analysis. It is evident that the trends obtained with N, P and K on a dry weight basis, were quite similar to those found by analysing the nutrient solution (fig. 18).

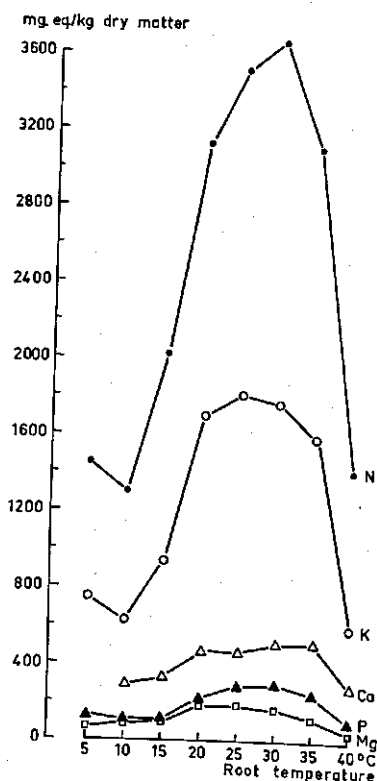


FIG. 19. Effect of root temperature on the mineral content of the shoots (dry weights) after 12 days at 20°C and 8 days at the different root temperatures (analysis of plant material)

To facilitate comparisons between the different nutrients the values in fig. 19 have been expressed as percentage of the average content of 20°, 25°, 30° and 35°C. The data, presented in table 9 indicate that the relative content of N, P and K were quite similar at the root temperatures tested. Some indication does exist that phosphate uptake at 15° and 20°C was relatively less than that of N and K.

TABLE 9. Relative mineral content of shoots after exposure to the different root temperatures for eight days (dry weight basis)

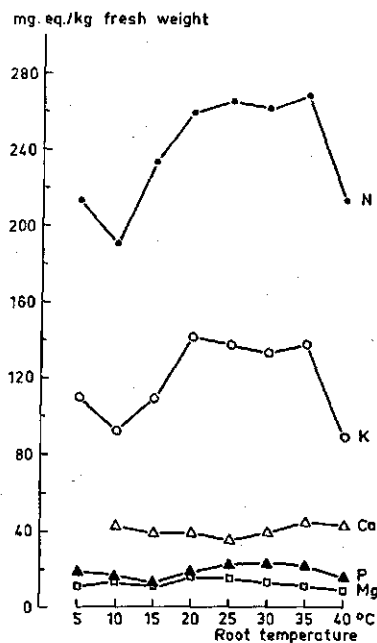
Nutrient	Temperature - °C							
	5°	10°	15°	20°	25°	30°	35°	40°
P	47.4	42.5	41.4	83.8	109.0	112.8	94.7	38.7
K	43.6	36.6	55.1	99.1	105.5	102.8	92.5	34.4
N	43.3	38.8	60.3	93.2	104.7	109.6	92.5	42.0
Ca	-	59.1	67.9	95.5	94.9	104.3	105.1	58.3
Mg	43.8	52.7	58.6	111.8	114.2	100.0	73.4	32.5

Fig. 19 further indicates that Ca accumulation in the shoot apparently increased with a rise in temperature from 25° to 35°C whereas Mg accumu-

lation decreased. The effect of root temperature beyond this temperature range seems to be similar, a corresponding decrease in Ca and Mg content being evident at 10° and 15°C.

Since large differences in dry matter percentage occurred in the shoots at the various root temperatures (fig. 11) the method of expressing mineral content on a unit dry weight basis may result in disputable conclusions. An alternative approach is to express the mineral content on a fresh weight basis. This procedure may eliminate the effect of a relatively larger increase in dry weight to some extent.

FIG. 20. Mineral content of the shoots on a fresh weight basis, previously presented on a dry weight basis in fig. 19



The mineral content of the shoots in milligram equivalent per kilogram fresh weight, previously presented in fig. 19 on a dry weight basis, is given in fig. 20. The data indicate that the trends for N, P and K are similar to those obtained on a dry weight basis (fig. 19) with the exception that differences are much smaller and practically eliminated in the temperature range 20°–35°C.

The relative content as percentage of the mean concentration at 20°, 25°, 30° and 35°C is presented in table 10.

The data in table 10 demonstrate that the differences in relative content between the various root temperatures were much less than previously found with the dry weights. The differences in N, P and K content previously encountered in the range 20°–35°C with the dry weights seem to have been caused by a relatively greater increase in dry weight at 20° and 35°C resulting in a lower content per unit of dry weight. When compared on a fresh weight basis it is evident that per unit of shoot weight no differences in uptake occurred between 20°, 25°, 30° and 35°C for P, K and N except

TABLE 10. Relative mineral content of shoots (fresh weight) after exposure to the different root temperatures for eight days

Nutrient	Temperature - °C							
	5°	10°	15°	20°	25°	30°	35°	40°
P	87.7	77.8	59.9	87.3	103.8	106.6	102.8	74.1
K	80.3	67.2	79.6	102.9	100.0	97.1	100.7	65.7
N	81.0	72.2	89.0	98.5	100.8	99.2	101.9	81.0
Ca	-	107.7	97.7	99.0	89.5	98.2	113.5	109.9
Mg	80.0	96.3	85.2	116.3	108.1	94.1	80.0	62.2

that P uptake at 20°C seems to have been limited. Table 10 further indicates that uptake of N, P and K was limited at 5°, 10°, 15° and 40°C. The larger content at 5°C compared to 10°C seems to be the result of a relatively greater accumulation of N, P and K in the shoot at 5°C than growth, whereas the opposite condition occurred at 10°C.

The relative values for Ca (table 10) in the temperature range 10°–30°C were quite similar, with indications that it increased at the temperatures above 30°C. The relative Mg content, however, decreased with a rise in temperature from 20°–40°C. At the temperatures 10° and 15°C the relative content of Ca and Mg seems to have been influenced similarly (table 10).

Table 10 also illustrates that the uptake of Ca and Mg, judged by the relative contents of the shoot, was decreased conspicuously less at 10°C when compared with N, P and K at this temperature.

The mineral content of the shoots (fresh weight) of plants exposed to the various root temperatures for five days is given in fig. 21. These plants

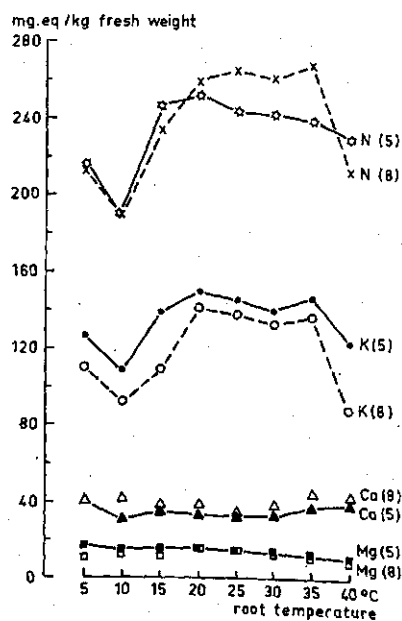


FIG. 21. Mineral content of shoots (fresh weight basis) of plants exposed to the root temperatures for 5 and 8 days respectively (analysis of plant material)

were grown at 20°C for 20 days before subjecting their root systems to the different temperatures. The mineral composition of the shoots of younger plants, previously presented in fig. 20, is included for comparison.

From fig. 21 it is evident that the effect of root temperature on the mineral content has in general been similar to that encountered in younger plants.

It is evident that no differences in N and K content existed in the shoots in the temperature range 15°–35°C after an exposure period of five days. This, however, was not the case with younger plants after eight days at similar temperatures; here the content at 15°C was decidedly lower. Similar results were also obtained with phosphate.

The N and K content of the shoot at 5°, 10° and 40°C seems to be less than that of the shoots in the temperature range 20°–35°C (fig. 21).

The trends of the Ca and Mg contents in the temperature range 5°–40°C appear to be similar for both exposure periods. Some discrepancy occurred at 10°C where Ca increased to a relatively greater extent after eight days of exposure.

The preceding results on mineral uptake have been obtained during periods in which pronounced differences in growth were evident. Since a close correlation may exist between growth and absorption of minerals in whole plants (STEWART and SUTCLIFFE, 1959; SUTCLIFFE, 1962), it is difficult to establish whether the growth differences were actually related to a limited nutrient uptake.

To eliminate the effect of growth as far as possible, the uptake of radioactive rubidium was determined during an exposure period of 24 hours (16 hours photo- and 8 hours nyctoperiod) to the various root temperatures. The plants used were grown at 20°C for 10 days and the rubidium uptake determined within 24 and 72 hours after transference to the root temperatures. The uptake of rubidium in counts per minute (cpm) per kilogram fresh weight of the roots and shoots separately, after 24 and 72 hours respectively, are presented in fig. 22 (a) and (b).

The data in fig. 22 (a) indicate that pronounced differences in the shoots and roots occurred within 24 hours after exposure. Some indication that an increased fresh weight per plant had also occurred after 24 hours seems to exist (fig. 22 (a)). It is nevertheless evident that in the temperature range 15°–35°C, where practically no differences in fresh weight of the shoot occurred, uptake was retarded at 15°C. Furthermore, that accumulation by the shoots and absorption by the roots at 5° and 10°C were decreased to a greater extent than at 15°C (fig. 22 (a)).

The marked retarding effect of 40°C on absorption by the shoots and roots after 24 hours of exposure is demonstrated in fig. 22 (a).

The uptake after 72 hours of exposure (fig. 21 (b)) was similar in the temperature range 20°–35°C for both shoots and roots. Beyond this temperature range accumulation by the shoot was still retarded. The values of the roots in the temperature range 15°–40°C varies, exhibiting no clear trend. Uptake by the roots and shoots at 5° and 10°C still remained less than that obtained with increased root temperatures.

3.2.5. Discussion

The results presented in this chapter demonstrate that exposure of the

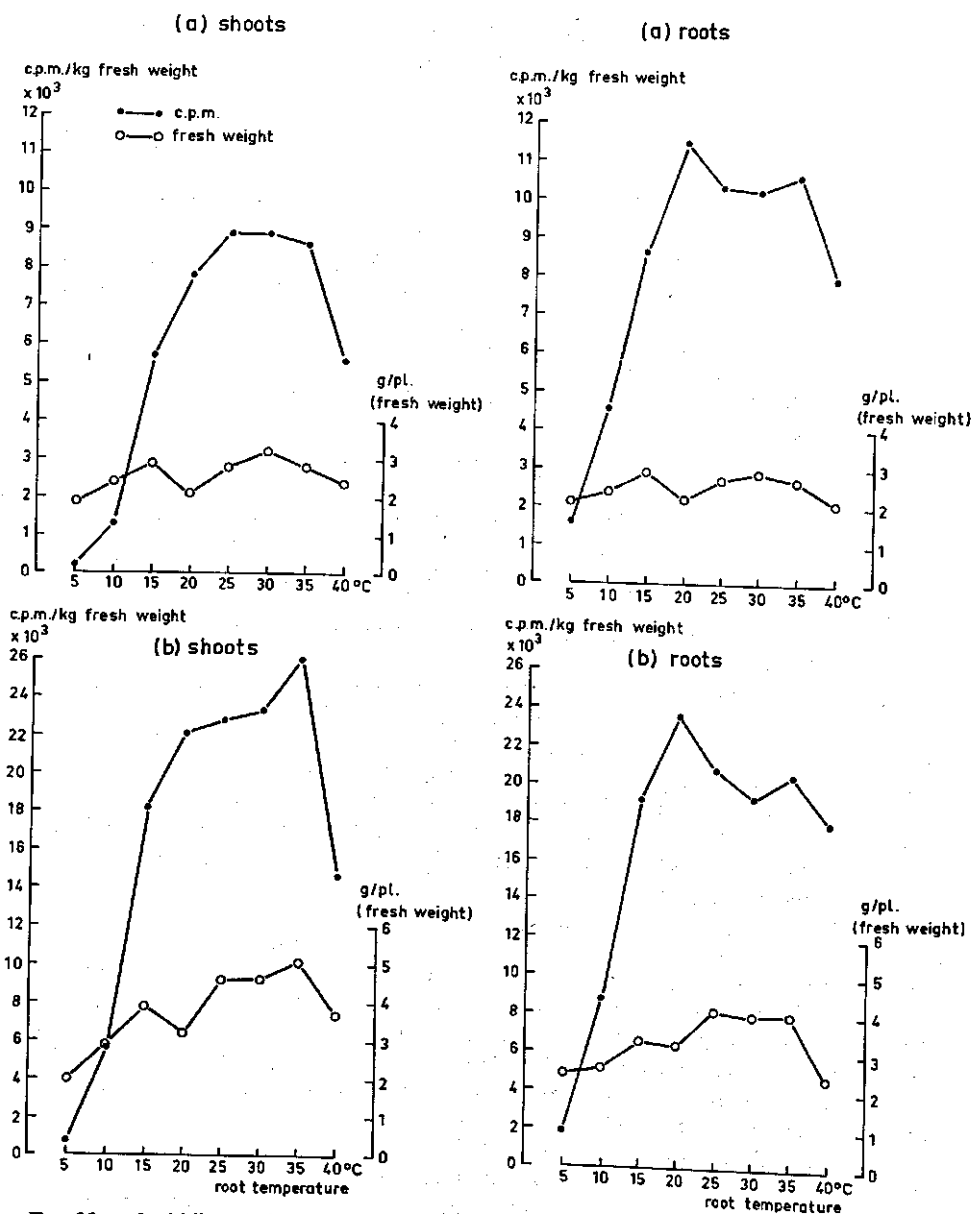


FIG. 22 *a* Rubidium (Rb^{86}) content per unit fresh weight, and the fresh weights of the shoots and roots, after 24 hours at the different root temperatures
b As 22*a* but after 72 hours at the different root temperatures

root system and base of the plant to various temperatures had a pronounced effect on the net assimilation rate, transpiration and ion accumulation in the shoot, kept at a constant temperature of 20°C.

In the temperature range 15°–35°C the net assimilation rate (NAR) was

found to be similar. A much lower value was, however, obtained at 10°C and to some extent at 40°C.

The NAR is by no means a pure measure of photosynthesis (WATSON, 1952). It depends on the excess of dry matter gain by photosynthesis over loss by respiration. Consequently it cannot be assumed that the differences in NAR originated from variations in rate of photosynthesis only.

Large differences in plant height ultimately also occurred at the various temperatures (PLATE I). The upper leaves of the larger plants were therefore, receiving higher light intensities than those of the smaller plants. The results of GAASTRA (1959) further showed that leaf temperature also increased with increasing light intensity. These changes in environmental conditions of the shoot and their possible effect on photosynthesis and respiration is difficult to evaluate. Judged by the NAR calculated for each temperature an increase only occurred during the last two days at 20°, 25°, 30° and 35°C, whereas a notable decrease was evident at 10°, 15° and 40°C.

The increase in dry weight of the root system also contributed to the NAR. In the present experiments they were exposed to different temperatures. JENSEN (1960) studying the effect of root temperature on the respiration of intact root systems of maize, with the shoot exposed to 20°C, demonstrated a marked increase in respiratory quotient with rise in temperature from 5° to 35°C with 5°C intervals. Furthermore, from the graphs presented by him it is evident that the rate of carbon dioxide liberation and oxygen uptake of roots exposed to 30°C for 60–70 minutes followed by a similar exposure period to 35°C, was less at the higher temperature. The relative rates at 35°C, however, exceeded those of 30°C. If the plants were exposed to 35°C first and then transferred to 30°C the liberation rates were higher at 35°C. This indicates a marked time effect on respiration. A similar time effect has also been demonstrated where pea seedlings were exposed to different temperatures (MEYER et al., 1960).

Furthermore the NAR involves the expression of respiration rate as the total respiration of the whole plant per unit leaf fresh weight. The respiration of the whole plant per unit leaf fresh weight will vary with the leaf-weight ratio, independently of a change in the respiratory activity of the tissues merely because the respiration of a varying weight of plant material is referred to unit leaf fresh weight. Hence, a decrease in leaf-weight ratio involves an increase in rate of respiration per unit leaf weight purely as a result of a relatively larger increase in the non-photosynthetic system.

This review indicates that it is exceptionally difficult to relate the differences found in NAR at the root temperatures 10° and 40°C to a decreased rate of photosynthesis. WATSON (1952) discussing NAR admits that changes in these values may originate from a drift in rate of photosynthesis, or in rate of respiration per unit dry weight or in leaf-weight ratio.

The NAR data of the present study indicate that the differences in relative growth rate which were observed in the temperature range 20°–35°C cannot be ascribed to the rate of increase in dry weight per unit leaf fresh weight. A factor which probably did contribute was leaf-weight ratio. HANWAY (1962) also concluded from field studies with maize that differences in NAR appeared to be of much less importance in determining rate of dry matter production than does the weight of leaves. Even at temperatures of 10° and 40°C it seems to be improbable that the retarded rate of dry matter pro-

duction per unit of leaf fresh weight contributed to the less rapid relative growth rates. The water soluble carbohydrate content of the shoots at these temperatures exceeded that of the plants in the optimum temperature range (cf. fig. 12). The effect of the root temperatures 10° and 40°C on the leaf-weight ratio, however, was relatively more pronounced, indicating that relative leaf area per plant was decreased to a greater extent. The retarded relative growth rates, therefore, seem to be related to a decrease in leaf-weight ratio.

BROUWER and VAN VLIET (1960) however, measured a similar rate of dry matter production per unit leaf fresh weight with peas which had been exposed to root temperatures of 5°, 10°, 15° and 20°C. Leaf orientation of pea plants with regard to light source is probably not influenced by root temperature whereas with maize it certainly has an effect (PLATE I). The leaves are oriented more parallel to the light source. This then may account for the difference in results.

A marked effect of root temperature on the efficiency of water use (transpiration ratio) has been demonstrated. Less water was used in the production of a unit dry weight at 10°, 15° and 40°C than in the temperature range 20°–35°C. This seems to indicate that increase in dry matter was relatively less affected than transpiration at root temperatures of 10°, 15° and 40°C. In the temperature range 20°–35°C the amount of water transpired to produce a gram of dry matter was similar, indicating that growth differences in this temperature range were probably not related to water use.

Similar results were obtained, in respect to the low temperatures, by NIELSEN et al. (1961) for oats and lucern as well as by BROUWER and VAN VLIET (1960) for peas.

Data presented by RICHARDS et al. (1952) indicate that climate is an important factor influencing water use efficiency. Also, that the climatic factors influencing the evaporative power of the aerial environment are principally involved in the climatic effect.

ILJIN (1957) concluded that the reaction of photosynthesis and transpiration to environmental conditions is not necessarily alike. Transpiration is checked in air saturated with water vapour with no modificatory effect on the absorption of carbon dioxide.

The transpiration rate per unit leaf fresh weight showed a corresponding decrease at 10°, 15° and 40°C whereas similar rates occurred in the temperature range 20°–35°C. This indicates that under the present experimental conditions root temperatures reduced the transpiration ratio by changing the transpiration rate.

Data presented by LUNT et al. (1960) clearly demonstrate that with red kidney beans no differences in transpiration rate occurred between root temperatures of 13°, 21° and 29°C at a relative humidity of 96 per cent, whereas notable differences were evident at a relative humidity of 40 per cent.

The differences in water use efficiency at the various root temperatures described by NIELSEN et al. (1961) for oats and lucern may to some extent be the result of lower relative humidities applied which accentuated differences in the high temperature range.

It has, however, been established that species differences exist in water use efficiency; oats and lucern being less efficient than maize (RICHARDS

et al., 1952). This has been confirmed by DE WIT and ALBERDA (1961) under controlled conditions for oats in comparison to maize.

The transpiration of oats and lucern may be more sensitive to root temperatures resulting in differences in transpiration ratio in a temperature range where maize does not seem to be affected. This probably also explains the increased transpiration ratio reported by BROUWER and VAN VLIET (1960) for peas with rising root temperatures from 5° to 31°C where the light intensity and relative humidity was approximately similar to that which prevailed in the present experiments with maize.

The results reported with maize have been obtained with plants subjected to an abrupt change in root temperature which occurred when transferred from 20°C to the required temperature.

KRAMER (1949) noticed that rapidly cooled plants transpired less than did plants which were slowly cooled to the same temperature. He concluded that slow cooling possibly affords time for the occurrence of changes in protoplasmic properties that mitigate the effects of cooling on absorption.

The effect of gradual and abrupt changes in root temperature has been studied by BÖHNING and LUSANANDANA (1952) for sunflower, tomato and red kidney bean. These investigators found that although the rate of absorption under the gradual change of root temperature was generally higher than the rates under abrupt changes, the differences were not very great except when such an abrupt change brought about some permanent injury to the plants e.g. when red kidney beans were subjected to an abrupt change in root temperature from 25° to 5°C.

Since no injury was observed it, therefore, appears to be improbable that the results on transpiration obtained in the present investigation could have been altered to a marked extent if the plants were subjected to the different root temperatures gradually.

A pronounced effect of root temperature on the mineral content of maize plants has been established.

Analyses of the nutrient solution for nitrate, phosphorus and potassium (N, P and K) indicated that uptake on a dry weight basis by the whole plant in the temperature range 20°–35°C, exceeded that of temperatures beyond this range averaged over a period of fourteen days.

The effect of temperature on physical processes (diffusion, exchange and adsorption) is relatively less than its effect on active accumulation (BROYER, 1951; SUTCLIFFE, 1962). The large differences which have been obtained, therefore, seem to be mainly the result of active accumulation.

The pronounced effect of root temperature on the relative proportion of shoot to root weight has previously been discussed. Since the plants in the optimum temperature range contained a relatively larger proportion of roots, the increased content in N, P and K may to some extent be the result of a relatively greater contribution by the root system. Furthermore, ZHURBITZKY and SHTRAUSBERG (1958) as well as GUKOVA (1962) have noticed that translocation seems to be retarded at lower root temperatures. The nutrient uptake by the whole plant consequently is not necessarily an indication of the content of the shoot.

An analysis of the N, P and K content of the shoot, on a dry weight basis, revealed similar trends to that found for the whole plant. The content of N, P and K at 10°C and 40°C being approximately 35 per cent of that at 30°C.

KETCHESON (1957) reported large differences in yield and phosphorus percentage for the shoots of maize on a loam soil without additional phosphate fertilizer when subjected to root temperatures of 13° and 20°C. Additional phosphorus banded near the seed, however, increased the phosphate percentage at the low soil temperature but decreased it at 20°C resulting in no difference in phosphorus percentage at the two temperatures. A higher yield was still produced at 20°C. The decline in phosphorus percentage of the fertilized plants grown at the higher temperature was explained to be the result of a growth stimulation without a corresponding increase in phosphorus uptake. This seems to be in accord with data presented by SMITH (1962) where it was shown that practically no change in mineral composition of tissue can occur although large differences in yield are obtained even in the case of insufficient supply.

In another experiment with maize using a fine textured soil DORMAAR and KETCHESON (1960) measured the effect of three soil temperatures (15°, 21° and 27°C), on growth and phosphorus uptake. A pronounced increase in growth and phosphorus uptake (mg/unit dry weight) was evident with rising temperatures from 15° to 27°C. Increased levels of nitrogenous fertilizer had no effect on the phosphorus content at 15°C but significantly increased phosphorus uptake at 21° and 27°C. After an optimum had been reached the phosphorus content declined with further increments of nitrogenous fertilizer. The authors emphasize that the results pertain to treatments mixed throughout the rooting medium. Placing phosphorus and nitrogen in specific bands would present a different situation in respect to growth and nutrient uptake.

NIELSEN et al. (1961) established an increase in yield of tops for maize in soil culture with rising soil temperatures (5°, 12°, 19° and 27°C) without corresponding effects on the N, P and K percentages. The nutrients were mixed throughout the soil. The highest percentage of N, P and K was obtained at the lowest soil temperature (5°C). Nitrogen showed no constant relation to soil temperature, being similar at the three highest temperatures. The phosphorus percentage decreased at 12°C, and increased at 19° and 27°C; the content at 27°C still being less than that obtained at 5°C. Potassium content decreased progressively with an increase in soil temperature.

It is evident that the method of fertilizer application and soil type exerted a marked effect on the nutrient status of the shoots of maize in these experiments. A high N, P and K content was not necessarily associated with increased yields.

The present experiments in solution culture also exhibited some increase in N, P and K content at 5°C compared to 10°C, although larger yields were obtained at 10°C. Furthermore, an increase in dry weight production with rising root temperatures was clearly associated with a higher N, P and K content.

An important difference between the plants of the soil culture experiments and those obtained in the present study in solution culture was the age of the tissue. The plants were exposed for prolonged periods (6-8 weeks) in the soil culture experiments.

According to LOEHWING (1951) three fairly distinct stages in the metabolism of the plant are evident from the period of germination to flowering. These are:

- a. an initial anabolic phase in which intake of inorganic nutrients and synthesis of proteins is rapid;
- b. a second phase where accumulation of carbohydrates is accelerated while rate of protein synthesis gradually diminishes;
- c. a catabolic phase which becomes evident as flowering is approached in which hydrolysis of reserves begins to overbalance synthesis and a general internal redistribution of nutrients is initiated.

It therefore, seems probable that with prolonged periods of exposure (6–8 weeks) to favourable soil temperatures, the plants have passed the anabolic phase. An actual dilution of elements may then occur resulting in less conspicuous differences between soil temperature treatments. In younger plants still in the anabolic phase, as in the present study, dilution effects are probably less in the optimum temperature range resulting in higher concentrations.

It has also been demonstrated that the mineral content on a dry weight basis is influenced conspicuously by the dry matter percentage. SMITH (1962) discussing growth as a factor in the mineral composition of tissues stated that the accumulation of dry weight dilutes all elements unless an influx of minerals offsets this effect.

A comparison of the mineral content of tissue on a fresh weight basis does eliminate the effect of differences in dry matter percentage to a large extent. In experiments where pronounced treatment effects are produced in dry matter percentage, the fresh weight basis seems to be more appropriate. On this basis it has been shown that practically no differences in N, P and K content occurred in the temperature range 20°–35°C except that the accumulation of phosphorus in the shoot, however, seems to have been less at 20°C. Less N, P and K was accumulated by the shoot at 5°, 10°, 15° and 40°C. The content at 5°C, however, seems to be higher than that obtained at 10°C. This is most probably due to a dilution effect mentioned by STEENBERG (1951) and SMITH (1962), since higher yields were obtained at 10°C. It nevertheless demonstrates that an increased concentration of N, P and K was without effect on shoot growth when compared with 10° and 15°C.

The temperature of the nutrient solution in the range 15°–30°C does not seem to have affected calcium uptake by the shoot. Some increase, however, was evident at 10°, 35° and 40°C. The magnesium content decreased with increasing temperature from 20°–40°C. At 10° and 15°C the relative response seems to have been similar to that obtained with calcium.

No consistent effect of soil temperature on the calcium and magnesium content of plant tissues is evident from data reported in the literature (NELSON, 1956; DIKSHOORN and 'T HART, 1957; LINGLE and DAVIS, 1959; NIELSEN et al., 1960; NIELSEN et al., 1961).

Considering the results obtained with radio-active rubidium (comparable to potassium) the effect of root temperature on absorption and accumulation has clearly been demonstrated. These results are in some respects similar to those obtained by McEvoy (1960) with tobacco. The detrimental effect of 40°C, however, occurred within 24 hours after exposure with maize whereas McEvoy noted such an effect only after 4 days. Furthermore, a certain optimum temperature range occurred corresponding to that

of growth. McEvoy (1960) presented no growth data but rates of P^{32} uptake increased with root temperature up to 35°C .

The results obtained in the present study after 24 hours for the shoots and roots are quite similar to those presented by SHTRAUSBERG (1958) for maize. He subjected maize plants to root temperatures of 7° and 21°C for five hours and measured the uptake of P^{32} . Uptake by the shoots and roots at 21°C significantly exceeded that obtained at 7°C .

ZHURBITZKY and SHTRAUSBERG (1958) presented additional results with maize confirming the reduction in rate of uptake by low root temperatures (7°C compared to 18°C). An absorption period of only 3–4 hours was used.

These results indicate that low temperatures of the solution culture retarded uptake of rubidium and phosphorus. The shoot temperature does not seem to have any marked effect on uptake. This has been verified experimentally by ZHURBITZKY and SHTRAUSBERG (1958) for P^{32} uptake of maize.

4. GENERAL DISCUSSION

If the growth response of the shoot to different root temperatures is regarded in conjunction with simultaneously occurring physiological processes *viz.* net assimilation rate, ion uptake and transpiration rate, interesting relationships are evident.

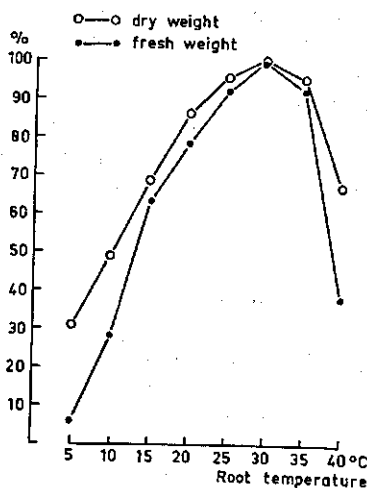
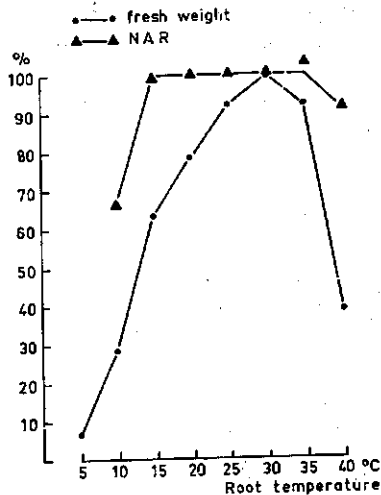


FIG. 23. Effect of root temperature on relative growth rate of shoots, on a fresh weight basis, as compared to the effect on relative growth rate on a dry weight basis

The relative growth rate of the shoot on a fresh and dry weight basis is presented in fig. 23 and the net assimilation rate in comparison to the relative growth rate (fresh weight) in fig. 24. These have been expressed as percentage of the values determined at 30°C .

The relative rate of dry weight accumulation seems to have been affected relatively less than the relative rate of fresh weight production beyond the optimum temperature range. This is substantiated by the fact that NAR remained practically unaltered over a wide temperature range, being lower

FIG. 24. Effect of root temperature on net assimilation rate (NAR) as compared to the effect on relative growth rate (fresh weight basis)



at temperatures beyond the range 15°–35°C (fig. 24).

No indication was found that the net rate of dry matter production per unit of leaf weight was responsible for the differences in relative growth rate in the temperature range 15°–35°C. This is in agreement with results of BROUWER and VAN VLIET (1960) who concluded that rate of dry weight production per unit leaf fresh weight was not influenced over a wide range of root temperatures for peas.

The differences in relative growth rate encountered in the temperature range 15°–35°C cannot therefore, be ascribed to net dry weight accumulation per unit of leaf fresh weight. It has, however, been indicated (cf. fig. 15) that the ratio of leaf fresh weight to total dry weight, which can be considered as an indication of relative leaf area, varies considerably in this temperature range. A decrease in this ratio was associated with decreased relative growth rates of the shoot. Leaf area per plant therefore, seems to be the main determinant of differences in relative growth rate as influenced by root temperature. WATSON (1956) also concluded from numerous field studies with various species, that differences in leaf area and not NAR was primarily responsible for differences in growth.

At the temperatures below 15°C and above 35°C, root temperatures do decrease the NAR. The adverse effect of these temperatures on the leaf-weight ratio is, however, relatively more pronounced.

The growth reaction to all root temperatures tested may therefore, be elucidated by searching for the factors affecting leaf area per plant.

The resultant leaf area per plant is influenced by rate of leaf initiation and rate of leaf growth (MILTHORPE, 1956). It has been established that the rate of leaf emergence (leaf initiation) as well as leaf elongation was the most rapid at 25°, 30° and 35°C (cf. fig. 2) during the experimental period of fourteen days. Since only embryo leaves were visible at 5°, 10° and 15°C the retarded rate of leaf emergence detected at these temperatures is mainly the result of leaf extension although an effect on cell division cannot be disregarded, especially at 5°C.

WATSON (1956) has stated that cultural practices which increase yield do so mainly by influencing leaf growth. Nitrogen increases leaf area throughout the growth period; phosphorus increases leaf area particularly in the early stages of growth; potassium on the other hand is most effective in the later stages of growth and tends to delay senescence of the leaves.

The rate of radio-active rubidium accumulation by the shoot, expressed as percentage of that at 30°C, has been found to show a marked correlation with the relative growth rate (fig. 25). Data of ZHURBITZKY and

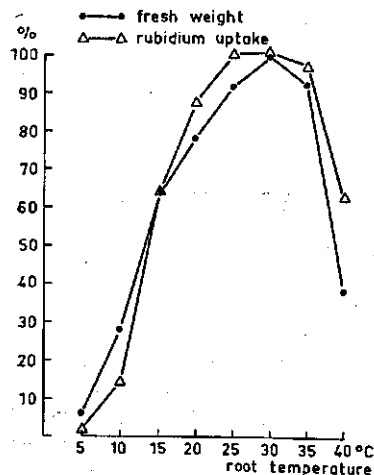


FIG. 25. Effect of root temperature on rate of rubidium uptake of the shoots as compared to the effect on relative growth rate (fresh weight basis)

SHTRAUSBERG (1958) as well as SHTRAUSBERG (1958) have also indicated that P^{32} accumulation in the shoot is retarded by low root temperatures. These authors have furthermore determined that absorption of nitrogen by the root system is retarded at low root temperatures. It can therefore, be assumed that the rate of N, P and K accumulation by the shoot proceeds less rapidly at low root temperatures. DAVIS and LINGLE (1961), however, have noticed no differences in K and P concentrations in the shoot of tomato plants within 24 hours after exposure to 13° and 25°C. These observations are at variance with those found in the present study as well as with the other limited data reported in the literature.

A decreased accumulation of mineral elements does not necessarily imply that rate of nutrient uptake is responsible for differences in growth at various root temperatures. Considering the tissue content of these elements in the shoot (*cf.* fig. 20 and 21) it is evident that a higher content of N, P and K was not associated with high yield at the temperatures 5° and 10°C.

Phosphorus applications to tomato plants on sand culture increased P uptake by the shoot at low root temperatures without any increase in yield (LINGLE and DAVIS, 1959). KETCHESON (1957) observed in sand culture applications, did result in increased growth but it was still much less than that obtained at higher root temperatures.

LOCASCIO and WARREN (1960) noted in soil culture with tomato plants that the phosphorus content increased at soil temperatures of 13°, 21° and

29°C with increased levels of phosphate application. A significantly higher tissue content only occurred at 21° and 29°C at the upper two levels of phosphate application when compared to 13°C. No differences were evident at the lower levels of application. The dry weight production, however, increased linearly with level of phosphate application at 13°C. A similar response did not occur at 21° and 29°C where the response to phosphorus decreased after the first increment to such an extent that practically no response was obtained after the second increment. Dry weight production at 21° and 29°C, however, significantly exceeded that of 13°C at all increments of phosphate except that no differences were evident where no phosphate was applied (lowest level).

The dry weight production of annual rye grass (*Lolium multiflorum* L.) was decreased at soil temperatures of 10°C in comparison to 20° and 30°C in soil culture (PARKS and FISHER, 1958). A highly significant response to nitrogen applications was noted at all temperatures; the greatest yield response occurring at 20°C and the least response at 10°C. The nitrogen content of the forage, however, was significantly greater at 10° and 30°C than at 20°C. The phosphorus content was the highest at 20°C as well as potassium.

These experiments indicate that in the majority of cases dry weight production at low soil temperatures has been increased by additional applications of nitrogen and phosphate. In some instances, however, no response was obtained by increased fertilizer applications. The composition of the tissue also varied in response to increased nutrient concentrations of the soil. A pronounced increase in mineral content generally seems to have occurred at low temperatures in some instances exceeding that of the tissues at temperatures where growth was more rapid.

Dry weight production at low soil temperatures, however, never approached that obtained at higher and favourable soil temperatures.

Growth can therefore, be improved in soil at low temperatures by additional phosphorus and nitrogen applications. This has not been found in solution culture by DAVIS and LINGLE (1961) and in the present study (cf. fig. 8). Furthermore, no differences in fresh or dry weight production could be obtained on sand culture by LINGLE and DAVIS (1959) with increased phosphate concentrations. The different concentrations were applied by means of daily applications of Hoagland's nutrient solution modified to provide the necessary phosphorus levels.

These results seem to indicate that growth limiting factors may occur in soil culture which are absent in water culture or in sand culture (with daily applications of nutrient solution).

Root extension is of less importance in solution culture where the nutrients are continually being circulated in the solution. A similar condition evidently seems to exist in sand culture with regular applications of nutrient solution. In cold soil, however, root extension seems to be of primary importance. Most ions are relatively immobile in soil and the roots must therefore grow to the available supply. By increasing the concentration of ions in the soil either with additional applications or concentrated in bands close to the root system uptake is increased.

The growth response to increased nutrient concentrations at low tem-

peratures, however, has been limited and it has not been possible to eliminate retarded growth.

In the present experiments the plants received a sufficient supply of nutrients during the ten days prior to transfer. LOEHWING (1951) stated that many annuals tend to absorb the major portion of their total mineral supply in very early life and early absorption is in general in excess of current needs when the external supply is favourable. BROUWER et al. (1961) also established that the growth of plants, which have been well supplied with N, only diminished two days after withholding N. The immediate depression of growth which occurred in the present study when the plants were transferred to 5°, 10° and 15°C (cf. fig. 1 and 2) seems to indicate that some other factor was responsible for the retarded growth. If the contents at 20°–35°C are considered, indications of a luxury consumption are evident at 20°, 25° and 35°C. It therefore seems doubtful to ascribe the lower relative growth rate at 5°, 10° and 15°C to a shortage of N, P, K, Ca or Mg in the tissue. Furthermore, results obtained by doubling the concentration of macro-elements did not increase growth at these temperatures (cf. fig. 8 and table 4).

The mineral composition of the shoots at 5°, 10° and 15°C also illustrates the pronounced effect of small temperature increments (5°C) on accumulation by the shoot.

The reduction in relative growth rate at 40°C may, to some extent, have been caused by a decreased uptake of nutrients. This, however, seems obvious since the roots were unable to withstand this temperature and eventually died. Passive absorption was probably eliminated since decomposition of the roots was evident. Although these roots were not yet destroyed they may have been plugged up by the activities of micro-organisms. As will be discussed later (cf. p. 62) water uptake may have been the main determining factor.

The evidence obtained on mineral uptake and tissue content, with solution culture experiments as well as soil culture studies, do not indicate that this was the primary cause of differences in growth at various root temperatures. The decreased mineral content at the low root temperatures, however, seems to indicate that with prolonged exposure periods mineral uptake may become a limiting factor.

Since elongation of stems and enlargement of leaves are dependent on a turgid condition of the cells, these processes decrease or cease when water deficits occur.

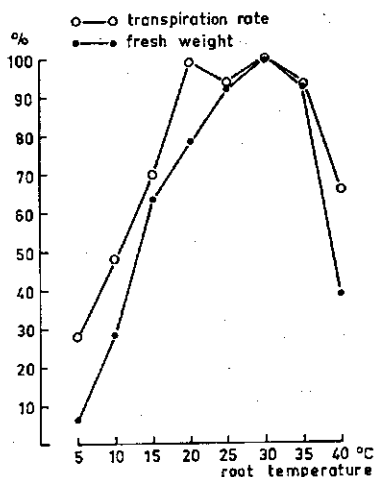
LOOMIS (1934) as well as THUT and LOOMIS (1944), concluded that a liberal supply of water to the growing point of maize was one of the main factors controlling growth.

Furthermore, in the present study, growth, as measured by increase in leaf length and fresh weight, was immediately depressed when subjected to the root temperatures 5°, 10° and 15°C. In addition noticeable wilting of the plants was evident at 5°C.

These observations suggest that water supply was the main determinant of decreased growth at the lower temperature. Similar results have been reported by KRAMER (1949); ABD EL RAHMAN et al. (1959); LUNT et al. (1960); BROUWER and VAN VLIET (1960).

Fig. 26 demonstrates that the rate of transpiration as percentage of that

FIG. 26. Effect of root temperature on transpiration rate as compared to the effect on relative growth rate (fresh weight basis)



at 30°C closely followed the relative growth rate trend at temperatures of 5°, 10° and 15°C. Such a relationship was absent at 20°, 25°, 30° and 35°C where no difference in transpiration rates was evident although the relative growth rate was less at 20°, 25° and 35°C.

The lower transpiration rate obtained in the present study at 5°, 10° and 15°C does not seem to have been the result of different shoot environmental conditions such as light intensity, temperature or humidity. A hampered absorption by the roots was probably the limiting factor which decreased rate of transpiration.

The principal cause of reduced intake of water by transpiring plants in cold soil is a physical effect of increased resistance to water movement across the living cells of the roots (KRAMER, 1949). ABD EL RAHMAN et al. (1959) also concluded that the effect of soil temperature on 'permeability' for water, which includes all factors governing water uptake of the living root cells, is the most important factor in water uptake by plants.

A marked depression in water flow rates in cotton plants was measured by BLOODWORTH (1961) at soil temperatures of 10° and 15°C. Increased viscosity of the water probably contributed to these decreased flow rates but increased resistance to water uptake across the living cells to the xylem may have been the main cause.

This implies that internal water deficits developed in plants at the low temperatures which largely reduced growth (BROUWER, 1961).

Additional data on this aspect were obtained by subjecting plants, previously kept at a root and shoot temperature of 20°C, to the different root temperatures for two hours. The decrease in weight of the shoots during this period, as percentage of the original shoot fresh weight, is given in table 11.

The data in table 11 indicate that the water loss by transpiration at 5°, 10°, 15° and 40°C could not be replenished at a similar rate.

The water content of the leaves consequently also decreased. The reduction in the water content of the leaves may influence photosynthesis by reducing the diffusive capacity of the stomates and decreasing the hydration

TABLE 11. The decrease in weight of the shoot as percentage of the original shoot fresh weight, during an exposure period of two hours to the root temperatures indicated

	Temperature - °C						
	5°	10°	15°	25°	30°	35°	40°
	%	%	%	%	%	%	%
Loss . . .	9.9	7.9	2.0	0	-0.1	0.1	5.4

of the chloroplasts and other parts of the protoplasm which in some manner diminishes the effectiveness of the photosynthetic mechanism (MEYER et al., 1960).

This seems to be one reason for the reduction in net assimilation rate at temperatures of 10° and 40°C (*cf.* fig. 15).

The decreased growth at 20°, 25° and 35°C without any difference in transpiration rate (fig. 26) may also be the result of a relatively higher internal diffusion pressure deficit compared to 30°C. BROUWER (1963) has indicated that within certain limits of an increased external osmotic pressure of the nutrient solution a marked decrease in growth was observed while transpiration remained unaltered. Furthermore by removing various quantities of the root system he demonstrated that transpiration was less sensitive to a decreased water supply than growth; growth was retarded immediately whereas transpiration decreased relatively less.

Since wilting and desiccation of the plants occurred at 40°C, water supply to the shoot seems to have been primarily responsible for the diminishing relative growth rate at this temperature.

DAVIS and LINGLE (1961), however, could not improve the growth of tomato plants which was reduced as a consequence of a low root temperature by placing a portion of the root system in warm distilled water. Furthermore, they noted no difference in diurnal moisture loss of plants held at root temperatures of 18° and 24°C. ABD EL RAHMAN et al. (1959) however, did measure differences in rate of transpiration at root temperatures of 16.8°, 20° and 25.3°C with tomato plants at an air temperature of 25°C and a mean relative humidity of 44 per cent. DAVIS and LINGLE stated that air temperature fluctuated from a constant night temperature of 18°C to a daily maximum of 35°C. Relative humidity at night approximated 70 per cent and during the day it seems to have been 40 per cent. On the average the relative humidity must have been higher which may account for the absence of differences in transpiration rate. Growth, however, was not enhanced at the lower root temperature in their experiments by increasing the relative humidity. Since ion uptake and water uptake was eliminated as the growth determining factors at low root temperatures they proposed an endogenous mechanism *viz.* root produced substances having shoot regulatory activity.

After considering the results of the present study it seems more likely that water deficits rather than ion uptake was the factor limiting growth under the present experimental conditions over a wide temperature range and not only at the extremes.

The possible role of hormones and micro-elements, however, was not

explored. These are additional factors which require further study to provide a better understanding of the effect of soil temperature on plant growth.

The statement of WENT (1957) that warming of the soil has not been found to be beneficial to the growth of plants when growing conditions are optimal, and the root medium well aerated, has been disproved by the present and numerous other studies. LOCASCIO and WARREN (1960) remarked that in cases where growth was not reduced at relatively low root temperatures the results may have been due to sub-optimal light intensities. They stated that plants grown in a greenhouse in midwinter were restricted in growth by insufficient light so that the influence of soil temperature on growth could not be clearly expressed. This seems to have been the primary factor which eliminated effects of root temperature on shoot growth in the experiments of WENT.

It would therefore, be worthwhile to include additional environmental variables of the shoot in future studies of root temperature.

SUMMARY

The effect of root temperatures on the growth, water uptake and ion uptake of the maize single cross $K_{64r} \times E_{184}$ has been studied during the early vegetative phase in solution culture in temperature controlled rooms. A root temperature range of 5°–40°C with 5°C increments, a constant air temperature of 20°C, and a constant light intensity were employed throughout.

The optimum temperature range for root growth was found to be 20°–30°C; growth at 35°C being distinctly less. The poorer growth at 35°C was mainly caused by a depressing effect on seminal root growth. Crown root production was similar to that obtained at 25°C. The initiation of crown roots was retarded progressively with a decrease in root temperature from 20°–5°C.

Pronounced effects on shoot growth were obtained. The optimum temperature range appeared to be 25°–35°C. The shoot apex of the plants, however, was also exposed to the root temperatures concerned up to the age of 20 days. Root temperature effects on older plants (20 days), where the shoot apex was also subjected to the air temperature, were nevertheless similar to those encountered with younger plants.

An excellent rate of leaf initiation at 25°, 30° and 35°C was shown to be one factor which contributed to the higher growth rate of the shoot at these temperatures. In addition rate of leaf elongation also appeared to be the most rapid in the range 25°–35°C. Ultimate size of individual leaves, however, seemed to be favoured by temperatures below the optimum range, the longest leaves being obtained at 15° and 20°C. The total increase in leaf length per plant, however, proceeded the most rapidly at 25°, 30° and 35°C.

Pronounced differences in the dry matter percentage and the water soluble carbohydrate content, presumably sucrose, occurred due to root temperature. A progressive increase in the shoot was evident at temperatures beyond the optimum range. This seemed to be the result of a relatively greater decrease in growth, than photosynthesis. Due to the limited growth, photo-

synthates could not be fully utilized and consequently accumulated in the plant.

The dry matter percentage and water soluble carbohydrate content of the roots increased relatively less than in the shoot at temperatures beyond the range 20°–30°C. At 5°C the dry matter percentage remained unchanged throughout the exposure period applied. This probably also applies to the water soluble carbohydrates. In the temperature range 20°–30°C these values diminished and commenced to rise again during the latter four days.

An increase in dry matter percentage, however, was not related to a limited supply of nutrients or water in the root environment. The internal physiological condition may be of importance *e.g.* an increase may occur prior to the initiation of flower primordia.

Root temperature influenced the proportion of roots to shoots. A relatively greater increase in shoot weight, in comparison to root weight, was evident at all temperatures studied. Root growth, however, was retarded to a relatively greater extent at temperatures beyond the range 20°–30°C which resulted in an increase in shoot-root ratio. Shoot and root growth was practically inhibited at 5°C with the consequence that the shoot-root ratio, based on the fresh weight, remained constant. On a dry weight basis, however, a progressive increase occurred. This could be ascribed to the fact that growth was practically inhibited at this temperature, whereas photosynthesis was influenced relatively less.

It was also established that root growth at 10° and 15°C ultimately increased to a relatively greater extent than shoot growth, resulting in a diminishing of shoot-root ratio at 15°C and no further increase at 10°C, where the ratio remained constant. At both temperatures the increased root growth seemed to have been caused mainly by the initiation and growth of new crown roots in the transition temperature zone.

In the temperature range 20°–30°C the shoot-root ratio remained constant during the major part of the experimental period. Some increase, however, was noted at 25° and 30°C during the last four days of exposure. The shoot-root ratio at 35°C exceeded those of 20°, 25° and 30°C. This higher ratio, however, was caused by a relatively larger increase in shoot growth during the first few days after transference to 35°C. Once established it remained constant.

Since root growth at 40°C was inhibited while shoot growth proceeded at a retarded rate, a progressive increase in shoot-root ratio occurred.

An analysis of the physiological processes, net assimilation rate, transpiration rate and rate of ion uptake in comparison to the relative growth rates revealed interesting relationships.

The relative rate of dry weight accumulation was influenced relatively less than the relative rate of fresh weight production at temperatures beyond the range 25°–35°C. This seemed to be ascribable to the fact that the rate of dry matter production per unit of leaf fresh weight was not affected in the temperature range 15°–35°C whereas it decreased relatively less than growth at temperatures of 10° and 40°C. It was indicated that the differences in relative growth rate obtained were associated with the relative leaf area per plant.

Root temperature did affect the uptake of nitrate, phosphorus, potassium, calcium and magnesium. In general the root temperatures 5°, 10°,

15° and 40°C retarded uptake of N, P and K. Indications of a luxury accumulation by the shoot seemed to exist at temperatures of 20°, 25° and 35°C. Shoot growth of young and older plants, however, could not be increased at the temperatures 5°, 10° and 15°C by doubling the concentration of macro-elements in the nutrient solution. In fact, some depressive effect on growth occurred in the optimum temperature range of young plants.

The retarded rate of uptake of mineral elements in the low temperature range (5°–15°C) as well as at 40°C did not seem to be the primary cause of the retarded growth rates at these temperatures.

It was proposed that under the present experimental conditions a hampered absorption of water by the roots, which decreased the transpiration rate at temperatures below 20°C and at 40°C, increased the internal diffusion pressure deficit of the plants. This seemed to be responsible for the immediate decrease in growth of the shoot at these temperatures. In addition, the retarded growth at 20°, 25° and 35°C may also have been the result of a relatively higher internal diffusion pressure deficit, although no differences in transpiration rate could be determined.

The transpiration ratio, employed as a measure of the water use efficiency, decreased at the temperatures 10°, 15° and 40°C. Less water was therefore transpired per gram increase in dry weight.

The possible role of hormones and micro-elements as growth determining factors was not explored.

SAMENVATTING

De invloed van de temperatuur van het wortelmilieu op de groei, water- en ionenopname in het vegetatieve stadium van de maïs hybride K_{64r} × E₁₈₄ werd bestudeerd. Hierbij werd gebruik gemaakt van voedingsoplossingen, waarvan de temperatuur geregeld kon worden. Aangewend werden constant gehouden temperaturen van 5°–40°C met intervallen van 5°C. De proeven werden genomen in klimaatkamers met een constante luchttemperatuur van 20°C en een constante lichtintensiteit.

De wortelgroei was optimaal in het traject van 20–30°C. De geringere groei bij 35°C werd vooral veroorzaakt door een remming van de groei van de kiemwortels. Het gewicht aan kroonwortels was gelijk aan dat bij 25°C. De aanleg van kroonwortels was sterker vertraagd naarmate de temperatuur in het wortelmilieu lager gehouden werd tussen 20 en 5°C.

Er werden ook duidelijke effecten op de groei van de spruit waargenomen. Hierbij bleek het optimum te liggen in het gebied van 25–35°C. Tot aan de leeftijd van 20 dagen was ook de groeipunt van de spruit blootgesteld aan de betreffende worteltemperatuur. Daarna bevond hij zich geheel „bovengronds” in de heersende luchttemperatuur. De invloed van de temperatuur in het wortelmilieu was echter bij jongere en oudere planten nagenoeg gelijk.

Bij 25, 30 en 35°C bleek een versnelde bladaanleg een der factoren van de groeiverschillen te zijn. Ook de bladstrekking vond in dit temperatuurtraject met de grootste snelheid plaats. De uiteindelijke afmetingen van de individuele bladeren bleken echter het grootst te zijn bij temperaturen be-

neden het optimale traject (15 en 20°C). De totale bladlengte per plant nam echter het snelst toe bij 25, 30 en 35°C.

Ten gevolge van de uiteenlopende worteltemperaturen traden in de spruit uitgesproken verschillen op in het droge-stofpercentage en het gehalte aan in water oplosbare koolhydraten, waarschijnlijk sucrose. Deze gehalten namen aan beide zijden van het optimale traject duidelijk toe. Dit bleek het gevolg te zijn van een relatief sterkere afname van de groei dan van de fotosynthese. Ten gevolge van de geremde groei konden de assimilaten niet geheel worden gebruikt en hoopten zich daardoor in de plant op.

De gehalten aan droge stof en in water oplosbare koolhydraten in de wortel namen aan beide zijden van het traject 20–30°C relatief minder sterk toe dan in de spruit. Bij 5°C bleef het droge-stofpercentage zelfs onveranderd gedurende de gehele proefperiode. Dit was waarschijnlijk ook het geval bij de in water oplosbare koolhydraten. In het temperatuurtraject 20–30°C namen deze gehalten aanvankelijk af en begonnen later weer te stijgen. Een toename van het drogestofpercentage bleek niet in verband te staan met een tekort aan voedingsstoffen of water in het wortelmilieu. De interne fysiologische toestand kan van belang geweest zijn daar b.v. een toename kan optreden kort voor de bloeiaanleg.

De worteltemperatuur beïnvloedde de spruit-wortelverhouding. Een relatief grotere toename van het spruitgewicht ten opzichte van het wortelgewicht, trad duidelijk op bij alle bestudeerde temperaturen. De wortelgroei werd echter relatief sterker geremd bij de temperaturen aan beide zijden van het traject 20–30°C, hetgeen daar een sterkere toename van de spruit-wortelverhouding ten gevolge had. Bij 5°C in het wortelmilieu bleek praktisch geen groei van zowel spruit als wortel mogelijk als gevolg waarvan de spruit-wortelverhouding, gebaseerd op het verse gewicht, constant bleef. Gebaseerd op het drooggewicht werd echter wel een toename waargenomen. Dit kan worden toegeschreven aan het feit dat de groei bij deze temperatuur praktisch volledig geremd was, terwijl de fotosynthese reëltief minder sterk werd beïnvloed.

Er werd ook vastgesteld dat het wortelgewicht bij 10 en 15°C uiteindelijk relatief sneller toenam dan het spruitgewicht. Dit resulteerde in een afname van de spruit-wortelverhouding bij 15°C en geen verdere toename bij 10°C, waar de verhouding constant bleef. Bij beide temperaturen lijkt de sterkere wortelgroei vooral te worden veroorzaakt door de aanleg en groei van nieuwe kroonwortels in het gebied van de temperatuurovergang tussen spruit- en wortelmilieu.

In het temperatuurtraject 20–30°C bleef de spruit-wortelverhouding gedurende het grootste deel van de proefperiode constant. Er werd echter bij 25 en 30°C gedurende de laatste dagen van de proef een kleine toename gevonden. De spruit-wortelverhouding bij 35°C lag hoger dan die bij 20, 25 en 30°C. Deze grotere waarde werd veroorzaakt door een relatief sterkere toename van de spruitgroei gedurende de eerste dagen na overbrenging op een worteltemperatuur van 35°C. Gedurende de verdere duur van de proef bleef deze verhouding constant.

De spruit-wortelverhouding bij 40°C nam ook toe, nu als gevolg van het feit dat de wortelgroei volkomen stilstond en de spruitgroei, hoewel geremd, doorging.

Er werd een vergelijking gemaakt tussen de snelheid van de netto droge-

stoftoename per eenheid van bladoppervlak, de transpiratiesnelheid, de ionenopname, de relatieve toename in versgewicht en de relatieve toename in drooggewicht.

De invloed van de worteltemperatuur op de drooggewichtstoename was geringer dan die op de versgewichtstoename. Dit kan toegeschreven worden aan het feit dat de droge-stofproductie per eenheid van bladversgewicht in het temperatuurtraject van 15–35°C nagenoeg niet beïnvloed werd terwijl in dat traject een duidelijke invloed op de groei werd waargenomen. Bij 10° en 40°C waren zowel droge-stofproductie als groei geremd maar de groei in veel sterkere mate dan de droge-stofproductie. Er werden aanwijzingen verkregen dat de verschillen in relatieve groeisnelheid in verband stonden met het aandeel van het bladgewicht in het gewicht van de gehele plant.

De worteltemperatuur had ook invloed op de mineralenopname. Over het algemeen was de opname van nitraat, fosfaat en kalium vertraagd bij worteltemperaturen van 5, 10, 15 en 40°C. Het lijkt dat bij 20, 25 en 35°C een luxe consumptie plaats heeft. De spruitgroei van jonge en oudere planten kon bij de temperaturen 5, 10 en 15°C niet verbeterd worden door de concentratie van de macro-elementen in de voedingsoplossing te verdubbelen. In het optimum gebied gaf deze verdubbeling van de concentratie zelfs een groeiremming te zien. Het lijkt niet waarschijnlijk dat bij de temperaturen 5, 10, 15 en 40°C de geremde mineralenopname de voornaamste oorzaak van de vertraagde groei was. De reactie op de overgang van hoge naar lage worteltemperaturen trad zo snel op dat hierbij aan een factor gedacht moet worden, die zich zeer snel kan wijzigen. Bovendien was het mineralengehalte ook bij de lage worteltemperaturen nog zodanig hoog dat op grond van onze huidige kennis geen deficiëntie verondersteld moet worden.

Aangenomen wordt dat onder de omstandigheden van deze proeven de wateropname door de wortels bij de onderzochte temperaturen beneden 20°C en boven 35°C zodanig bemoeilijkt werd dat de zuigspanning in de plant te groot werd. Dit bleek uit de verminderde transpiratie en de verhoogde zuigspanning lijkt verantwoordelijk voor de onmiddellijke groeiremming van de spruit bij deze temperaturen. Alhoewel de snelheid van de transpiratie bij 20–35°C dezelfde was zijn er toch aanwijzingen verkregen dat mogelijk ook in dit traject de groeiverschillen een gevolg geweest zijn van verschillen in zuigspanning.

De transpiratiecoëfficiënt als maat voor de efficiëntie van het watergebruik was lager bij de temperaturen 5, 10, 15 en 40°C.

De mogelijke rol die hormonen en micro-elementen in deze temperatuurreacties gespeeld hebben is niet onderzocht.

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PLATES

PLATE I



PLATE II



PLATE I. Maize plants grown during 14 days at the various root temperatures. The plants were allowed to grow at 20°C for 10 days before transference to the different root temperatures (scale numbers indicate decimetres)

PLATE I

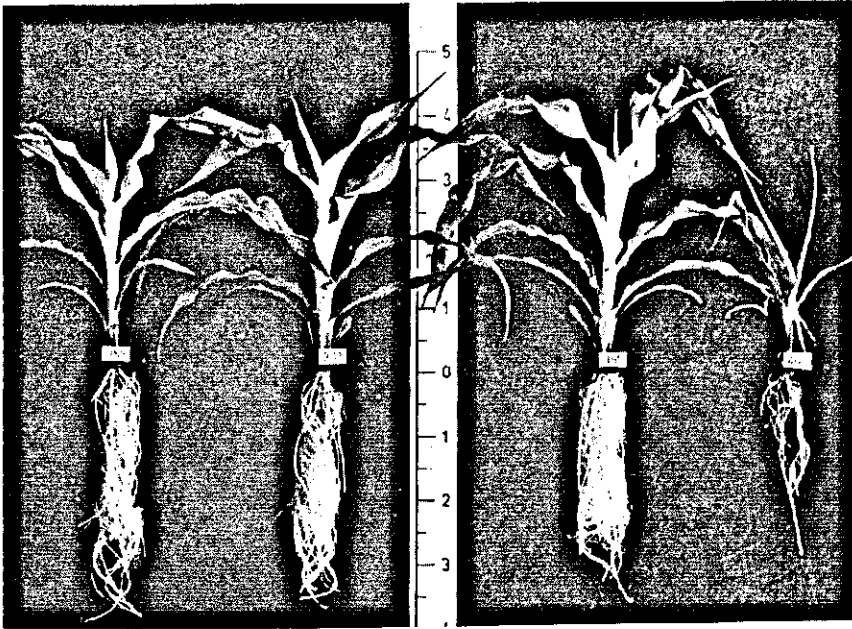


PLATE II

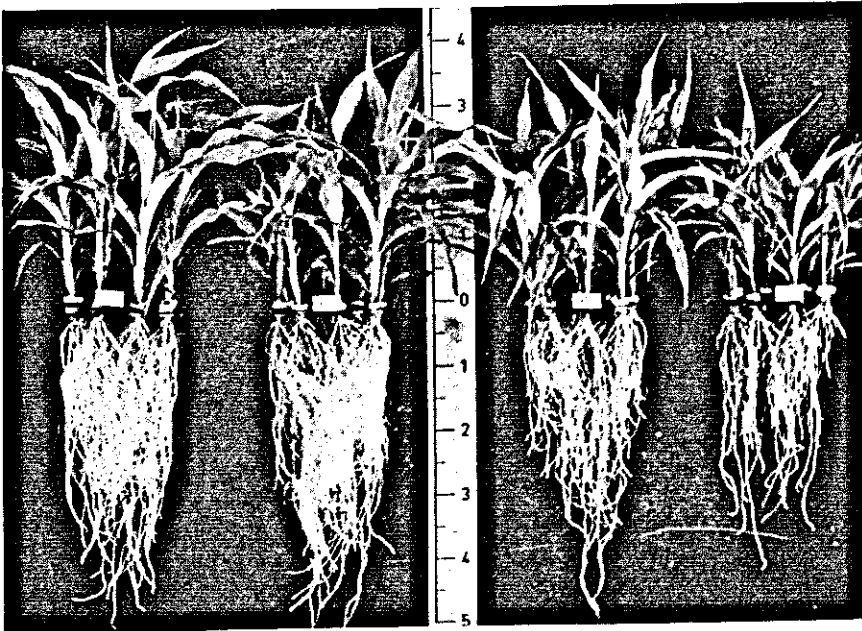


PLATE II. Maize plants grown during 8 days at the different root temperatures. Plants were transferred to the various root temperatures after growing at 20° C for 12 days (scale numbers indicate decimetres)