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TEMPERATURE, LIGHT AND THE TOMATO

MET SAMENVATTING: TEMPERATUUR, LICHT EN DE TOMAAT

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWKUNDE
OP GEZAG VAN DE RECTOR MAGNIFICUS DR J. H. BECKING,
HOOGLERAAR IN DE HOUTMEETKUNDE, DE BOSBEDRIJFSECONOMIE,
DE BOSBEDRIJFSREGELING EN DE HOUTTEELT
EN BOSBESCHERMING IN DE TROPEN,
TE VERDEDIGEN TEGEN DE BEDENKINGEN
VAN EEN COMMISSIE UIT DE SENAAT
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP VRIJDAG 25 NOVEMBER 1955 TE 16 UUR

DOOR

KAY VERKERK



H. VEENMAN & ZONEN – WAGENINGEN – 1955

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STELLINGEN

I

Voor het effect van de bestuiving bij tomaten geldt de wet van het minimum.

II

Het verdient aanbeveling het woord vernalisatie slechts dan te gebruiken, als een duidelijke omschrijving van de betekenis wordt toegevoegd.

III

Een te laag percentage zaaddragers bij de stullenteelt van sluitkool is niet een gevolg van een te zachte winter.

IV

Bij een hoogstaande teelt is geen praktisch belangrijk heterosiseffect te verwachten.

V

Bij een hygiënische bedrijfsvoering is de tomatenkanker van weinig betekenis.

VI

De duur van de jeugdphase bij spruitkool is afhankelijk van de lichtintensiteit.

VII

Er bestaat geen verband tussen bloemaanleg en een verandering van het suikergehalte.

VIII

Een selectie op hoge schieterresistentie heeft zijn bezwaren.

IX

De steden zijn verplicht om hun afvalstoffen in bruikbare vorm ter beschikking te stellen van het platteland.

X

Bij ruimere internationale handelsmogelijkheden en bij verbetering van vervoersmogelijkheden zal de teelt van stooktomaten in Nederland verdwijnen.

*Eer wij wat weten,
zijn wij versleten.*

GUIDO .GEZELLE

*Aan de nagedachtenis van mijn Vader
Aan mijn Moeder*

WOORD VOORAF

Deze gelegenheid wil ik niet laten voorbijgaan zonder enige woorden van dank te richten tot de velen die mij dit werk mogelijk, ja dikwijls aangenaam gemaakt hebben.

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Met veel genoegen heb ik bij U, Hooggeleerde QUANJER, gewerkt aan planten-ziektenkundige problemen.

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Daar ik hier niet iedereen met name kan noemen wil ik volstaan met verder allen, werkzaam aan het Laboratorium voor Tuinbouwplantenteelt te danken voor de mij geboden hulp, in welke vorm dan ook.

CONTENTS

CHAPTER I. Introduction 176

CHAPTER II. Experimental 177

1. Introduction 177

1.1. Experiments carried out in Pasadena 178

1.2. Experiments carried out in Wageningen 178

2. Temperature 178

2.1. Introduction 178

2.2. Accidental discoveries 179

2.3. In greenhouses 181

2.3.1. Night temperatures from March till July 181

2.3.2. Day and night temperatures from June till November 183

2.3.3. Day and night temperatures from November till February 192

2.4. In artificially lighted rooms 194

2.4.1. Introduction 194

2.4.2. Night temperature 194

2.4.3. Day temperature 195

3. Light 196

3.1. Introduction 196

3.2. Differences in light energy 197

3.2.1. Introduction 197

3.2.2. Reduced light intensity 197

3.2.3. Variation in day length 198

3.3. Plant growth with extra artificial light during winter 200

3.3.1. Young plants 200

3.3.2. Older plants 202

4. Temperature and light 205

4.1. Introduction 205

4.2. In artificial-light rooms 205

4.3. In greenhouses during winter months 205

CHAPTER III. General discussion 207

1. Introduction 207

2. Growth 208

2.1. Vegetative growth 208

2.2. Generative growth 208

2.3. Carbohydrates 209

2.4. Balance between vegetative and generative growth 209

3. Growth and photosynthesis 210

3.1. Introduction 210

3.2. Extra light in winter 210

3.3. Vegetative growth 210

3.4. Generative growth 211

3.5. Carbohydrates 211

3.6. Balance between vegetative and generative growth 212

4. Growth and respiration	212
4.1. Introduction	212
4.2. Vegetative growth	212
4.3. Generative growth	213
4.4. Carbohydrates	213
4.5. Balance between vegetative and generative growth	213
5. Growth and transport of carbohydrates	213
6. Growth, photosynthesis and respiration	214
7. Growth, photosynthesis and transport of carbohydrates	215
8. Growth, respiration and transport of carbohydrates	215
9. Growth, photosynthesis, respiration and transport of carbohydrates	216
10. Additional remarks	218
SUMMARY	219
SAMENVATTING: Temperatuur, licht en de tomaat	220
REFERENCES	221

CHAPTER I

INTRODUCTION

The economic importance of the tomato for the Netherlands is growing every year as may be illustrated by table 1 (88).

TABLE 1

Supply of tomatoes brought to the auctions in weight and in value during the years 1949–1953

Year	Weight in 1000 kg	Value in 1000 guilders
1949	69428	33585
1950	75062	33653
1951	82529	49157
1952	91180	51960
1953	97532	56996

The export of the Dutch tomato makes up about 25% of the export of all vegetables. Nearly half of the yield is exported to England and Germany. This importance justifies the large amount of research work done on this crop.

Growth is an increase of size and of weight. Man is interested especially in growth of those parts of the plants he wants to use. From the tomato plants the fruits are wanted. These fruits are the parts of the plants containing the seeds which represent the next generation and as such they are more or less the final products of the plant. This means that a good fruit crop cannot be expected if there has not been a reasonable vegetative growth. Only then the plant can produce an appreciable number of fruits.

If the influence of certain factors on the yield has to be studied it is necessary to study the influence of these factors both on vegetative and on generative growth.

In the Netherlands most tomato varieties are grown on one stem. The axil shoots are pinched off. After developing 5–12 leaves a terminal cluster is initiated. The axil bud of the leaf under the cluster, however, will form a new stem and the terminal habit of the cluster is no longer apparent. After 3–5 leaves are formed by the new stem another cluster is initiated and so on. So there is a constant growth of leaves as well as clusters at the same time. Usually the top of the plant is pinched off a few leaves above the 5th–7th cluster.

In the tomato the whole growth cycle of the plant from seed to seed has to be completed to get the yield. In this respect the tomato corresponds closely with peas, beans, cucumbers and melons. They all have relatively little reserve material in the vegetative parts; from all, the fruits are used. These crops show a continuous vegetative growth which after some time is connected with a continuous generative growth. The yield will be spread over a relatively long time, and a harvest every few days will be necessary. There is not much difference between the culture as a vegetable crop or as a seed crop.

On the other hand are the crops from which the leaves, bulbs, tubers or roots are used. Here only vegetative growth is wanted to produce the marketable part of the plant as a vegetable crop. In most cases the harvest falls in a relatively short period. These crops have another type of development. Their growth can be divided into a pronounced vegetative phase and a generative phase. Without a smaller or larger change in environment the vegetative phase will not change into the generative phase. Hence, there is a big difference between the culture for a vegetative crop and for a seed crop.

The tomato plant, not having much reserve material in the vegetative parts, has the disadvantage or perhaps advantage that it will react as a result of changing environmental factors rather quickly.

As a self-fertilizer it has the advantage that all the plants of a variety tend to be genetically the same (iso-homozygotic). Differences among plants of the same variety can be found only if the environments are different. For this reason the amount of plants per treatment necessary to study the influence of a certain factor can be relatively small.

The influence of temperature and light on the tomato has been studied by the writer. In the experimental part the influence of temperature will be treated first because in efforts to get an artificial climate to grow plants, temperature was controlled first. Next the influence of light will be discussed, followed by a treatment with both factors in their mutual relationship. In the general discussion the experimental results will be compared with data from the literature.

CHAPTER II

EXPERIMENTAL

1. INTRODUCTION

The experiments on the influence of temperature and light on tomato plants can be divided into two groups: those done in the Earhart Plant Research Laboratory of the California Institute of Technology in Pasadena, California

(94) and those done at the Horticultural Laboratory, Agricultural University in Wageningen, the Netherlands.

1.1. *Experiments carried out in Pasadena*

In the greenhouses and the artificially lighted rooms of the Earhart Plant Research Laboratory temperature can be kept constant. Different temperatures are maintained in different rooms, so that a whole series of temperatures is provided and by moving the plants from one compartment to another any combination of these temperatures can be realized. In the artificially lighted rooms the light source is Westinghouse fluorescent tubes supplemented by some incandescent lamps.

Naturally space is limited in such a laboratory and consequently in most cases the number of plants in one treatment had to be rather small. This, however, need not to be a disadvantage, because:

- a) the environment could be regulated so well that the variation between the plants within a treatment was very small;
- b) in many cases experiments were carried out in which a series of temperatures was used and if a trend was found in such a series it would have a certain significance in itself;
- c) most experiments lasted a considerable time and differences between treatments usually increased with time.

A mixture of gravel and vermiculite was used in order to exclude the unknown influence of soil. Nutrition and water were given once or, if necessary, twice a day by watering with a complete nutrient solution. Plant growth was satisfactory.

The above description shows that this laboratory is an excellent place to examine the influence of temperature and light and their interaction on the growth of plants. A disadvantage was that in the greenhouses day temperatures were about 6° C higher than night temperatures between 8 A.M. and 4 P.M. regardless of the natural day length. The time elapsing between day and night temperature was one half to one hour.

1.2. *Experiments carried out in Wageningen*

The plants were grown in the greenhouses in the usual way, pinching out the small axil shoots and taking off the top of the plants after 5–7 clusters. It was impossible to keep a certain constant temperature in these greenhouses and also the light could not be regulated.

Most of the experiments were laid out in replicated blocks. In most cases the easiest way to express the influence of a certain factor was to express its results as a percentage of the results with the control.

Plants were sown and planted in heated greenhouses because outside temperatures were too low to work outdoors or in unheated greenhouses. At that time of the year the natural light was very weak. To overcome this, artificial illumination was used, giving a light intensity of approximately 4000 lux.

2. TEMPERATURE

2.1. *Introduction*

The biochemical processes working in nature are, of course, all influenced by temperature. Plants, unlike mammals, do not have a constant temperature, but

are dependent on the temperature of the environment. We can expect an important influence of temperature on plants, which results in different types of growth at different temperatures or combinations of temperatures. These differences in the reaction of the plants, in this case tomato plants, can be of great importance for the grower. Research, in an effort to understand and predict the reactions of the plant to the environment in so far as temperature is concerned, was carried out in the Earhart Plant Research Laboratory at Pasadena.

In nature the temperature generally rises slowly after sunrise to a maximum and after that gradually drops. In our experiments this could not be done. We worked with a constant temperature the whole day or during part of the day followed by another constant temperature during the rest of the day.

After first mentioning some accidental discoveries about temperature influence the research done at Pasadena will be described.

2.2. *Accidental discoveries*

By accidental discoveries concerning temperature influence are meant influences, most probably the result of uncontrolled differences in temperature in the greenhouses at the Horticultural Laboratory, as the result of an improper heating system.

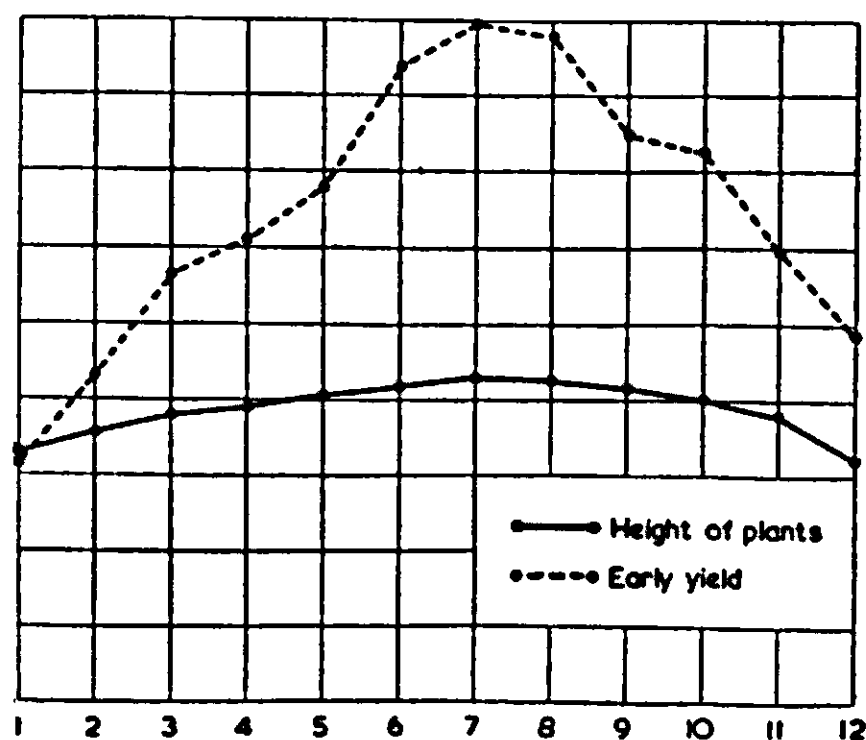
First example – The variety Ailsa Craig was grown in a heated greenhouse, in which the ends were not properly heated.

Differences in height were observed between the plants at the ends and the plants in the middle. In the 38 days from planting on March 9 till April 16 those differences became so pronounced that measurements were taken. The plants were divided into twelve groups, each of three rows of 48 plants each. The mean height and early yield (= yield during first three weeks of harvest period) of each group were determined, see graph 1.

From this graph it can be seen that both the early yield and the height of the plants on April 16 were greatest in the middle of the greenhouse and decreased gradually to both ends. There was a highly significant correlation between height and early yield of 0.74 (odds 99:1).

Minimum night temperature measurements during the second half of April disclosed that the minimum temperatures in the middle of the greenhouse were about 1.2–1.4° C higher than at the ends. In March these differences probably were even larger, because the outside temperatures were lower. This seems to indicate that the taller plants and higher early yields in the middle of the greenhouse are the consequence of the higher temperatures there.

Second example—This discusses the relation between cluster growth and temperature in the variety Dominant. Photograph 1 (see at the end), taken March 23 of plants planted in the heated greenhouse December 7, shows plants on the left to be much



GRAPH 1

Ordinate: average height (one unit is 20 cm) and early yield (one unit is 140 g) of 12 groups of plants (abscissa) spaced from one end of the greenhouse to the other.

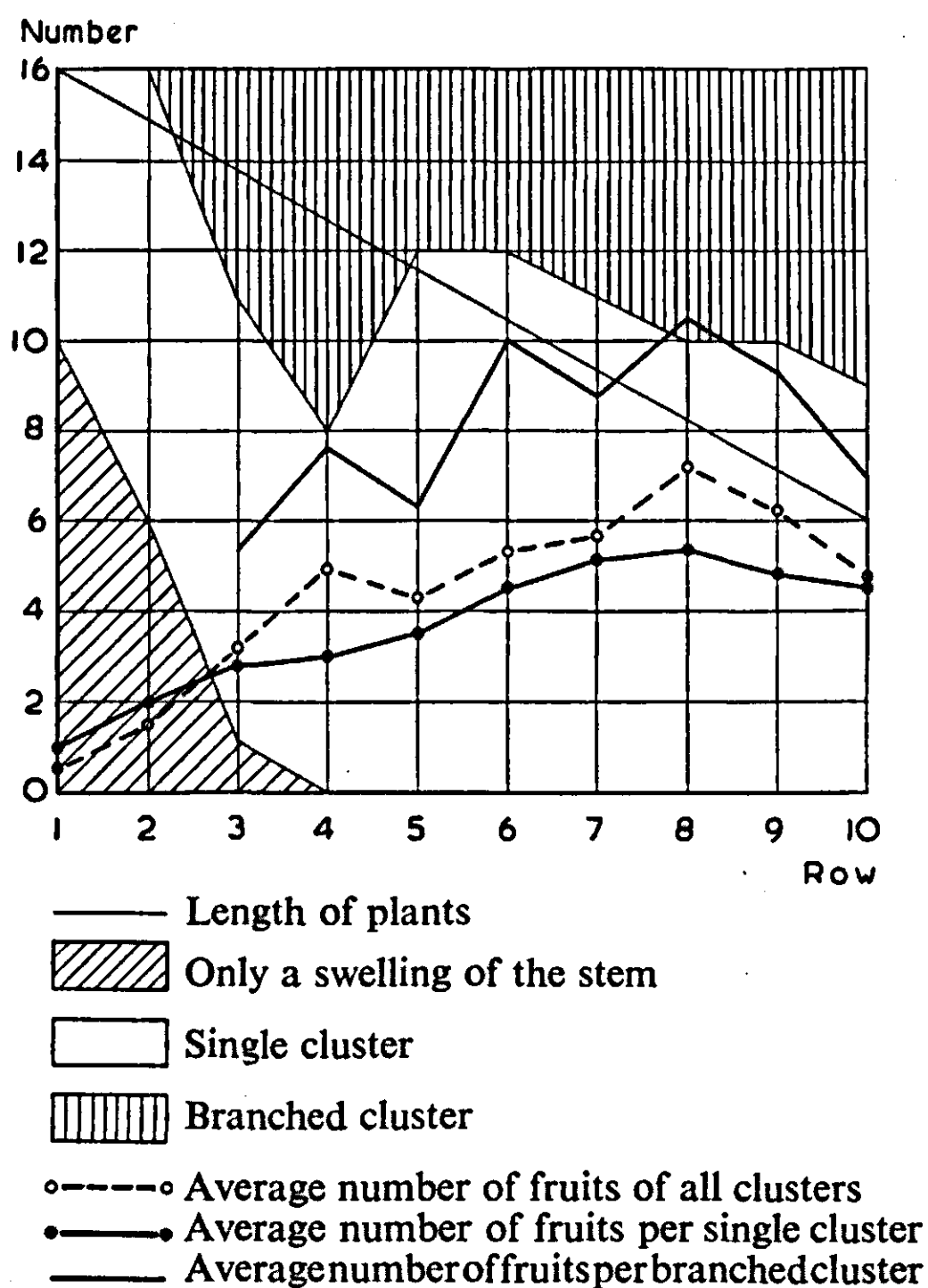
taller than those on the right, unmistakably the result of slower growth on the right. The only explanation for this which can be offered is the temperature distribution in the greenhouse. The left side adjoins another heated part of the greenhouse, beyond the right side is the cold outside air. The heating pipes are the same on both sides and this results in a non measured temperature fall from left to right, schematically indicated by the length of the plants on the photograph.

There were ten rows, each of sixteen plants, in this compartment of the greenhouse, between the above mentioned walls. Of the first cluster of each plant were determined:

- a) the size, divided into three groups:
 - only a little swelling of the stem
 - a single cluster
 - a branched cluster
- b) the number of fruits.

The result is given in graph 2. In this graph the rectangle 10×16 refers to the 10 rows of 16 plants from the warm inside wall on the left to the cold outside wall on the right. The thin line indicates the lengths of the plants schematically.

The distribution of the three sizes of the first clusters is given by the divisions in the rectangle. This shows that the fastest growing plants have the poorest



GRAPH 2

Relations between decreasing length of growth of plants and size and number of fruits per single or branched cluster. Details in text.

clusters (only a swelling of the stem). The first two rows do not have any branched cluster. Going from left to right (lowering temperature) there are more branched clusters in each row, with the exception of the fourth row.

The number of fruits on the first cluster is larger with slower growth of the plants, having its maximum at row 8. To the right of that probably the temperature is too low for maximum fruit set (compare p. 209).

The differences in fruit number on single and branched clusters can be seen in the graph, showing the same type of curve and showing at the same time that the number of fruits on the branched clusters is about twice as large as on the single clusters.

Conclusion: In winter, when plant growth in length is less, probably as a result of lower temperature, the first cluster is better, there are more branched

clusters, more fruits per cluster and a higher yield, providing that temperature is not too low for fruit set.

Example from practice – Practical experience demonstrated that before the second world war careful growers who heated their greenhouses well both day and night had poorer results than growers who were less careful and maintained at night a considerably lower temperature than during the day time.

Later on it will be seen that the temperature influences found here are exactly the same as those found in the experiments done in the Earhart Plant Research Laboratory.

2.3. In greenhouses

2.3.1. Night temperatures from March till July (experiment I)

Introduction – The tomato variety Ailsa Craig was used to investigate the influence of different night temperatures on growth and yield.

The plants were sown on January 16, and transplanted on February 26 into crocks with a diameter of about 20 cm. The day temperature was 23° C (from 8 A.M.–4 P.M.) and the night temperature 17° C. On March 10 these plants were divided into three groups: day temperature 23° C with night temperatures of 22°, 17° and 11° C respectively (abbreviated 23–22, 23–17 and 23–11). Each group contained 12 plants.

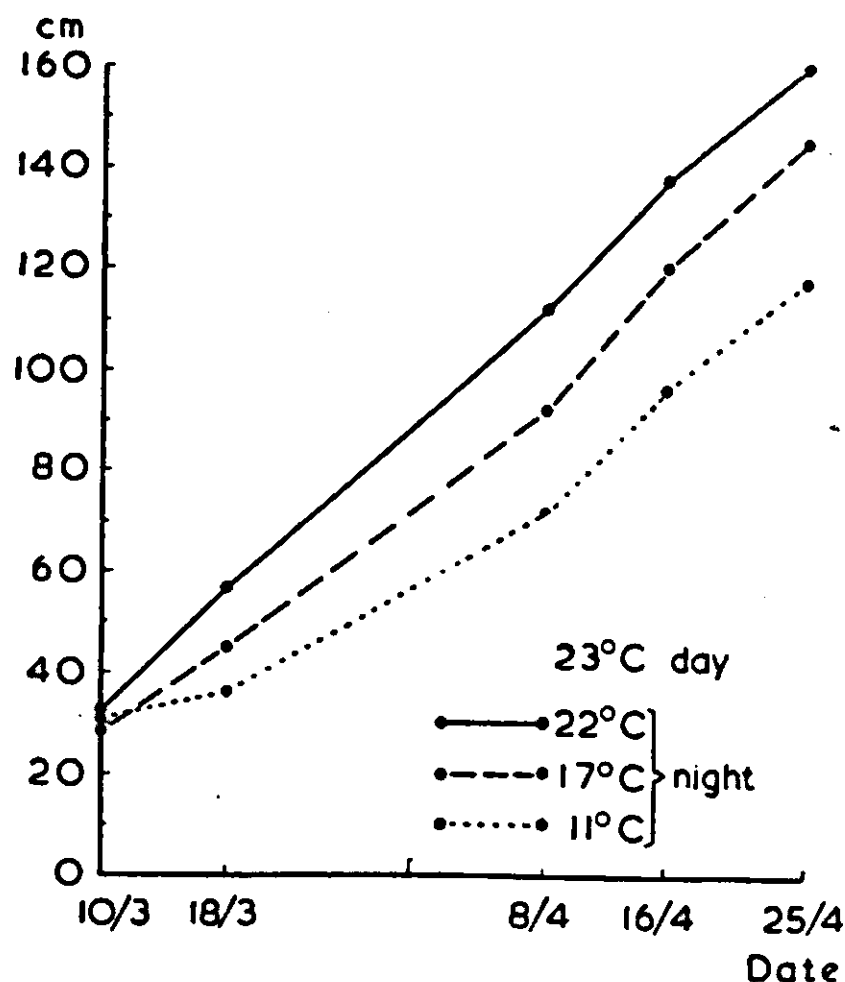
The auxiliary shoots and the top above the 5th cluster were removed, so each plant was grown as one stem with 5 clusters. There were 4 plants in a space of 0.5 × 0.5 meter. The 23–22 group soon showed light green leaves, the 23–11 group dark green leaves and the 23–17 group was in between. Many fruits of the high night temperature (22° C) had blossom-end rot, a disease that probably was the result of the high night temperature in this case.

Ripe fruits were picked every third day. When discarding the plants, weights of roots, stems, leaves and clusters were determined. The length of the plants was measured once a week from March 10 till April 25. By that time most of the plants were topped, so further measurements were senseless. From these measurements an average stem growth in mm per day was calculated.

Growth rate of the stem – The mean length of the plants of each group is given in graph 3.

Starting March 10 with plants of the same length, by March 18 there were highly significant differences in length as the result of the different night temperatures. At a night temperature of 17° C the growth is faster than at 11° C, at 22° C faster than at 17° C. The mean growth is 19.3, 25.2 and 27.6 mm per day for the 23–11, 23–17 and 23–22 groups respectively.

By the method of Student the reliability



GRAPH 3
Mean length of 12 plants of the variety Ailsa Craig grown at a day temperature of 23° C and night temperatures of 22°, 17° or 11° C.

of the differences of the mean length of the plants of each group can be shown:

differences in cm between groups 23-11 and 23-17				23-17 and 23-22			
on March 10	0.8 ± 1.0	$t = 0.8$	3.2 ± 1.2	$t = 2.6$		
on March 18	6.7 ± 1.5	$t = 4.4$	7.3 ± 1.6	$t = 4.5$		
on April 25	26.5 ± 2.8	$t = 9.1$	14.3 ± 3.3	$t = 4.1$		

Hence, at the beginning on March 10 there are no highly significant differences in length among the groups, while on March 18 and April 25 they occur ($t_{11} = 3.105$ for odds 99:1), which means a faster growth at higher night temperatures.

Root and stem weight – For comparing the results of the different temperature treatments the difficulty is to decide at what time to compare the plants. The moment was chosen on which the harvest was practically completed. For the 23-22 group this was on June 9, for the other two groups July 29, because the growth of the fruits, as will be shown, is also faster at higher temperatures.

The dry weight of the root system on these dates in grams was 4.9, 6.1 and 8.0 for the groups 23-22, 23-17 and 23-11 respectively. Not only did the 23-22 group with the highest night temperature and the shortest time for growth have the lightest root system, but also the 17 °C night group had a root system lighter than the 11 °C night group, notwithstanding the fact that they were harvested on the same day.

The height of the 5th cluster was nearly the same in the three groups. The mean dry weight in milligrams of 1 cm stem up to the 5th cluster was smallest for the high night temperature plants (140 mg). For the other two the weights were nearly the same (222 mg and 203 mg). So at the high night temperature the stem is less sturdy than at a lower night temperature.

The mean dry weight of the leaves between the 3rd and 5th cluster was 1.8, 3.4 and 2.8 grams, so, also, the lightest leaves were on the plants at the highest night temperature.

Clusters – In connection with the differences in growth of roots, stems and leaves at different night temperatures, it will be interesting to compare the clusters from which the yield comes.

For each of the clusters the following was determined:

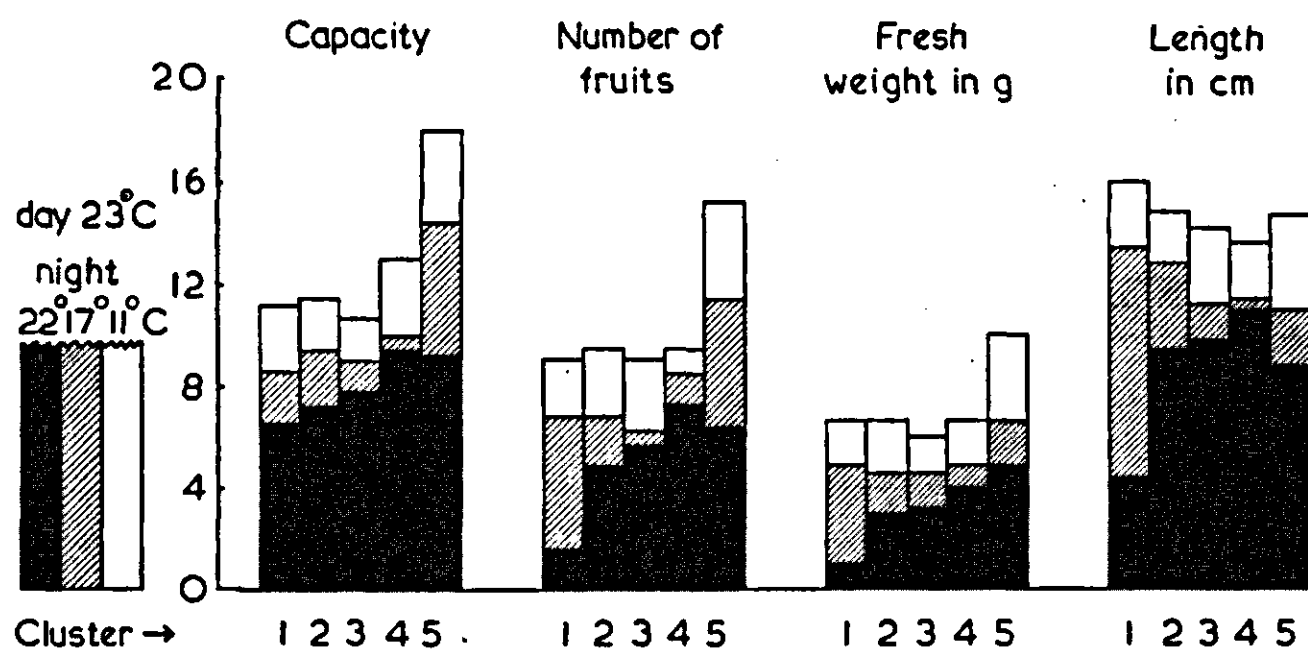
- a) the number of flower buds, flowers, ripe and green fruits together, including fallen flower buds and flowers; this is the number of fruits that would have been on the cluster if all flower buds had grown to fruits (called capacity);
- b) the total number of fruits;
- c) the fresh weight without fruits in grams;
- d) the length from the stem to the tip in cm.

Graph 4 shows convincingly that all the above mentioned values are smaller as the night temperature is higher.

Fruit yield – Not only the numbers of fruits alone, but also the time of the harvest is very important. Graph 5 shows how many grams of fruits per plant had been harvested cumulatively up to a given day. At higher night temperatures the harvest is earlier, but the total yield is lower. The dates on which half of the fruit weight had been picked are about three weeks apart. The mean fruit weight of the three groups was 49, 58 and 56 grams at 22°, 17° and 11 °C night temperature respectively. This is an indication that high night temperature may cause small fruits.

Summarizing, it was found that a higher night temperature in comparison to a lower one results in:

- faster stem growth;
- less heavy roots, stems and leaves;
- less fruiting capacity, number of fruits, weight and length of clusters;
- smaller but earlier yield.



GRAPH 4
Capacity, number of fruits, fresh weight of clusters without fruits in grams and length of clusters in cm of plants grown at a day temperature of 23° C and night temperatures of 22°, 17° or 11° C.

2.3.2. Day and night temperatures from June till November (experiment II)

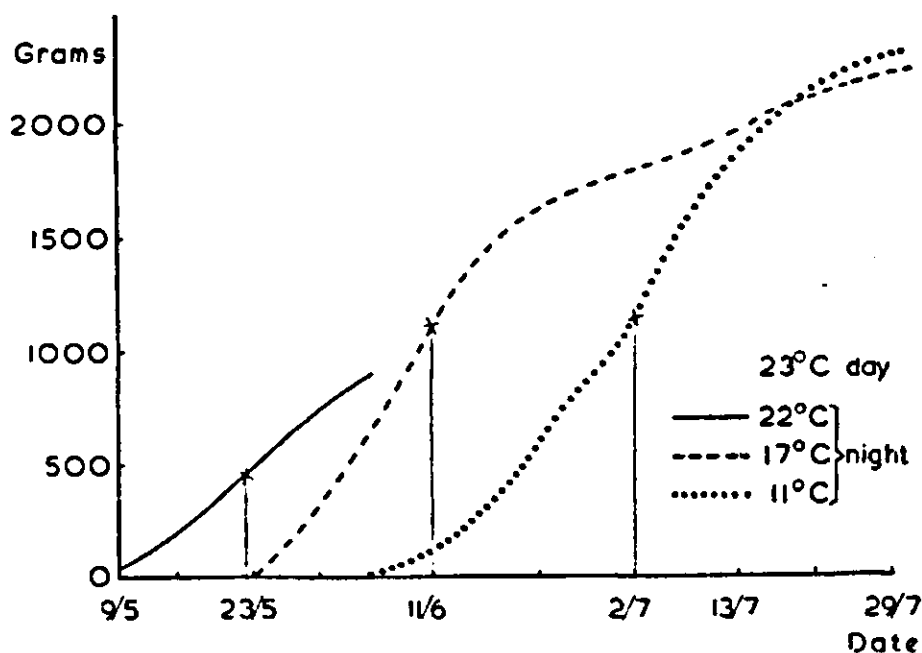
Introduction – In the experiment described above one variety, one day temperature and three different night temperatures were involved. To get more information on the influence of temperature, this experiment with 6 varieties and different day as well as night temperatures was carried out in the greenhouses during summer.

In consequence of the large number of objectives only two plants of each variety could be used in each temperature combination. Nevertheless the results of this experiment show some significant influences of temperature and certain conclusions can be drawn, keeping in mind the results of the above described experiment also.

The plants were sown May 19 and grew till July 5 at a day temperature of 23 °C and a night temperature of 17 °C. Then they were divided into 9 different temperature groups.

The following 6 varieties were used:

- 1) Tuckqueen, a greenhouse tomato of the Netherlands,
- 2) Michigan State Forcing, a greenhouse tomato of Michigan, U.S.A.,
- 3) Essex Wonder, a greenhouse tomato of England,
- 4) Rutgers, an outdoor tomato of the Eastern United States,
- 5) Improved Pearson, an outdoor tomato of the Western United States,
- 6) Beefsteak, an outdoor tomato for home gardeners.



GRAPH 5
Harvest of fruit from plants grown at a day temperature of 23° C and night temperatures of 22°, 17° or 11° C and date (x) on which half of the yield was harvested.

Thus there were three greenhouse varieties (1 to 3) and three outdoor varieties (4 to 6).

The 9 temperature treatments are given in table 2. The order of the treatments 1 to 9 is the order of rising mean temperature.

TABLE 2. The 9 temperature treatments

Number of treatment	Mean temperature	Temperature	
		day	night
1	13.00	17	11
2	15.00	23	11
3	16.00	20	14
4	17.00	17	17
5	19.00	23	17
6	21.33	30	17
7	22.00	26	20
8	22.33	23	22
9	24.66	30	22

The mean temperature is calculated from the formula

$$\frac{1 \times \text{day temperature} + 2 \times \text{night temperature}}{3}$$

since the day temperature lasted from 8 A.M. till 4 P.M. or for 8 hours a day and the night temperature covered the other 16 of the 24 hours. A treatment with a day temperature of a °C and a night temperature of b °C will be abbreviated as $a-b$.

With these 9 temperature treatments comparisons can be made between treatments with

- different, almost constant temperatures: treatments 4(17-17) and 8(23-22);
- the same day, but different night temperatures: treatments 1(17-11) and 4(17-17); 2(23-11), 5(23-17) and 8(23-22); 6(30-17) and 9(30-22);
- the same night, but different day temperatures: treatments 1(17-11) and 2(23-11); 4(17-17), 2(23-17) and 6(30-17); 8(23-22) and 9(30-22);
- both higher day and night temperatures: treatments 2(23-11) and 6(30-17), day and night temperature about 6 °C higher; 1(17-11), 3(20-14), 5(23-17), 7(26-20) and 9(30-22), day and night temperature progressively about 3 °C higher; 4(17-17) and 8(23-22), day and night temperature about 6 °C higher;
- rising mean temperatures in the order in which they are given in table 2.

Because both day and night temperatures are involved, three-dimensional graphs are needed to show the results, the measured value being the third dimension. Night temperatures are given on the x-axis, day temperatures on the y-axis. Along the vertical, the z-axis, the measured values are given. The ends of all verticals are connected and in this way vertical faces are formed; the shading is horizontal, so the height of different points may be more easily compared (see graphs 6-10).

Stem growth rate – During a three week period the length of each plant was measured once a week and from this the mean growth rate in mm per day was calculated.

Table 3 shows the results for the six varieties with their mean and the mean of the different temperature treatments.

TABLE 3. Mean growth rate of stem in mm per day

Treatment				Variety						
Number of treatment	Mean temperature	Temperature		Tuckqueen	Michigan State Forcing	Essex Wonder	Improved Pearson	Rutgers	Beefsteak	Mean
		day	night							
1	13.00	17	11	13	15	15	9	10	15	13
2	15.00	23	11	21	22	24	18	18	26	22
3	16.00	20	14	28	25	31	20	19	30	26
4	17.00	17	17	22	19	22	12	14	25	19
5	19.00	23	17	29	27	33	27	23	42	30
6	21.33	30	17	33	32	41	22	27	43	33
7	22.00	26	20	38	36	44	31	29	47	38
8	22.33	23	22	28	29	30	30	21	35	29
9	24.66	30	22	39	44	45	35	35	48	41
Mean				28	28	32	20	22	35	28

From this table the influence of day and night temperature can be studied. Making the comparisons mentioned above:

- different, almost constant temperatures: treatments 4 and 8 (the italicized figures) show a faster growth at a higher temperature;
- the same day, but different night temperatures (treatments 1 and 4; 2, 5 and 8; 6 and 9); with a higher night temperature a faster growth is found; only treatment 8, with a nearly constant temperature, shows a slower growth than expected;
- the same night, but different day temperatures: treatments 1 and 2; 4, 5 and 6; 8 and 9 show that faster growth is found at higher day temperature; there is only one exception, namely the 30-17 treatment of Improved Pearson: this is a variety with a determinate type of growth, which stops growth sometimes after the fourth, sometimes after the fifth cluster, so this exception is not amazing;
- both higher day and night temperatures: treatments 2 and 6; 1, 3, 5, 7 and 9; 4 and 8; the data indicate also a faster growth at higher day and night temperatures;
- a higher mean temperature gives faster growth except the nearly constant temperature of treatments 4 and 8, which fall out of the range in all varieties and which are much lower than expected.

Practically all mentioned differences are significant (odds 19:1).

In the three-dimensional graphs 6 a-f (see pp. 188-189) the same picture is shown. This gives a convenient way of showing the conformity between the varieties as to temperature influence on growth. To the right (higher night temperature) as well to the back (higher day temperature) and in the direction of the diagonal (higher day and night temperature) growth rate is faster.

Earliness of yield - The earliness of yield was measured by the number of days between the day on which half of the yield had been picked and November 11, the date on which half of the yield had been picked for the last group. The greater the number of days, the earlier the yield.

Table 4 gives this number of days. There are four open spaces, because no

fruits were harvested from these groups. These are all outdoor varieties. This shows that the greenhouse varieties have a wider temperature range than the outdoor varieties. Probably the reason for this is that the greenhouse varieties have been selected to give a yield in less favourable conditions of temperature than the outdoor varieties.

TABLE 4

Earliness of yield measured by the number of days between the day on which half of the yield had been picked and November 11

Treatment				Variety						
Number of treatment	Mean temperature	Temperature		Tuckqueen	Michigan State Forcing	Essex Wonder	Improved Pearson	Rutgers	Beefsteak	Mean
		day	night							
1	13.00	17	11	14	7	0	0	—	25	9
2	15.00	23	11	36	36	36	32	28	32	33
3	16.00	20	14	49	49	56	36	36	49	46
4	17.00	17	17	36	36	36	28	25	32	32
5	19.00	23	17	56	49	60	54	43	54	53
6	21.33	30	17	56	60	66	63	43	81	62
7	22.00	26	20	63	63	60	54	56	—	59
8	22.33	23	22	66	70	74	70	66	74	70
9	24.66	30	22	66	70	70	—	66	—	68
Mean				49	49	51	42	45	50	48

Following the same scheme for earliness as was followed for the growth rate, a surprisingly great conformity will be found between these two. So it would be superfluous to go over all the comparisons again. If earliness is read instead of growth rate on page 185 the following is found:

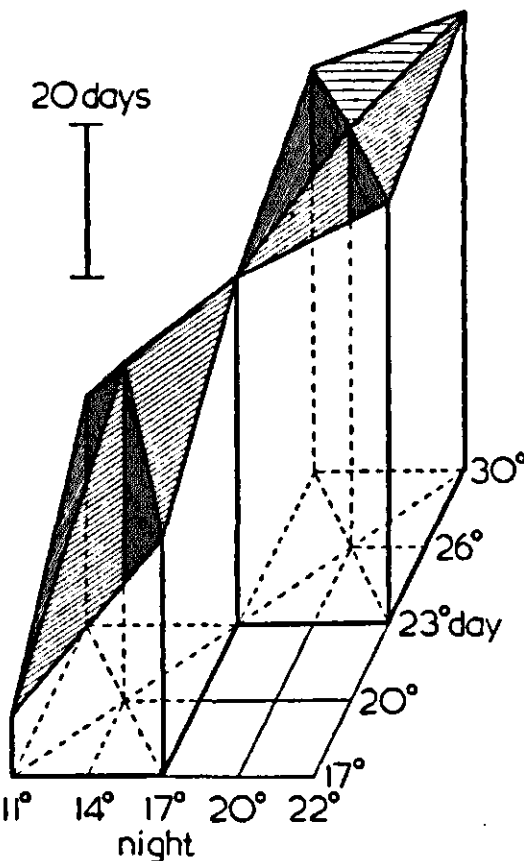
- the same;
- the same, only the exception for treatment 8 is lacking here;
- the same, only treatments 8 and 9 do not show differences;
- the same;
- the same, of the two treatments 4 and 8 that did not fit in only 4 remains. Treatment 4 differs greatly from the other treatments with a night temperature of 17 °C, giving the suggestion that 17 °C day temperature is rather low for good fruit set.

Graphs 7a–f (see pp. 188–189) show the earliness of yield and from a comparison with graphs 6 a–f the great conformity between growth rate and earliness can be seen readily. It seems clear that the growth rate of the stem and of the fruits is related to temperature in the same way. This seems to be even more the case considering the time of development from flower to ripe fruit, as will be discussed below.

Duration of fruit growth – By tagging some flowers with the date of anthesis, it was possible to find the time involved in development from flower to ripe fruit. For the three greenhouse varieties the mean is given in graph 8, showing the time in days subtracted from 100. This gives a larger value for a faster growth. This graph, having the same shape as those for growth rate and earliness also shows the close relation of fruit and stem growth.

Fruit yield – The total fruit yield is given in table 5. If the same comparisons as for growth rate (page 185) are made, the following results are found for

- a) different, almost constant temperatures (treatments 4 and 8): in four of the six varieties (excepted Rutgers and Improved Pearson which cannot well stand a day temperature of 17 °C) the yield is much higher at 17 °C than at 23 °C;
- b) the same day, but different night temperatures: treatments 1 and 4: the 17–11 group has a very low yield, not only is the 17 °C day temperature probably on the low side, but in conjunction with a 11 °C night temperature the result is very poor; this group had only 25% fruit set, the lowest of all groups; in this comparison, as an exception, the group with a higher night temperature has a higher yield; in treatments 2, 5 and 8 a higher night temperature almost always shows a lower yield, as does the 6 and 9 comparison;
- c) the same night, but different day temperatures: treatments 1 and 2: here the exception of 17–11 is found again; treatments 4, 5 and 6 give a lower yield at higher day temperatures for the greenhouse varieties; for the outdoor varieties 17 °C day temperature is too low, so that the 23 °C day temperature is much better; treatments 8 and 9: higher day temperatures again give a lower yield;
- d) both higher day and night temperatures (treatments 2 and 6; 1, 3, 5, 7 and 9; 4 and 8): at higher temperatures the yield is lower, except for the 17–11 group for all varieties and the 17–17 group for some varieties;
- e) higher mean temperatures tend to result into a lower yield, except 17–11 in all varieties and 17–17 in all except Tuckqueen and Michigan State Forcing; the day temperature of 17 °C seems to be rather low; the night temperature of 11 °C is not too low, as is shown by treatment 2 which has an 11 °C night temperature, but a very good yield.



GRAPH 8
Mean growth rate of the fruits of the varieties Tuckqueen, Michigan State Forcing and Essex Wonder: 100 minus number of days of fruit development.

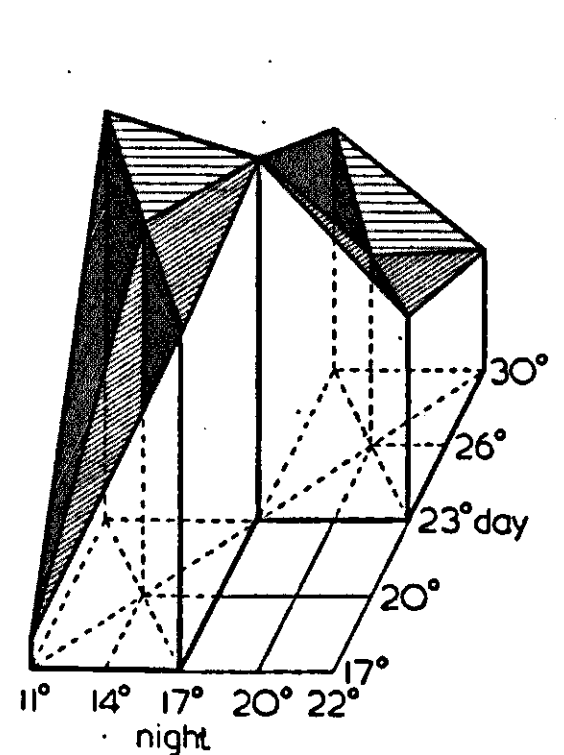
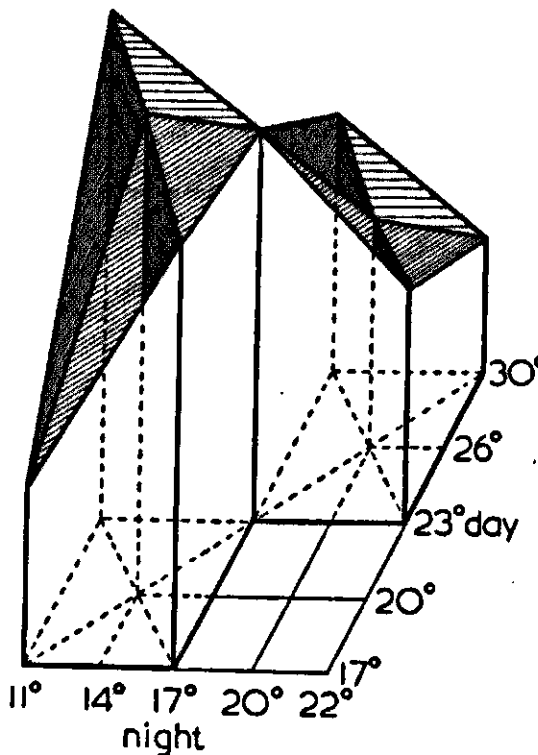
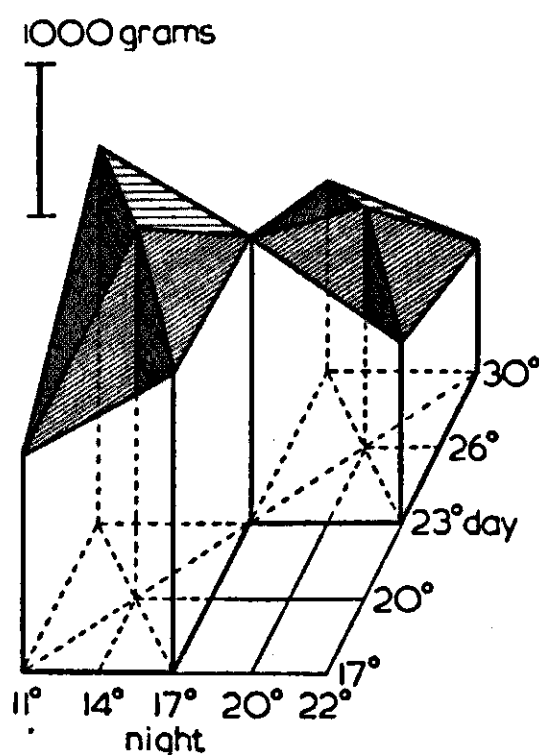
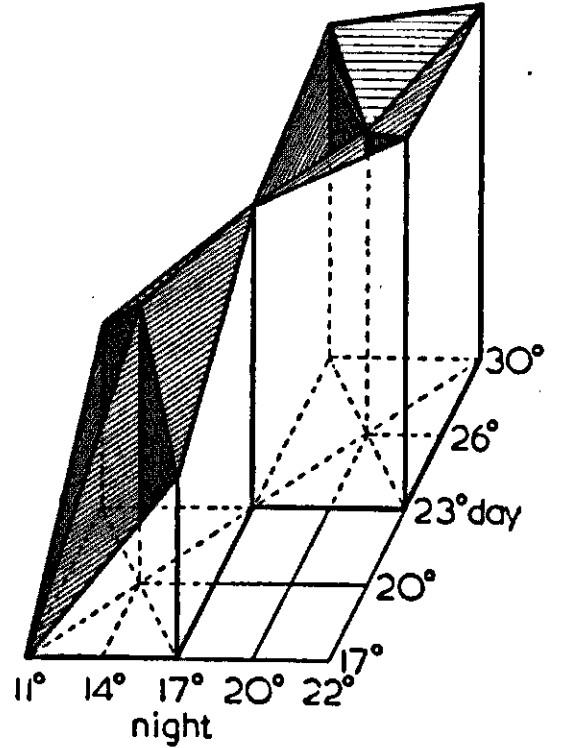
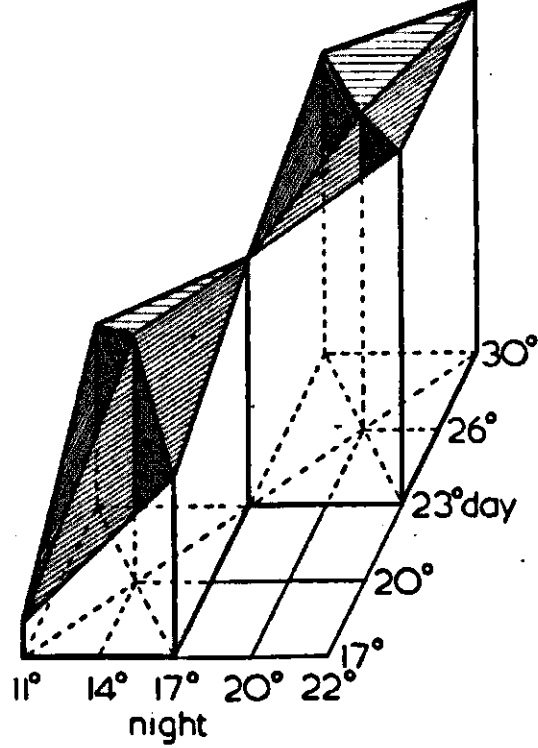
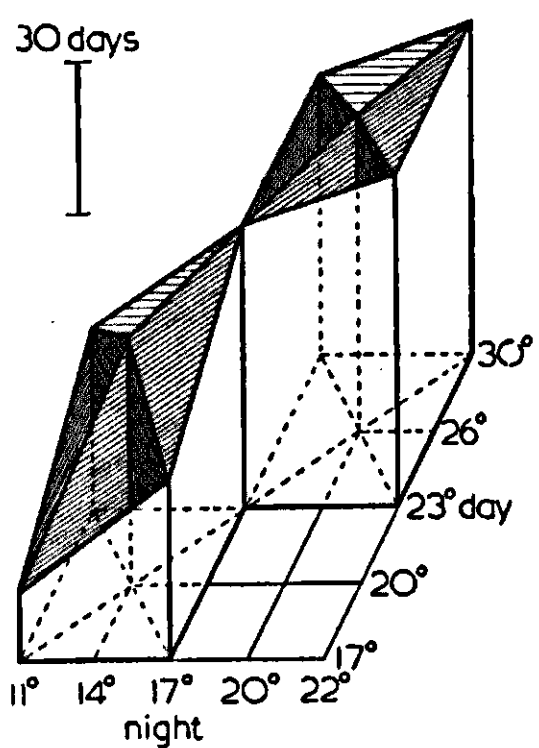
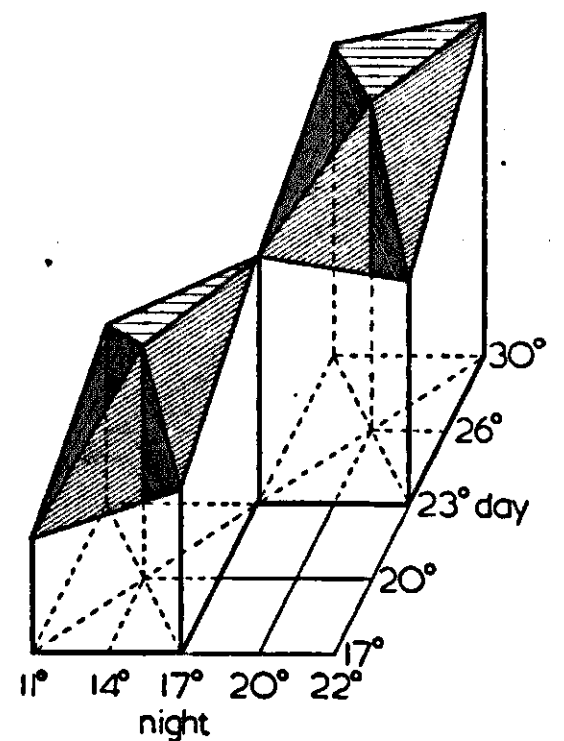
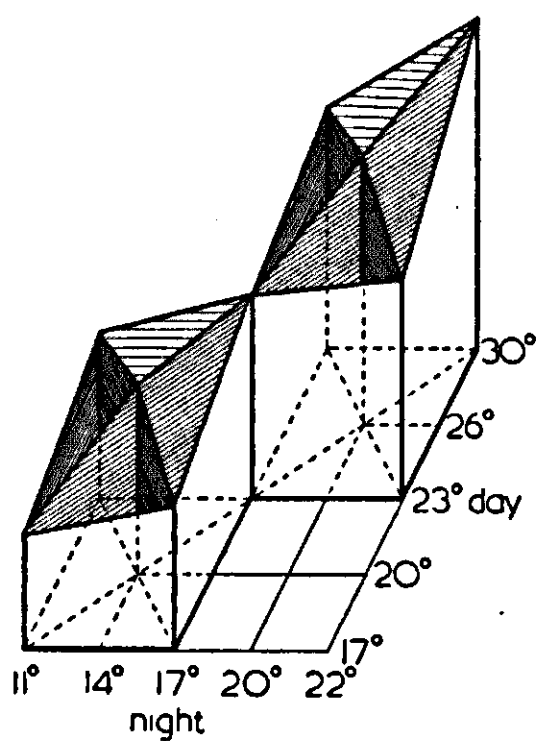
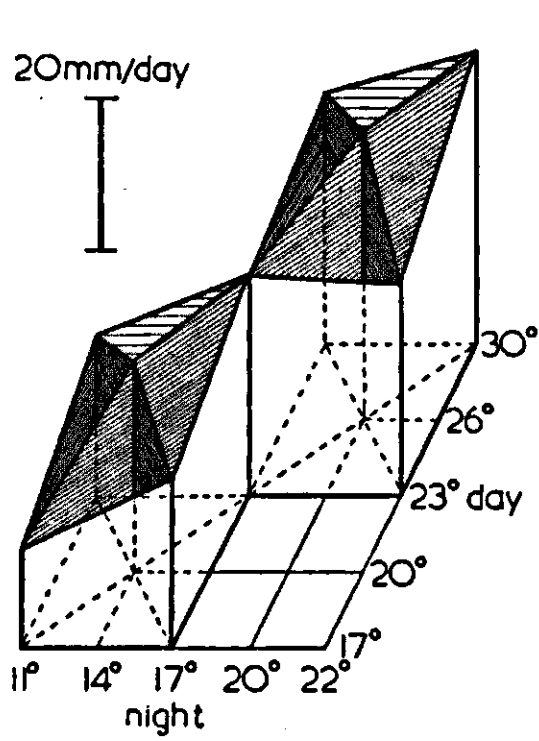
TABLE 5. Fruit yield per plant in 100 grams

Treatment				Variety						
Number of treatment	Mean temperature	Temperature		Tuckqueen	Michigan State Forcing	Essex Wonder	Improved Pearson	Rutgers	Beefsteak	Mean
		day	night							
1	13.00	17	11	14.5	12.0	2.0	3.5	0.0	1.0	5.5
2	15.00	23	11	25.0	33.5	27.0	18.5	25.5	7.5	23.0
3	16.00	20	14	24.5	32.0	24.5	22.0	24.5	11.0	23.0
4	17.00	17	17	20.0	28.5	22.5	10.5	6.5	4.0	15.5
5	19.00	23	17	19.0	26.0	24.0	20.0	18.5	6.0	19.0
6	21.33	30	17	12.5	17.0	16.0	5.5	9.0	2.5	10.5
7	22.00	26	20	16.0	15.0	12.5	6.5	10.5	0.0	10.0
8	22.33	23	22	12.0	15.5	13.5	11.5	13.0	1.5	11.0
9	24.66	30	22	8.5	9.0	8.0	0.0	2.0	0.0	4.5
Mean				17.0	21.0	16.5	11.0	12.0	3.5	13.5

a. Tuckqueen

b. Michigan State Forcing

c. Essex Wonder



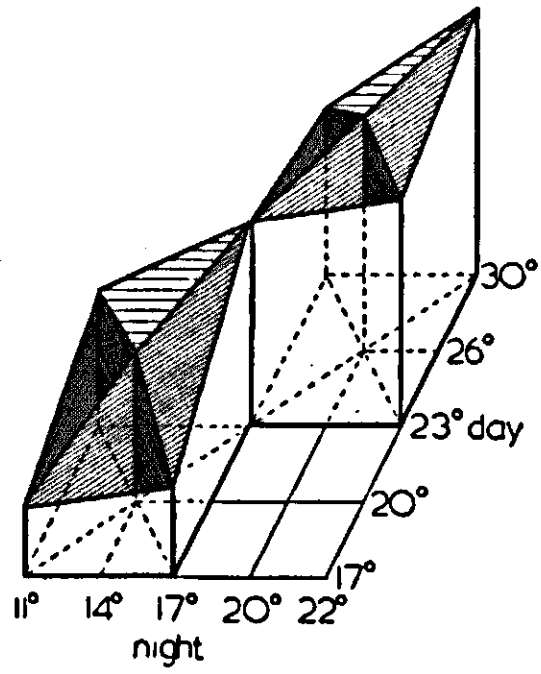
GRAPHS 6 a-f (upper row)

Stem growth rate in mm per day of the six varieties at different temperature combinations.

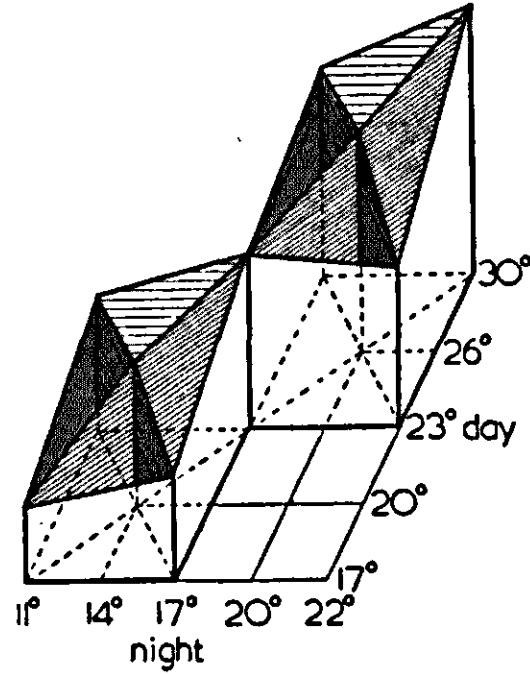
GRAPHS 7 a-f (middle row)

Earliness of yield in days of the six varieties at different temperature combinations.

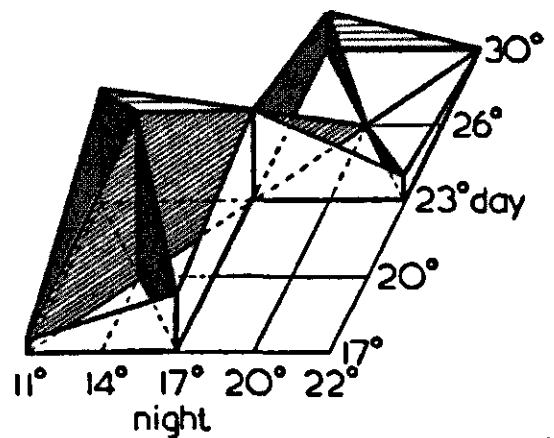
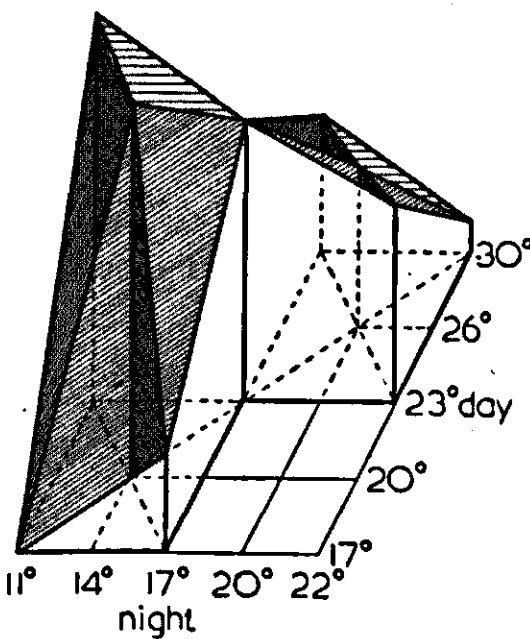
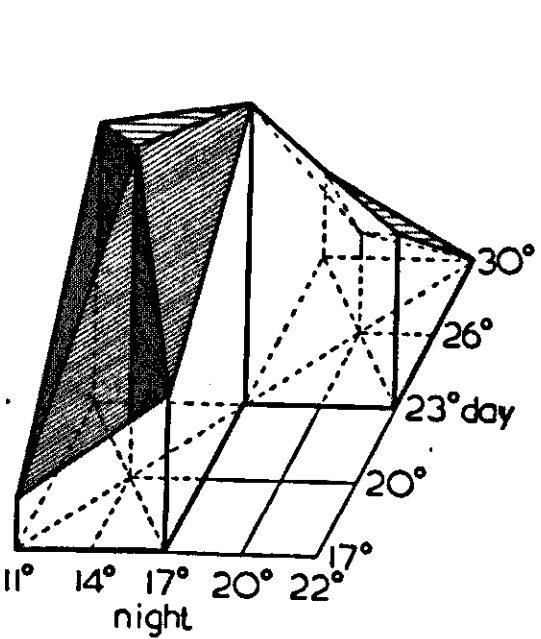
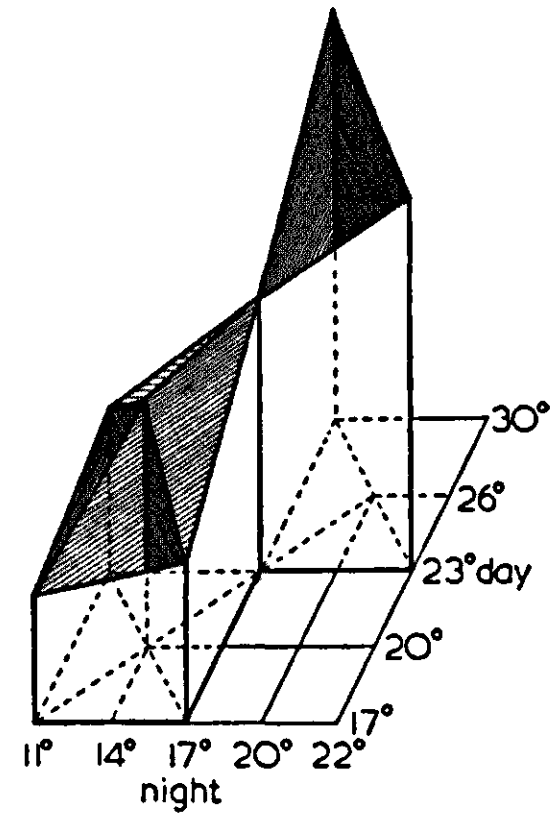
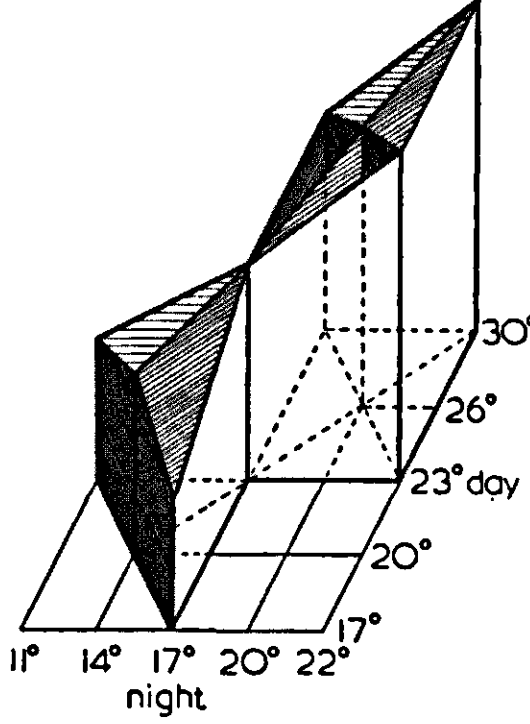
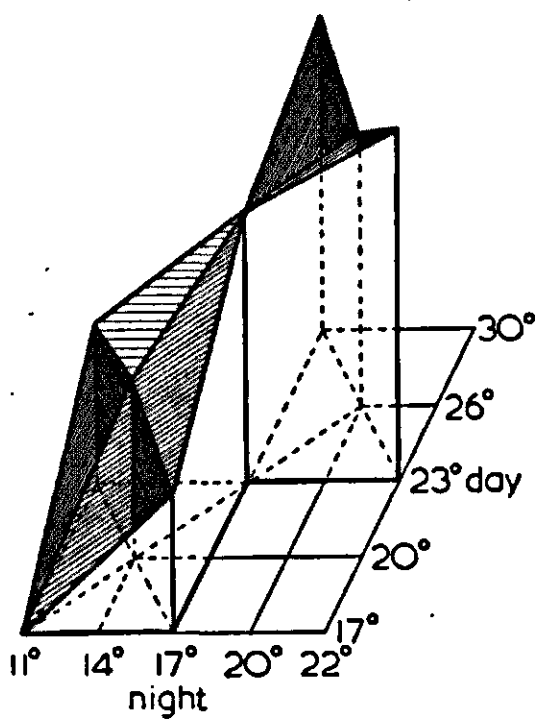
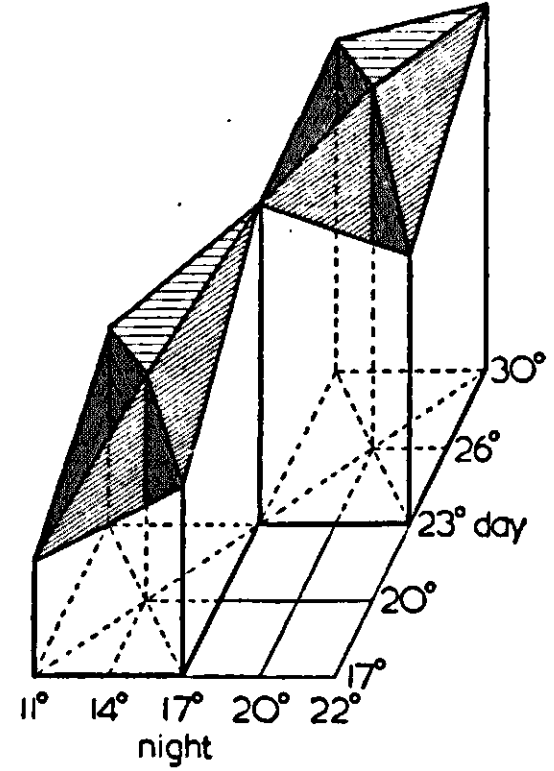
d. Rutgers



e. Improved Pearson



f. Beefsteak



GRAPHS 9 a-f (bottom row)
Fruit yield in grams of the six varieties at different temperature combinations.

Graphs 9 a–f (see pp. 188–189) also show these results. They demonstrate very clearly, if 17–11 is left out, the reverse influences of temperature on yield on the one hand and on growth rate of stem and fruit on the other hand. Also the differences between greenhouse and outdoor varieties are shown again.

From the same graph the following may be concluded about variety characters as far as yield is concerned. Tuckqueen is least affected by temperature differences and will be the best variety when temperature control is not possible at all. Michigan State Forcing has a very high yield in the case of certain temperature combinations (20–14 and 23–11). This shows that large temperature differences between day and night, even up to 12 °C, are not unfavourable for yield (as opposed to earliness). Essex Wonder yields almost nothing at treatment 17–11. Improved Pearson and Rutgers are very much alike. They are bad at both high and low temperatures or have a very small temperature range for good yield. Beefsteak is always very poor.

Correlations between mean temperature, growth rate of stem, earliness of yield, duration of fruit growth and fruit yield – Using the mean of the three greenhouse varieties which show the most regular picture, correlations between mean temperature and the values found for growth rate of stem, earliness of yield, duration of fruit growth and fruit yield have been calculated. The always exceptional 17–11 group is omitted for the fruit yield.

The following highly significant correlations are found:

mean temperature	+0.91	+0.90	–0.91	–0.98
	growth rate of stem	+0.90	–0.92	–0.83
		earliness of yield	–0.99	–0.86
			duration of fruit growth	+0.88
				fruit yield

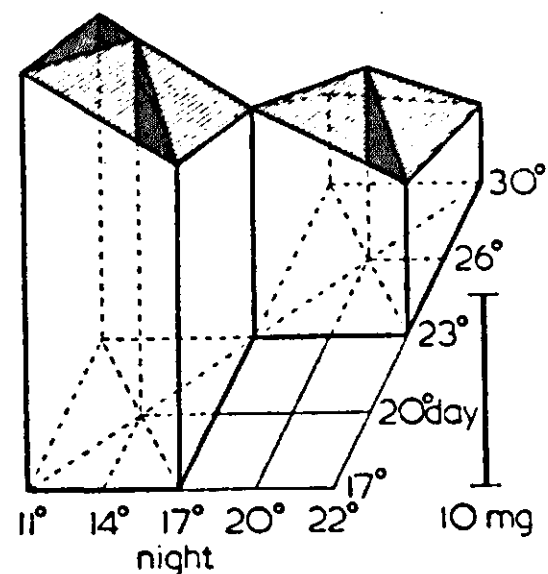
From the practical viewpoint the most difficult to overcome is the negative correlation between earliness of yield and fruit yield.

Disks of leaf blades – Because leaf blades are the main parts for photosynthesis in the plant, the influence of temperature on leaf disks was studied. With a corkborer 10 disks of about 1.6 cm² each were punched out of full grown leaves from each temperature group and dried at about 80 °C. This was done once every 4 hours for 24 hours on July 31 for the variety Tuckqueen. The mean weight, for convenience sake diminished by 40 mg, of the six values for each temperature treatment is given in the three-dimensional graph 10. This shows that heavier disks were produced at lower temperatures. So in combination with slower growth at lower temperatures heavier weight of the same leaf area is found. The weight of the disks is positively correlated with the fruit yield; the 17–11 treatment exception is not found here.

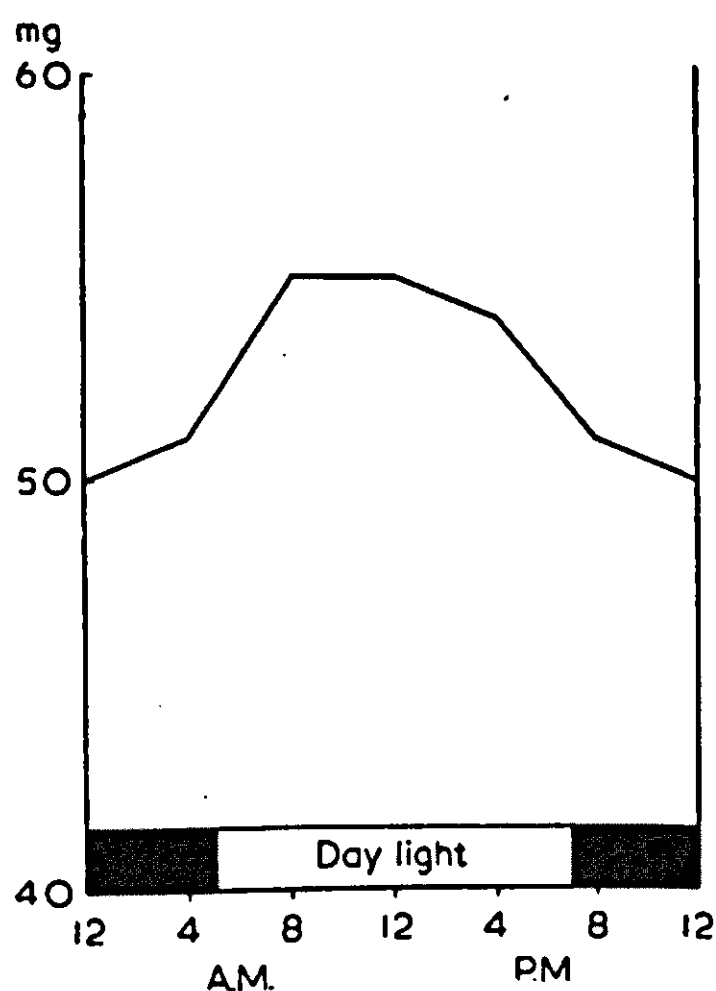
Taking all the temperature treatments together, changes in weight of disks during the day and night are found as given in graph 11.

Sugar was determined in these disks (64). The means of the sugar figures of all temperature groups are summarized in graph 12.

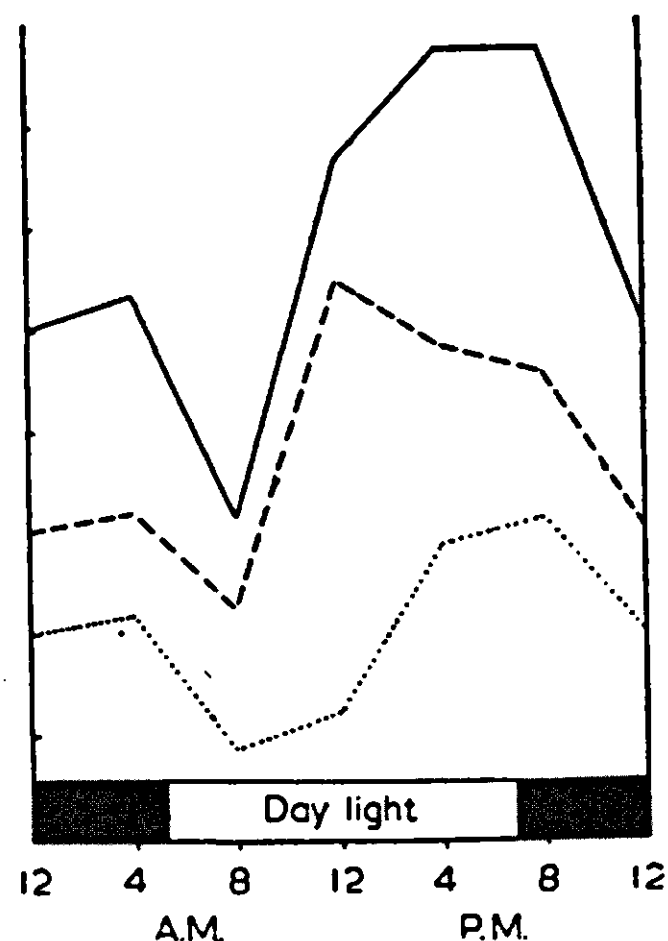
Comparing the values of graph 11 and in 12 the line for the sucrose between 8 A.M. and 8 P.M. it can be seen, that during the time that the dry weight of the leaf disks is decreasing the sucrose is increasing, probably due to a high transport of carbohydrates from the leaves in that period of the day (compare p. 217).



GRAPH 10
Mean dry weight less 40 mg
of 16 cm² leaf blade samples
at different temperature
treatments.



GRAPH 11
Dry weights at different times during the day of about 16 cm² samples of leaf blade in mg.



GRAPH 12
Relative sugar figures of leaf disks:
—— total sugars
----- reducing sugars
..... sucrose

Temperature influence on the sugar content was not very clear. Mostly the amount of sugar was higher at lower temperature and this could be the cause of better clusters and more fruits at lower temperatures.

Varietal differences – Some differences among the varieties greatly in excess of temperature effects are given in table 6, in which the values for the different temperature treatments have been averaged. Tuckqueen has the thinnest stem and lowest root weight and yet the fruit yield was good. Beefsteak, on the other hand, having a very heavy stem and root system, had practically no fruit yield; probably as a result of very irregular flowers with a long style extending beyond the stamens, nevertheless the temperature influence on yield was clear in this variety too.

TABLE 6

Some values for the six varieties, independent of the temperature treatments

Variety	Tuckqueen	Michigan State Forcing	Essex Wonder	Improved Pearson	Rutgers	Beefsteak
Dry weight of 1 cm stem in mg .	126	177	192	169	205	291
Dry weight of roots in g	3.4	6.6	5.4	7.3	7.0	15.3
Mean weight of 1 fruit in g . . .	64	107	45	96	110	131
Fruit yield per plant in kg . . .	1.9	2.3	1.8	1.2	1.3	0.4

In this experiment the greenhouse varieties have a much higher yield than the outdoor varieties and a wider temperature range for fruit yield.

Conclusions – All six varieties respond in the same way to temperature. However, there are large differences in yield between the varieties.

At higher temperature faster length growth, faster fruit growth, less fruit and consequently an earlier but lower yield were found. The weight of the same leaf area was smaller.

Optimal temperatures to get a moderate growth and a high fruit yield are 20–23 °C during day time and only 11–17 °C at night.

A night temperature at least 6 °C lower than the day temperature is advisable.

It has to be considered, however, that all results mentioned above, are found with 2 plants for each treatment and 4 plants grown in an area of $\frac{1}{2} \times \frac{1}{2}$ meter. It is possible, that with larger distances between the plants higher temperatures are needed to get maximum yield.

2.3.3. Day and night temperatures from November till February (experiment III)

Introduction – During the summer the differences in plant growth and yield as a result of temperature influence were very pronounced. The accidental differences in light intensity as a result of shadowing did not influence the results too much. In the growth and yield of plants during the winter, however, when light intensities were probably about a third of the summer intensities and day length was much shorter, large differences as a result of different light intensities were found; and consequently the differences between temperature groups were not always as pronounced as in the summer experiment.

The experiment during winter was carried out only with one variety: Tuckqueen which was used during the summer too.

Sown on November 1 the plants were divided into 14 different temperature groups of 4 plants each.

Temperature	day	30	30	30	26	23	23	23	20	20	20	20	17	17	17
	night	22	17	11	20	22	17	11	20	17	14	11	22	17	11

There was no time to wait for ripe fruits, so the plants were harvested at the moment when the fourth cluster was clearly visible. Dry weights of plants and green fruits were determined.

Group 20–14 had a light intensity very much lower than the other groups and therefore is not included in the results.

Results – The average stem growth per day was less during the winter than during the summer. As shown in table 7 growth in summer was about $1\frac{1}{2}$ times as fast as in winter.

TABLE 7

Mean growth of stem in mm per day at different temperature treatments during winter and summer

Temperature	day	30	30	30	26	23	23	23	20	20	20	17	17	17
	night	22	17	11	20	22	17	11	20	17	11	22	17	11
Growth	winter	21	20	13	24	18	19	15	16	16	14	10	11	9
	summer	39	33	–	38	28	29	21	–	–	–	–	22	13

Of course not much can be said about earliness of the harvest in this experiment. The first flowers were found in the 20–20, 20–17 and 23–17 treatment plants.

Some idea about earliness is perhaps obtainable by comparing the dates of harvest of the plants, as in the summer the faster growing plants had a higher early yield.

Somewhat more can be said about the expected yield. At the moment of harvest buds, flowers and fruits were counted and the clusters weighed. On the first three clusters of the plants one can expect at least as many fruits at harvest time as had already been set.

A survey of the results is given in table 8.

TABLE 8. Effect of day and night temperature in winter

1	2	3	4	5	6	7	8	9	10
Temperature		Date of harvest	Average stem growth in mm per day	Stem length in cm at harvest time	Average dry weight in mg of 1 cm stem	Dry weight of roots in g	Dry weight in mg of ± 26 cm ² leaf blade	Dry weight in mg of the first 4 clusters with fruits	Expected number of fruits on first three clusters together
day	night								
17	11	16/2	9	93	83	2.78	52	569	0.00
17	17	30/1	11	89	62	1.82	48	171	0.50
17	22	30/1	10	82	43	1.43	48	76	0.00
20	11	2/2	14	113	53	2.36	49	11387	11.25
20	17	19/1	16	110	45	1.60	44	158	2.25
20	20	19/1	16	109	43	1.38	45	4035	3.50
23	11	2/2	15	128	49	2.16	36	620	3.75
23	17	19/1	19	135	39	1.24	36	1079	3.25
23	22	19/1	18	128	36	1.17	33	58	0.50
26	20	13/1	24	153	35	1.16	42	299	0.75
30	11	30/1	13	107	63	2.70	51	1330	6.25
30	17	13/1	20	129	48	2.22	47	598	2.75
30	22	13/1	21	138	32	1.35	40	125	0.00

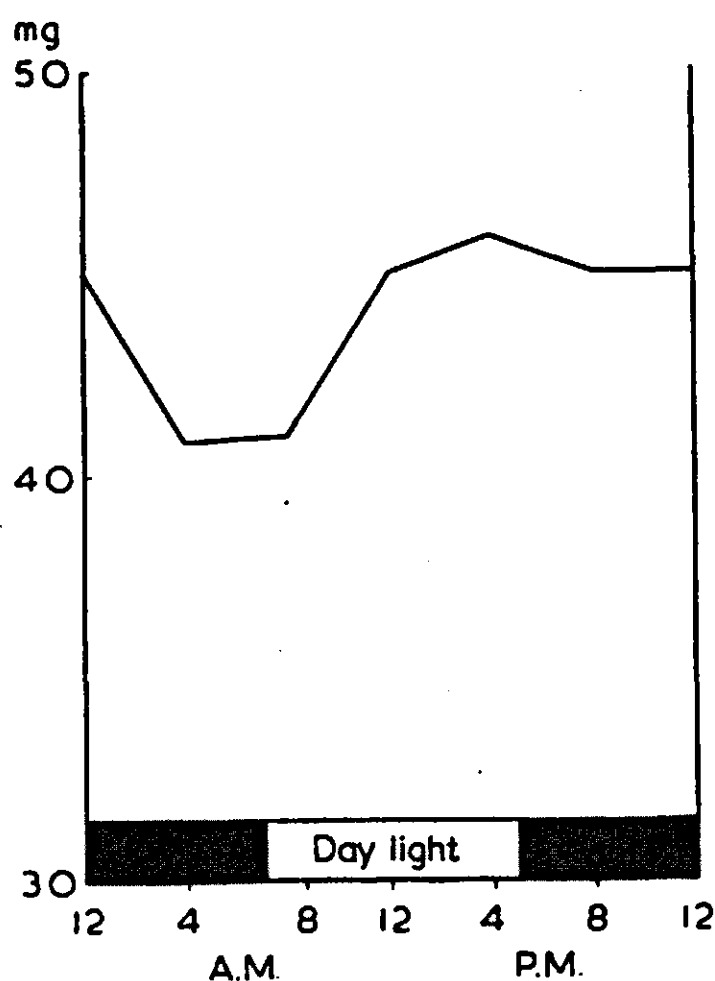
On the whole the plants of the higher temperature (especially night temperature) groups were ready for plant harvest earlier (column 3). These plants have a faster stem growth (4), are mostly longer (5) and have a thinner stem (6), a smaller root system (7), thinner leaves (8), smaller clusters (9) and the expected number of fruits is much less (10) than from the lower temperature groups.

In fruit development an exception are the plants with a day temperature of 17 °C. This temperature seems to be too low to get a good fruit formation;

though the clusters are quite well developed in 17-11, the flowers are pale and abnormal and many buds do not open properly.

Larger differences between day and night temperatures generally result in slower growth, shorter plants with heavier stem and roots as well as larger clusters and more fruits. In short: light deficiency in winter results in a very low yield. Night temperatures much lower than day temperatures are essential for fruit yield.

On December 18 for each temperature treatment 16 leaf disks ($\pm 26 \text{ cm}^2$) were taken every 4 hours during a 24 hour period and dried. Graph 13 gives the mean daily course of all temperature groups combined. The picture is not as clear as in the summer experiment (p. 191). The leaves are much thinner. The rise in weight starts, because of the shorter day, between 8 and 12 A.M., but the fall does not start until after 12 at night, much later than in summer. The differences between highest and lowest weight are, as in summer, about 10 %.



GRAPH 13

Dry weights at different times during the day of about 26 cm^2 samples of leaf blade in mg.

2.4. In artificially lighted rooms

2.4.1. Introduction

Plants, used for the experiments in artificially lighted rooms were grown to about first bloom in a greenhouse with a day temperature of 23°C and a night temperature of 17°C . This was a mistake. In this pretreatment the plants could make reserve material which was used up in the artificially lighted rooms at different speeds. This caused difficulties in comparing the various temperature groups. Nevertheless some conclusions can be drawn from these experiments. Again there were 4 plants on an area of $\frac{1}{2} \times \frac{1}{2}$ meter, two plants of the variety Ailsa Craig and two plants of the variety Tuckqueen. The mean of these 4 plants was calculated.

The lamps (Westinghouse fluorescent tubes and some incandescent lamps) were hung above the plants and the plants were moved downwards, when their tops reached the lamps. Light intensity was slightly above 10,000 lux at the top of the plants. It was much lower, however, further from the lamps. The light was not strong enough to get a good yield. It has to be considered that plants growing slower have a larger part closer to the lamps than plants growing faster.

On account of the low light intensity, the same difficulties as a result of uncontrollable differences in light intensities were found, as in the winter crop. Temperature influence is often confused by this.

2.4.2. Night temperature (experiment IV)

To study the influence of night temperature there were two series with day temperatures of 17°C and 23°C . Light period was 8 hours a day.

Some results obtained after three months of treatment are given in table 9. By far the slowest stem growth (column 3) is found in the groups with the lowest night temperature. The other night temperature groups do not show a clear picture.

The root systems (4) and stem weights (5) are largest at the lowest night temperature. For the lengths (6) and weights (7) of the clusters a more or less regular rise is found at lower night temperatures and some very small fruits (8) were formed only at the lowest night temperature with an exception for the 17-23 group.

TABLE 9. Influence of different night temperatures

1	2	3	4	5	6	7	8
Temperature		Stem growth in mm per day	Dry weight of roots in g	Dry weight of 1 cm stem in mg	Cluster length in cm	Cluster weight in mg	Fruit weight in g
day	night						
17	10	13	1.39	40	17.0	1291	12
17	14	19	0.83	23	8.7	906	2
17	17	22	0.88	30	5.8	558	0
17	20	19	0.85	28	3.5	100	0
17	23	17	0.88	29	6.6	401	10
17	26	23	0.97	24	6.1	220	0
23	10	15	1.12	42	22.1	2905	54
23	14	25	0.95	27	11.4	1005	4
23	17	27	0.99	27	5.7	517	0
23	20	21	0.86	26	2.7	37	0
23	23	33	0.70	24	3.4	101	0

So here was found, as in the greenhouses, at higher night temperatures a faster stem growth, a thinner stem and lighter root system and less developed clusters than at lower night temperatures. Differences are less pronounced and less clear than in the greenhouses.

2.4.3. Day temperature (experiment V)

To study the influence of day temperature two series were established, one of a day length of 8 hours, the other with 16 hours light a day. The night temperature was 17 °C in all cases.

Table 10 shows that most of the results found for a higher night temperature hold true for a higher day temperature too; for instance better clusters at low day temperatures. At the low day temperatures where cluster growth was the best, temperature, however, is too low for normal blooming and fruit set (7° and 10 °C). This is the reason that at the 16 hours day group at somewhat higher temperatures the greatest fruit weight is found, hence not on plants with the largest clusters. At the lowest day temperature groups with 8 hours light some very small seedless fruits were found.

TABLE 10. Influence of different day temperatures

	1	2	3	4	5	6	7	8
	Temperature		Stem growth in mm per day	Dry weight of roots in g	Dry weight of 1 cm stem in mg	Cluster length in cm	Cluster weight in mg	Fruit weight in g
	day	night						
8 hours day	7	17	9	1.69	54	17.4	1390	18
	10	17	13	1.22	50	13.5	800	14
	14	17	18	0.98	33	5.6	387	0
	17	17	22	0.88	30	5.8	558	0
	20	17	25	0.94	29	8.4	1234	0
	23	17	27	0.99	27	5.7	517	0
16 hours day	7	17	5	3.82	115	46.5	13550	1
	10	17	10	4.38	117	42.6	13250	14
	14	17	24	1.66	60	20.4	2556	108
	17	17	26	1.66	59	21.3	3530	126
	20	17	26	1.63	60	15.5	1687	64
	26	17	23	1.61	56	5.5	203	0

3. LIGHT

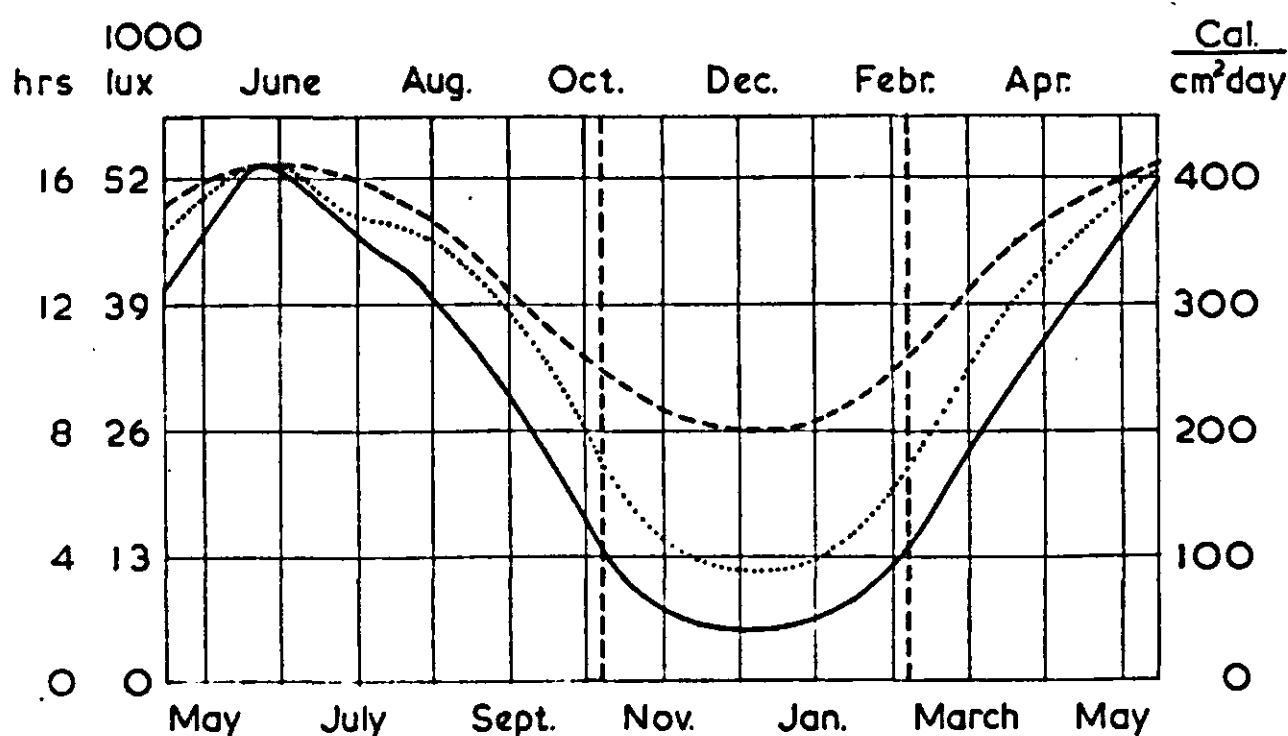
3.1. Introduction

Light provides the energy necessary for photosynthesis. This function, not regarding any other effect it might have, makes it essential for plant growth.

The light influence on growth can be split into influence of

- the intensity of the light and
- the length of the daily light period.

The light intensity of sunlight changes every moment. REESINCK (71) gives the mean course during the average day of each month during the year for the Netherlands. In graph 14 the distribution of light intensity at noon, averaged over ten years, is given. In winter this seems to be about one fifth of summer intensity resulting mainly from the lower altitude of the sun and the cloudiness in winter.



GRAPH 14

Yearly course of { day length in hours -----
light intensity at noon in lux
light energy per day in cal/cm² ———

Part of the data after REESINCK (71).

In addition to the low light intensity the days in winter are much shorter than in summer, about one half as long (graph 14). The two factors together result in a mean light energy on the longest days about 10 times as large as on the shortest days (graph 14). Furthermore, during winter tomatoes are grown in greenhouses where

This table shows that the total dry weight produced in the same time is smaller with weaker light. The first reduction of the light from 1 L to $\frac{1}{3}$ L and $\frac{1}{2}$ L gives a reduction of dry weight of approximately the same order as the reduction in light intensity. The second reduction to $\frac{1}{9}$ L and $\frac{1}{4}$ L, however, gives a reduction in dry weight of $\frac{1}{6}$ and $\frac{1}{3}$ of those at $\frac{1}{3}$ L and $\frac{1}{2}$ L, hence a much larger reduction. The weaker the light the larger the effect of a reduction of the light intensity. The expectation that all parts of the plants are influenced by the reduction of light intensity in the same way is wrong as will be shown.

With reduced light intensity the leaf blades are thinner, and the leaf area is less reduced than the weight of the leaves. With weaker light the leaves are thinner and paler green, the area is smaller, but not as reduced as are most other parts of the plant.

The differences in length are not as pronounced as are the differences in dry weight. With the light intensity reduced to $\frac{1}{3}$ L and $\frac{1}{2}$ L the length is nearly the same as with 1 L. Further reduction gives considerably shorter plants. The dry weight of 1 cm stem is heavier than would be expected. With reduction to $\frac{1}{3}$ L and $\frac{1}{2}$ L the internodes of the stem are longer than with 1 L and the first cluster is even higher on the stem.

The leaves at a lower light intensity contain relatively more water, as will be discussed further on p. 201.

As the light energy is reduced, the cluster is the first thing to be considerably reduced.

3.2.3. *Variation in day length*

Experiment VIII – Groups of plants were grown in day lengths of 6, 8, 10, 12, 14 or 16 hours. These different day lengths were given to plants at both 17 °C or 23 °C. The plants were grown under artificial light which was of an intensity of about 10,000 lux at the level of the tops of the plants. The plants were about 25 cm tall at the start of the treatments and the experiment was concluded after three months when the differences among the groups were determined (see table 12).

TABLE 12. Weights of certain plant parts from plants grown in different day lengths

Day length in hours		6	8	10	12	14	16
Weight of							
17 °C	roots (dry) in mg	770	880	1140	1600	1880	1660
	1 cm stem (dry) in mg . . .	20	30	41	59	68	60
	1 leaf between cluster 3 and						
	5 (dry) in mg	240	400	490	1070	1540	1390
	5 clusters with fruits (fresh)						
23 °C	in mg	80	560	4790	70330	100450	129530
	roots (dry) in mg	440	700	900	1060	1240	1200
	1 cm stem (dry) in mg . . .	13	24	30	32	38	37
	1 leaf between cluster 3 and						
	5 (dry) in mg	180	310	340	370	460	470
	5 clusters with fruits (fresh)						
	in mg	42	101	200	218	310	400

All measurements of plants grown at 17 °C gave larger values than the corresponding at 23 °C; 17 °C seemed to be a better temperature in the artificial light: at 17 °C fruits were formed at all day lengths longer than 10 hours, but

at 23 °C not even at 16 hours light a day. Up to 14 hours light per day all values increased under increasing longer days. The largest rate of increase was found in the clusters with fruits. The mean length growth of the stem at 23 °C was 32 mm/day and 25 mm/day at 17 °C.

Experiment V – An experiment already mentioned on page 195, where day and night temperatures are comparable and the day length was 8 or 16 hours, will be considered again (graphs 15a-f).

It is readily seen that between a treatment of 8 or 16 hours there are great differences except where growth rate (a) is concerned, so the growth rate seems to be more dependent on temperature than on day length. The dry weight of a certain leaf area (b) shows about the opposite picture: heavier leaf disks at lower temperatures. The opposite effect to stem growth was already found on page 190.

Both root and stem weights (c and d) of the 16 hours day plants are much heavier than those of the 8 hours day plants. For the roots this tendency is even greater than for the stems.

The clusters without fruits (e) are also heavier at the longer day and the differences in fruit production (f) are enormous.

The change in dry weight of leaf disks during the day is given in table 13. Again a rise is found during the light period, directly followed by a decrease to the original value.

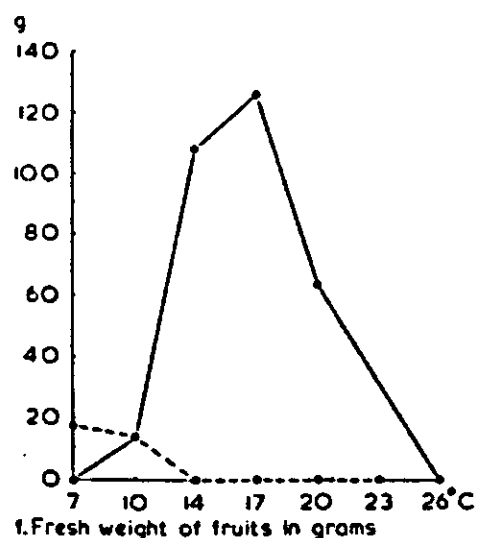
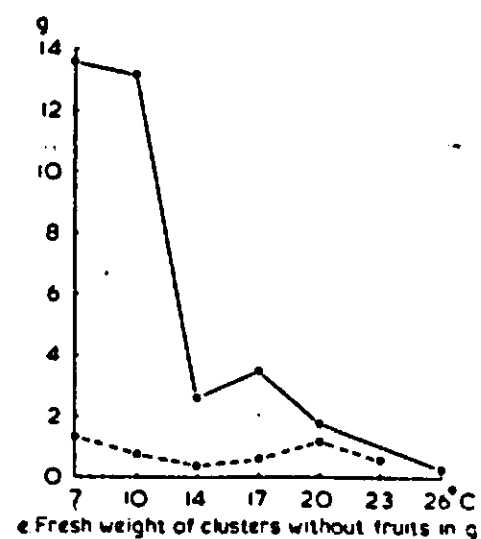
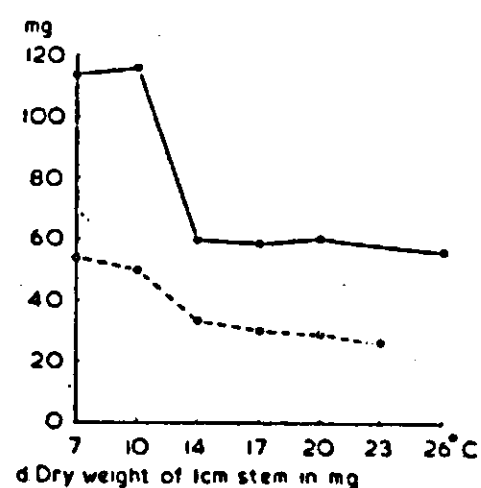
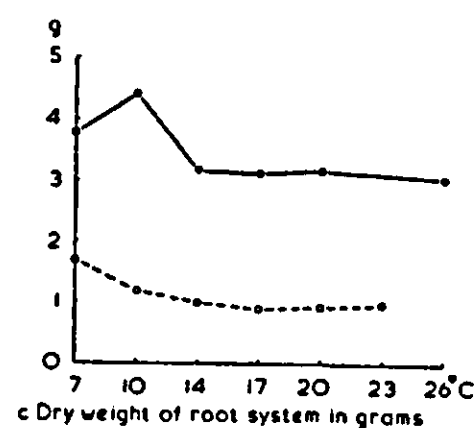
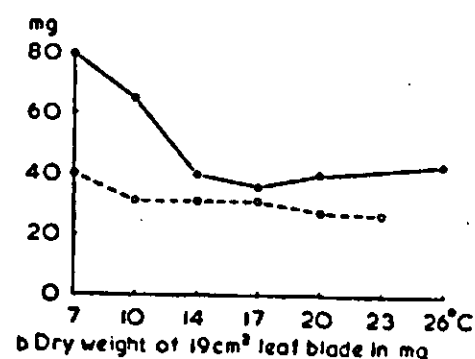
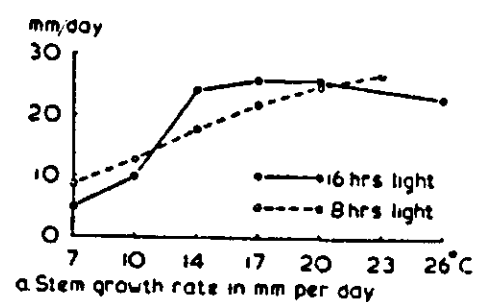
TABLE 13

Dry weights at different times during the day of about 26 cm² samples of leaf blade in mg

Time in hours after starting the illumination	Day length in hours	
	16	8
0	49.8	30.9
4	49.9	32.3
8	51.2	33.8
12	52.3	31.3
16	55.6	30.9
20	49.5	31.3
24	49.8	30.9

GRAPHS 15 a-f

Values for plants grown in artificial light for 16 hours a day (solid line) or 8 hours a day (broken line) at a night temperature of 17° C and day temperatures as indicated on x-axis.



3.3. Plant growth with extra artificial light during winter

3.3.1. Young plants

In Wageningen the influence of extra artificial light before planting was studied during the winter months.

Dry weight – In experiment IX plants of the variety Tuckqueen were used. They were sown on January 6 and received three different additional light treatments:

- a) no artificial light,
- b) 15 hours a day, also during the day light, light by TL tubes (fluorescent tubes), 4 tubes on 1 m² (+TL),
- c) 15 hours a day, also during the day light, light by HO 2000 lamps (= high pressure mercury lamps) (+HgL).

On a certain day at noon the light intensities were:

- a) -L = 4500 lux, b) +TL = 7200 lux and c) +HgL = 7200 lux. -L is not only weaker than the others, but also the time of light exposure is shorter and for these two reasons the light energy is much lower.

Dry weight determinations were made first on February 6, on which day only the above ground parts were harvested. For the subsequent four harvests the whole plants were used (table 14).

TABLE 14

Dry weights in mg of plants sown on January 6 and grown under natural light (-L), TL tubes 15 hours a day (+TL) and high pressure mercury light (+HgL)

Date	6/2	15/2	22/2	23/2	1/3
-L	16.1 ± 0.8	56 ± 2	119 ± 5	154 ± 11	261 ± 16
+TL	58.4 ± 4.0	226 ± 14	470 ± 54	551 ± 25	828 ± 45
+HgL.	43.4 ± 2.6	153 ± 13	425 ± 31	519 ± 28	824 ± 46

Plants under TL light and from the control had more anthocyanin than plants under the mercury light, probably as a result of a lower temperature.

Table 14 shows the effect of the extra light given in winter very clearly. The dry weights of the extra lighted plants are approximately four times as heavy as the dry weights of the plants under natural light conditions.

For experiment X plants of the variety Dominant were sown on November 14. Light from TL tubes was used 15 hours a day, in addition to and during the normal light, in comparison with normal day light alone. Dry weights of the above ground parts are given in table 15, where also the percentages dry matter

TABLE 15

Percentage dry matter and total dry weight in mg of plants under natural light (-L) or with extra illumination (+L)

Date	- L		+ L		Ratio of + L/- L × 100	
	% dry matter	total dry weight	% dry matter	total dry weight	% dry matter	total dry weight
28/11	5.22	4.25	6.89	5.92	132	139
1/12	4.48	5.39	6.18	10.24	138	190
5/12	4.95	7.48	7.44	17.94	150	240
8/12	5.06	9.31	8.92	24.13	176	260
12/12	5.65	13.23	6.36	62.40	113	472

are given and the relation of these values between the extra lighted and the not extra lighted plants.

The table shows:

- a) a higher dry matter content for the extra lighted plants (+L),
- b) the dry weight differences between +L and -L increase with time.

This must be the result of the decreasing natural light which makes the differences in light energy for the two groups steadily increase.

The two mentioned experiments (IX and X) show very clearly the influence of the extra light on the speed of plant growth and this speeding up in growth can result in an earlier yield (compare pp. 203 to 204).

Chlorophyll and dry weight content of leaf disks – Leaves from plants receiving extra light look darker green than those from plants grown under normal winter light conditions. It might be that the extra illuminated plants have relatively more chlorophyll. So chlorophyll content of leaf disks of extra lighted (+L) and not extra lighted (-L) plants was determined.

Leaf disks of both groups were put into boiling water for 20 seconds, extracted in 90% alcohol at 60–70 °C in a test tube. Then 3–4 cc alcohol was added and after three minutes the liquid was poured through a filter into another test tube. This action was repeated until the extract was colourless. After making up to a certain volume the density was measured.

Plant material from plants sown October 8 was used. On December 14 and 19 and January 5 leaf disks were taken. Half the amount of each group was used for dry weight determinations, the other half for chlorophyll measurements. The relation between dry weights was $+L/-L = 1.63 \pm 0.085$, between chlorophyll amounts $+L/-L = 1.69 \pm 0.061$. Because these figures do not differ, the conclusion must be that the amount of chlorophyll in the leaves of plants growing in different light energies is the same when expressed on a dry weight base. The darker colour will be the result of thicker leaves with more chlorophyll in the same leaf area.

The dry weight contents of the disks for the +L and -L plants were 12.6 ± 1.10 and 9.0 ± 0.34 , showing less dry matter in the leaves of the -L plants, the same as was found on this page for the above ground parts of the plants.

Summarizing, it can be said that plants receiving more light energy show a higher dry weight content, a heavier weight of the same leaf area, but a similar chlorophyll concentration. Whether this is the result of stronger light, longer light or a combination of these two cannot be told from this experiment.

Branched clusters – On page 180 it was shown that branched clusters have more fruits than single ones. The fruits of branched clusters may be smaller, but the yield is larger, mostly about $1\frac{1}{2}$ times as large, so branched clusters are desirable.

In experiments XII and XIII a, b and c (see p. 202) the influence of the extra

TABLE 16

Percentage of branched first clusters with (+L) or without (-L) extra light before planting

	Experiment XII	Experiment XIII a, b and c
+L	33	28
-L	7	12

light before planting on the appearance of branched first clusters was studied. Table 16 gives the results, showing a larger percentage of branched clusters on the extra lighted plants. So extra illumination may be one cause of more branched fruit clusters.

Habit of the plant – To show the influence of the extra light before planting in connection with more or less natural light, reference is made to photographs 2 a and b (see at the end). In each photograph the left two plants received 15 hours extra TL tube light, the right two plants receiving normal daylight. The extra light was the same in each case, the difference being the time of the year the plants grew. Picture 2a shows plants sown on October 8, photographed on December 12, plants in picture 2b were sown on November 14 and photographed on January 12. The age was nearly the same in the two cases, the natural light, however, was much stronger in the first case, showing less differences between the extra and not extra lighted plants than are found in the second case where the plants received less natural light. The growth habit of the plants of the first group is much better too.

3.3.2. Older plants

Description of experiments XI, XII and XIII – In experiment XI the influence of extra artificial illumination was studied. The extra light was given to increase the weak natural light and to have a light exposure longer than the normal one. Sixteen hours light were applied with 4 TL fluorescent tubes, 4×40 watt per m^2 . Seed of the variety Ailsa Craig was sown on November 18. The extra illumination was started on January 9. The lights were on from 4 A.M. till 8 P.M. daily. After planting on February 2 the extra light was continued. It was soon found, however, that the lamps and the frames in which they hung gave too much shade, so that the extra light was injurious rather than beneficial to the plants after planting.

In experiment XII the extra light was given only from sowing to planting. Five TL tubes were used instead of 4. During the night white paper above the tubes reflected as much light on the plants as possible. The extra illumination of 16 hours a day started as soon as the first leaves were visible after sowing on November 30. Planting was done on January 4. This time the variety Potentaat was used.

Experiment XIII done with the variety Dominant can be divided into three groups (*a*, *b* and *c*) based on time of sowing. Part of the plants had extra light till planting (+L), as in experiment XII. They had 15 hours a day instead of 16. In groups *b* and *c*, however, a few additional plants continued to receive extra illumination even after planting with 450 watt high pressure mercury lamps HO 2000 (++L). These lamps do not give much shade. Seven plants were illuminated by one lamp.

A survey of the dates is given in table 17.

TABLE 17. Summary of the dates of experiment XIII

	Group <i>a</i>	Group <i>b</i>	Group <i>c</i>
sowing	26/8	8/10	14/11
planting	19/10	7/12	12/1
+ L illumination until	19/10	7/12	12/1
++ L illumination until		8/3	1/4

Planting after the shortest day – The influence of extra light 16 or 15 hours a day even after transplanting (experiment XI) or only until transplanting (experiments XII and XIIIc) can be seen from table 18.

TABLE 18

Influence of extra light with TL tubes on number, mean weight and total weight of fruits up to a given date, expressed as percentages of the controls (+L/-L \times 100)

Experiment XI				Experiment XII				Experiment XIIIc			
Date	Num- ber	Mean weight	Total weight	Date	Num- ber	Mean weight	Total weight	Date	Num- ber	Mean weight	Total weight
9/6	101	100	101	4/6	641	47	307	6/6	1450	51	736
19/6	133	77	101	14/6	239	65	153	12/6	129	100	127
28/6	103	83	84	24/6	130	78	102	4/7	119	98	117
12/7	101	80	82	4/7	110	81	90	18/7	110	90	99
26/7	92	85	79	14/7	103	86	87	1/8	108	90	97
9/8	88	88	77	19/7	102	83	86	14/8	100	93	94

This table gives the fruit yield up to the given dates in number of fruits, mean weight of one fruit and weight of all fruits together. The results of the extra lighted plants (+L) are expressed as percentages of the controls which had no extra light (-L).

Plants of these three experiments were all planted in January–February, so light energy increased every day.

Experiments XII and XIIIc both show the influence of the extra light on earliness. The yields in the first harvest periods are much larger. The average fruit is smaller, because the fruits of the lighted plants have to grow in more unfavourable light conditions on account of earlier flowering.

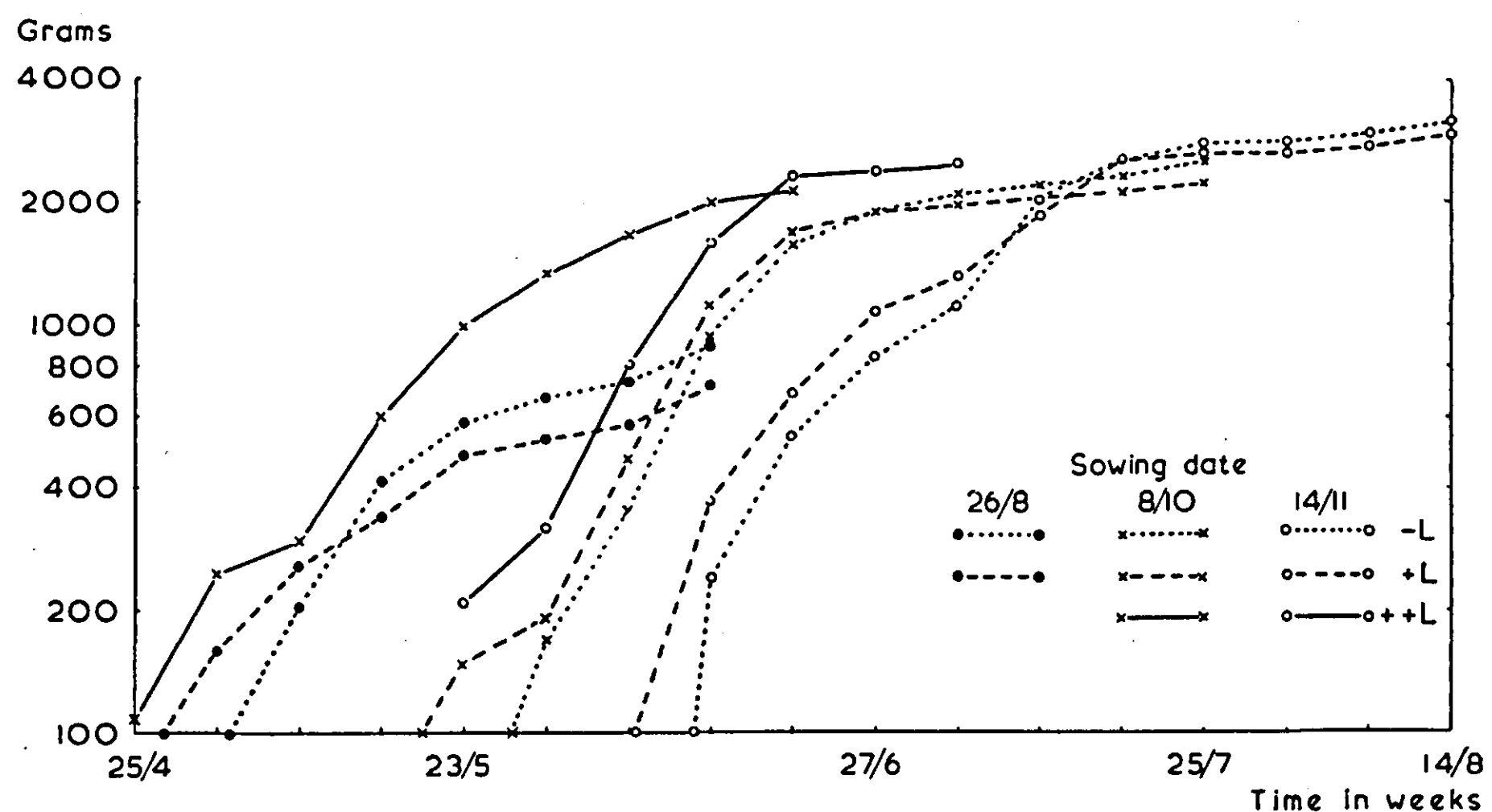
In experiment XI, however, there is no earlier yield from the lighted plants because the lamps, which were over the plants after planting, gave too much shade. Only on June 19 a larger number of fruits was picked, probably as a result of the earlier flowering of the lighted plants. In all cases the total yield of the lighted plants was less than from the controls. The explanation for this certainly must be again that the earlier flowering and fruiting plants (the lighted plants) had to develop fruits in a period with less light than the controls.

The results obtained with extra lighted plants will differ from year to year, the natural illumination being different every year.

Planting before the shortest day – In experiment XIII (see description on p. 202) the variety Dominant was used. Most outstanding in this experiment was:

- Part of the plants (group *a*) was planted before the darkest part of the year (see graph 14) and consequently the growth during winter could be studied.
- Part of the plants (++L) had extra light of 15 hours a day by high pressure mercury lamps even after being planted in the greenhouse. These lamps do not give much shade, so the difficulties from having too much shade from the lamps which were found in experiment XI were avoided here.

The yield of the different treatments is given in graph 16. On the y-axis a logarithmic scale is used to show better the small differences in early yield.



GRAPH 16
Yield in grams per plant without (-L) or with (+L) extra light before planting, or with extra light also after planting (++L). Logarithmic scale on the y-axis.

Comparing the +L and -L groups the same result is found as on page 203. The later the sowing of a group, the better the natural light conditions and the higher the yield. The groups receiving extra light even after planting were very much earlier than the other groups of the same sowing date, even earlier than the groups sown about five weeks earlier. Even though much earlier, the mean fruit weight was much higher (see table 19). Plants of group *a* planted on October 19 have much smaller fruits than the other groups. Furthermore, plants of group *a* grew fast, length growth being mostly dependent on temperature (compare p. 199), stems were thin and the colour of the leaves light green.

TABLE 19. Mean fruit weight in grams of the first 10 fruits per plant

Group	<i>a</i>		<i>b</i>			<i>c</i>		
Light	-L	+L	-L	+L	++L	-L	+L	++L
Mean fruit weight in g	28	26	44	47	75	48	45	100

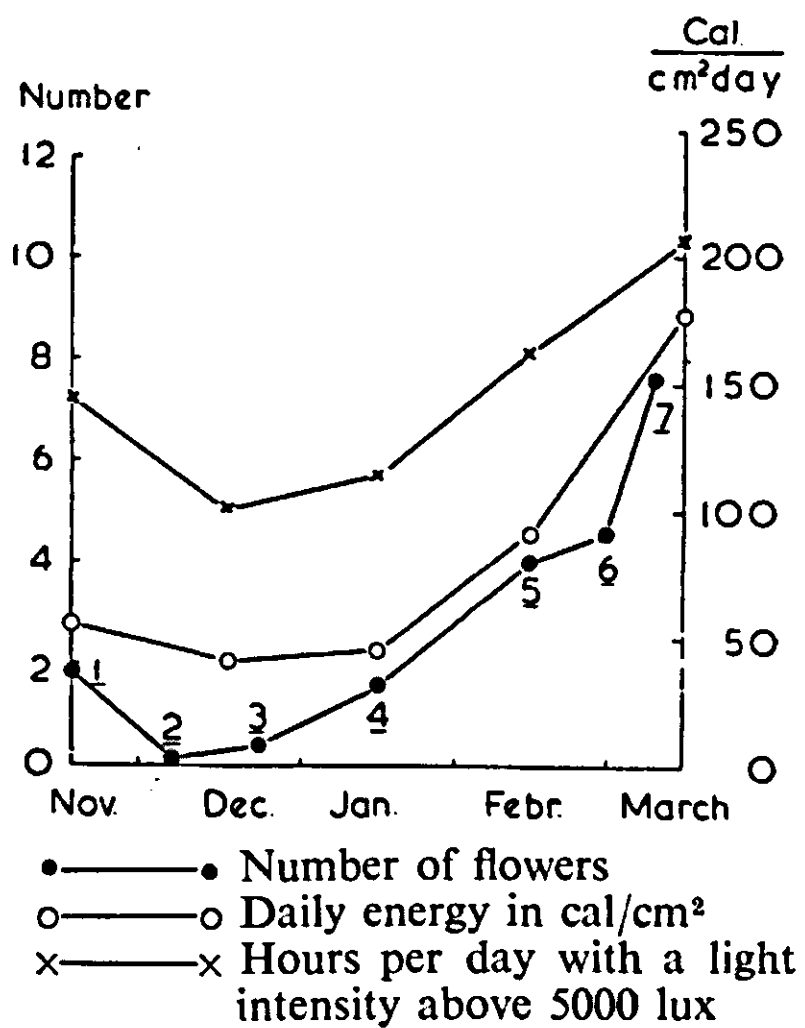
For a while after transplanting in the latter part of October and the first part of November some flowering occurred, the number of flowers, however, decreasing with decreasing light and increasing with increasing light (see graph 17). This was so striking that an effort was made to find a connection between:

- a) the number of flowers on each cluster resulting in fruits,
- b) the mean daily energy in cal/cm² outdoors,
- c) the mean number of hours per day having a light intensity above 5000 lux, this being an arbitrary value giving a light intensity of 2000–3000 lux in the greenhouse.

Graph 17 shows the close parallelism between the three values.

During the first part of February a reasonable number of flowers was again found in group *a*. In the meantime in the other comparable groups (*b* and *c*) hardly any flowers were present. This is probably the result of the large amount of leaves in group *a* which formed a much bigger photosynthetic apparatus than the other groups had.

Several times flowers were marked to find the time of fruit development from flower to ripe fruit. For a fruit set before winter one example took 166 days, whereas only 82 days were required in one of the groups in which light was continued after planting in the hothouse. In summer it takes a little over two months. The differences found here are certainly not the result of different temperatures, as it was in the experiment described on pages 183 to 192, but of the big differences in light energy received by the plants bearing the fruits under different circumstances.



GRAPH 17
Connection between a) number of flowers in each cluster resulting in fruits (cluster number underlined), b) the mean daily energy in cal/cm² outdoors and c) the mean number of hours per day having a light intensity above 5000 lux.

4. TEMPERATURE AND LIGHT

4.1. Introduction

In the chapter describing the influence of temperature on growth it was impossible not to mention the part that light played in the differences found between summer and winter crops. In this chapter the relation between temperature and light intensity will be discussed in more detail.

4.2. In artificial-light rooms

At constant temperature – As was demonstrated before (table 12 on p. 198), in artificial light of relatively low light intensity the results obtained at 17 °C were much better than those at 23 °C, showing that with insufficient light the lowest of the two temperatures gives the best results.

4.3. In greenhouses during winter months (experiment XIV)

Introduction – During winter in Pasadena the variety Tuckqueen was used to carry out an experiment with two light intensities: natural light (1L) and $\frac{2}{3}$ L. Daylight lasted 8 hours a day.

Temperature treatments were:

day	23 °C	23 °C	23 °C	17 °C	17 °C
night	23 °C	17 °C	10 °C	17 °C	10 °C

In winter the natural light intensity in Pasadena is on the low side for fruit production (compare p. 193) so that it could be expected that a light reduction to $\frac{2}{3}$ would have a considerable influence. In summer the influence of the same reduction would have only a minor effect.

Plants of this experiment were sown on November 1, divided November 10 over the treatments, while 8 plants were discarded on December 10 and 4 plants on December 30.

Results – The results will be shown with the help of three-dimensional graphs 18a–f, the solid lines showing the values for 1L, the dotted lines for $\frac{2}{3}$ L. These graphs show only the relative values of the different treatments on both dates.

The following items have been studied:

- a) Stem length – On December 10 at higher temperatures longer plants were found again regardless of whether day or night temperatures were higher. Only at $\frac{2}{3}$ L 23–23 shows much less growth than at 1 L, the other values for the length being practically the same for 1 L and $\frac{2}{3}$ L. So the greatest difference between 1 L and $\frac{2}{3}$ L is found at the highest night temperature. The same was true on December 30; here the 23–23 is not only shorter at $\frac{2}{3}$ L, but also at 1 L. The length is mainly influenced by temperature (compare p. 199). However, if light is too weak, the higher temperature group, in this case 23–23, is shorter than the lower temperature groups, so the high growth rate that would be expected at the high temperature cannot be maintained.
 - b) Total dry weight – For 1 L the total dry weight shows a picture nearly the same as was found for the stem length. Differences caused by the different light intensities on dry weight are much larger than on stem length. $\frac{2}{3}$ L shows a greater difference from 1 L at a higher temperature. With increasing time the differences become larger.
 - c) Leaf area – Because the leaves are the most important parts for photosynthesis, their area was studied. The leaf area data showed nearly the same picture as that for dry weight. Reduction in leaf area under reduced light was much less, however, than the reduction in dry weight. Again the reduction became larger as the temperature became higher.
 - d) Sturdiness of stem – The data for sturdiness of stem, a figure obtained by dividing stem weight by stem length, are shown in graph d. Bigger differences are found as a result of different light intensities than as a result of different temperatures. This is just the opposite from what was found for the length of the plants, where the temperature was the main factor.
- On December 30 for both light intensities the sturdiest plants were found at the lowest night temperature which was 10 °C. Again the reduction caused by low light intensity is less at the lower temperatures than at the higher.
- e) Weight of approximately 19 cm² leaf area – Because this item did not differ much with time only the mean of the values obtained on the two dates is given in graph e. Comparing the weight of the same leaf area in the different treatments, the smaller reduction caused by light differences is again found at the lower temperatures and the heavier leaf disks are found there also.
- At lower temperatures the leaves are thicker and a reduction in light intensity has relatively less influence than at higher temperatures.
- f) Fresh weight of the first cluster on December 30 – On December 30 the 17–10 treatment did not yet show a cluster. The influence of light as well as temperature on the weight of the cluster is enormous. The lowest temperature treatments showed by far the biggest clusters. The light reduction had a big influence on reduction of cluster weight. The influence again being relatively

smaller at the lowest temperatures. The lower the night temperature, or the larger the difference between day and night temperature, the bigger the cluster.

Lower temperatures result in better plants, which grow slower, but have thicker leaves and stems and much heavier clusters. If the winter light in Pasadena, which is already weak, is further reduced, it is still more important to have low temperatures and to have a night temperature lower than the day temperature to get a reasonable cluster development.

If temperatures are too high at a low light intensity no cluster will be found at all.

CHAPTER III

GENERAL DISCUSSION

1. INTRODUCTION

In the experimental part the growth of tomato plants under different temperature and light treatments was studied and described. Not only the length growth and increase in total dry weight are important, but also the distribution of the material over the different plant parts such as stems, roots, leaves and clusters.

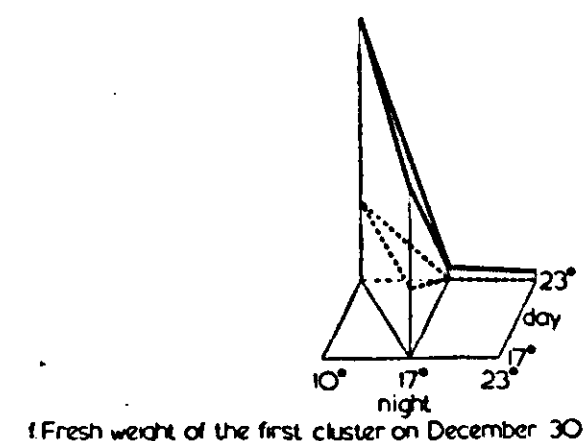
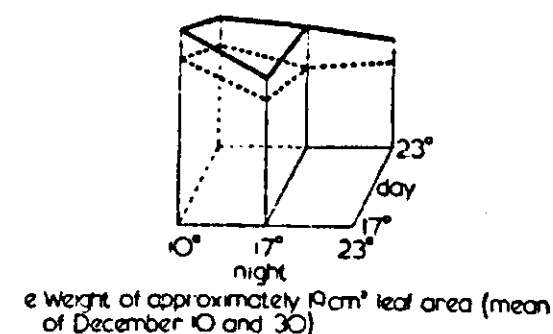
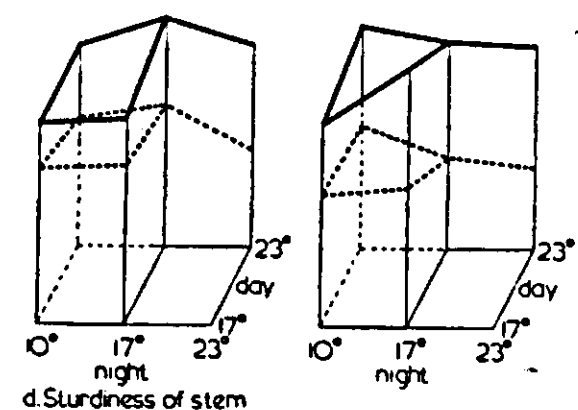
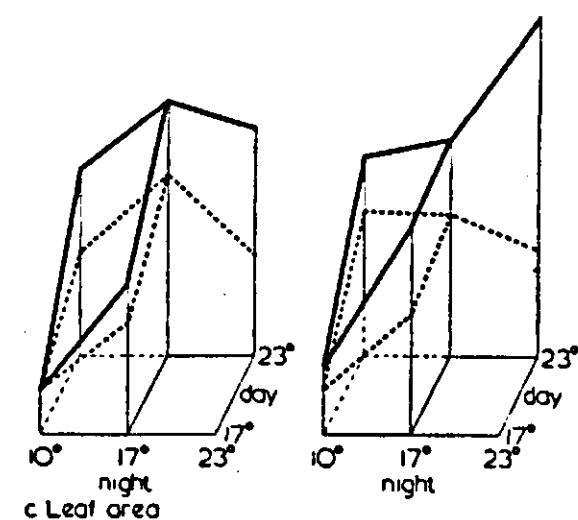
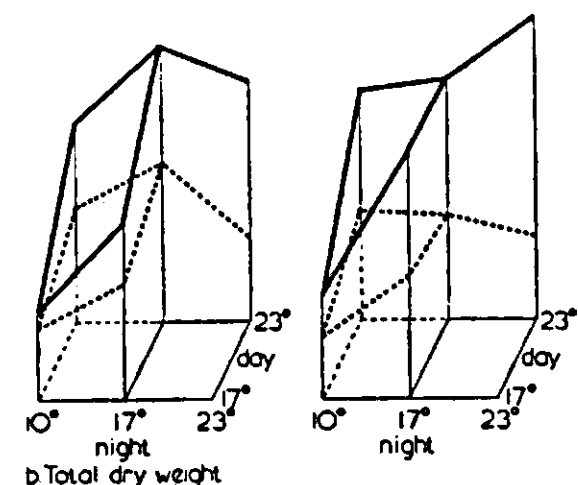
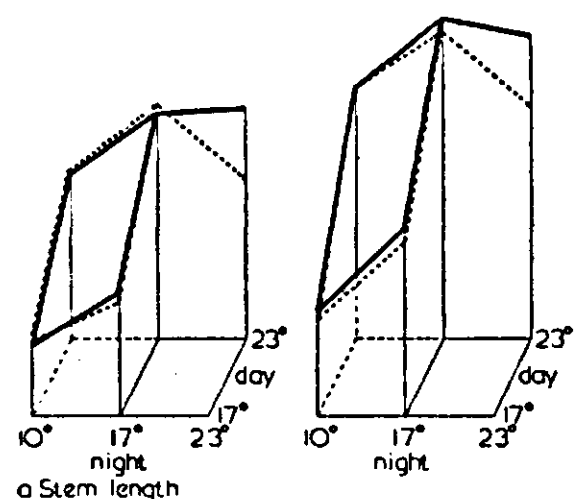
We shall now first discuss the influence of temperature on growth. Next the influence of photosynthesis, respiration and transport of carbohydrates on growth in connection with temperature and/or light differences will be considered and finally the different combinations of these factors.

These three processes are chosen because experiments were carried out with:

- different light energies, which strongly influence photosynthesis;
- different temperatures, which strongly influence photosynthesis and respiration, while to make growth possible transport of carbohydrates is necessary to bring material from the leaves to other parts of the plants.

GRAPHS 18 a-f

Relative values of the variety Tuckqueen grown at temperature combinations 23-23, 23-17, 23-10, 17-17 or 17-10 and light treatments 1L (continuous line) or 2/3L (dotted line). Left on December 10, right on December 30.



2. GROWTH

Growth, being the result of many processes each dependent on temperature, is strongly influenced by temperature.

2.1. *Vegetative growth*

In most cases at higher temperatures faster elongation of the *stem* was found than at lower temperatures within the used temperature range of 4–30 °C (see pp. 181 and 185, graph 3 on p. 181, graphs 6 a–f on pp. 188–189, table 8 on p. 193, graph 18a on p. 207 and literature 24, 39, 48, 66, 93). At higher temperatures the stem was thinner [(24, 39, 90) and as a result less mean dry weight of a 1 cm piece of stem was found at higher temperatures than at lower ones (compare p. 182, table 8 on p. 193, table 9 on p. 195, table 10 on p. 196). Stems grown at higher temperatures had relatively more pith and less xylem and phloem than stems grown at lower temperatures (41).

The influence of temperature on the *leaves* is similar. Length growth measurements were not taken. However, it was found that the same leaf area weighs less at higher temperatures than at lower ones (table 8 on p. 193, table 10 on p. 196 and graph 18e on p. 207), the leaves are thinner and weaker (6); the colour is lighter (24, 91, 93). A lower percentage of dry matter was not found convincingly, although FOSTER and TATMAN (24) do say so. In potatoes, also, it was found that at higher temperatures the leaf colour was lighter (19).

The amount of *root* system produced in a given time weighs less at higher temperatures than at lower temperatures (p. 182) and the ratio of the weight root/stem is lower at higher temperatures than at lower ones (see table 8 on p. 193 and literature 93).

2.2. *Generative growth*

It was found that at higher temperatures the fruits, like the stem, grow faster; the time elapsing between anthesis and ripe fruit will be shorter than at lower temperatures (graph 8 on p. 187 and literature 90, 95). As a consequence, the harvest is earlier at higher temperatures (graph 5 on p. 183, table 4 on p. 186 and graphs 7 a–f on pp. 188–189).

On the other hand it was found that at higher temperatures, in comparison with lower ones, the clusters themselves (without fruits) are shorter and not so heavy (graph 4 on p. 183, table 9 on p. 195, table 10 on p. 196, graph 18f on p. 207). The number of buds formed on the clusters is smaller, and so is the number of opening buds and the number of flowers giving good fruits (graph 4 on p. 183 and literature 90 and 93). As a result of this the fruit yield is lower at higher temperatures (graph 5 on p. 183, graphs 9a–f on pp. 188–189 and literature 5, 24, 69, 85).

From the work of OSBORNE and WENT (68) the conclusion can be drawn that fruits grown at higher temperatures are smaller than those grown at lower temperatures. At the highest night temperature treatment the smallest fruits were found (p. 182), and indication of the same effect of temperature on the individual fruit weight.

Fruit set and temperature – Normal fruit growth is only possible after fertilization which follows pollination with viable pollen. The time which elapses between pollination and fertilization at normal greenhouse temperatures may be two to three days (37, 82). It can be expected that if the temperature is rather low the pollen tube growth is too slow to reach the egg cell in time for fertiliza-

tion. SMITH (82) found a very slow pollen tube growth in vitro at 10 °C. WHITE (97) found no fruit set at a night temperature of 4–7 °C, a good fruit set at 13–15 °C night temperature. ODLAND and CHAN (67) found less and less fruit set as the number of nights the plants received a temperature of 4,5 °C increased. Only at night temperatures lower than 15 °C a good effect of hormone sprays was found, because at those low temperatures the natural fruit set was inadequate. WENT and COSPER (95) had no fruit set below 13 °C; at least 5 successive nights with a temperature above 12–14 °C were necessary to get good fruit set. OSBORNE and WENT (68) found a fruit set at 10 °C of only 29 %, with the use of hormones this was brought up to 73 %. This proves that the plant is capable of producing fruits of normal size at low temperatures, providing that hormones are used to start fruit growth when normal fertilization is inadequate.

In the summer experiment in the greenhouses (pp. 183–192) the fruit set (average of all six varieties) at the lowest temperature combination 17 °C day and 11 °C night, was only 25 % (p. 187), notwithstanding a good cluster growth. In the artificially lighted rooms with 16 hours light per day at 7 and 10 °C day temperature no fruits were formed, however these groups had the largest clusters (table 10 on p. 196). This heavy cluster growth at these low temperatures does not indicate a shortness of carbohydrates for fruit growth, especially because hormones, as said above, can improve the number of fruits set enormously at low temperatures.

The conclusion of LEARNER and WITTWER (48) was that the lowest temperature for tomato production is delimited by the lowest temperature for good fruit set, if no hormones are used.

2.3. *Carbohydrates*

Not many carbohydrate determinations were made (graph 12 on p. 191). However, the impression was gained that at higher temperatures less total sugars were present in the same leaf area than at lower temperatures.

In the literature the following points were found in this connection. Under circumstances which slow down growth such as low temperatures, dry soil or low nitrogen level of the soil, the carbohydrates (starch and sugars) in the plant are increased (24, 41, 47, 62, 66, 87, 93, 96). CURTIS and CLARK (21) assume in such cases a better root growth which was indeed found (p. 182). In potatoes at higher temperatures less sugars were found in the leaves (19).

At low temperatures in many cases a purple colour in the stems was found as a result of anthocyanin synthesis, in several occasions found to accompany high sugar content (10).

2.4. *Balance between vegetative and generative growth*

It was described in the preceding pages that at higher temperatures in comparison to lower ones, growth is faster, starch and sugars are less, stems and leaves are thinner, roots lighter, and the clusters less well developed, which results in a smaller, but earlier yield.

A negative correlation between yield and temperature and a positive one between growth rate and temperature were found. Consequently a negative correlation between yield and growth rate exists (p. 190). Sometimes this negative correlation is called the opposition between vegetative and generative growth (102). It seems better to speak of a balance in this case. The environment, for example temperature, will decide if the balance lies more on the vegetative or

on the generative side. Connected with a fast growth, hence at high temperatures, the balance is more on the vegetative side (30), with slow growth, hence at lower temperatures, it will be more on the generative side and the yield will be higher but later, provided that the temperature is not too low for good fruit set (see p. 209).

A special case of this balance, influenced so sharply by temperature, was found in England. With the same light intensity a lower temperature during the growth of the small plant, especially during the initiation of the first cluster, will result in more flowers on that first cluster (20, 40, 42, 50, 51). Thus the same was found both for the first cluster in the seedling stage and for the whole growth of five clusters.

3. GROWTH AND PHOTOSYNTHESIS

3.1. *Introduction*

Photosynthesis is the important process in which organic matter is made. Light is the energy source for this process.

If light is strong, the optimum temperature for photosynthesis is rather high, if light is weak the optimum temperature is much lower (8, 14, 56, 93).

On page 196 and in graph 14 on p. 196 are shown the difference sunlight energy throughout the year in the Netherlands. It is not surprising that in the darkest time (graph 14 between the vertical broken lines) growth of plants is bad. It is necessary that for an early tomato crop the seedlings are raised early, during this dark period. The knowledge of the influence of light on the plants could help this early seedling growth.

3.2. *Extra light in winter*

Much effort has been made to provide the seedlings with extra light during the dark winter period [(pp. 200–205 and literature 11, 12, 43, 44, 45, 46, 52, 53, 67, 77)].

At first an illumination during part of the night when the electric current was cheap was tried. In this way, however, more than one light and dark period in 24 hours occur and the tomato plant cannot stand this, no more than a light period longer than 18 hours a day. In such cases the leaves will show yellow spots and their activity will decrease. Only at rather low temperature (below 13 °C) this phenomenon will not show up (3, 33, 35, 46, 58, 77, 79, 86, 100). In our work no spots on the leaves were found with 24 hours of artificial light a day at 10 °C or lower, but spots occurred after about three weeks at 14 °C or higher.

After this discovery extra light was given directly after sunset or before sunrise, hence the weak day light is lengthened with artificial light. Some workers, as was done in this work also, gave extra light during the dark days, providing a long day with not too weak light. In the conviction that the tomato plant carries on photosynthesis only in the morning, which does not seem probable if light conditions are not very good (compare p. 216), REINDERS-GOUWENTAK and SMEETS gave artificial light at daytime only for 7–8 hours a day (74, 75). In experiment XIII during the dark time of the year extra illumination after planting was successful (graph 16 on p. 204).

3.3. *Vegetative growth*

If the light intensity is already low, still lower intensities will always produce a slower *stem* growth (table 11 on p. 197, literature 12, 23, 52, 53, 79, 83). If the

light intensity is not too low a small reduction will cause a faster stem growth (table 11 on p. 197, literature 70, 81). In both cases, however, light reduction gives thinner stems with less mean weight per cm with a relatively broad pith and small xylem and phloem tissue. The cell walls are thinner too (23, 70, 81). The stem will form a relatively larger part of the plant (table 11 on p. 197 and literature 9).

Less light produces thinner *leaves* (70, 81), paler green instead of dark green (12, 23, 47, 54, 86), more intercellular space; the same dry matter is spread over a larger area (table 11 on p. 197, table 12 on p. 198, table 15 on p. 200); the dry matter content is lower (table 11 on p. 197). As with stem length, a small light reduction, if the initial light is strong, will give a larger leaf area; if the light is already weak it will result in a smaller leaf area; the ratios: leaf area/plant weight and leaf area/leaf weight will be higher in reduced light (table 11 on p. 197 and literature 9).

With less light the *roots* are relatively smaller in nearly all cases (70, 79). Also root formation on cuttings from plants in winter without extra light was poor in relation to root formation of cuttings from extra lighted plants (59, 72, 73).

On the other hand, starting with the weak winter light, extra illumination will result, in most cases, in speeding up growth and will give sturdier plants, which are also much heavier (tables 14 and 15 on p. 200, literature 47, 58, 86).

3.4. *Generative growth*

More light during the whole growing season of the plant will result in a larger yield (compare summer pp. 183-192 and winter pp. 192-194 experiment), and with more light the cluster growth is better (table 11 on p. 197, table 12 on p. 198 and graph 15e on p. 199, graph 18f on p. 207 and literature 23, 70, 81, 90). HEMPHILL and MURNEEK (31) found a nice positive correlation between the light energy received from the first flower till the last picking date and yield among crops in different times of the year; while WITTWER (101) stated that the autumn crop received only $\frac{1}{2}$ of the light energy and the yield was about $\frac{1}{3}$ compared with the spring crop, hence in the autumn crop with less light, relatively more material is used by respiration and probably by vegetative growth too (compare p. 213). Our research showed a good correlation between number of flowers setting on each cluster and both the mean daily energy outside and the number of hours per day that light intensity was above 5000 lux outside at flowering time in winter (graph 17 on p. 205). It was shown that with less light the growth period for the fruits was longer (p. 205).

With extra light in winter before transplanting an earlier yield was obtained (table 18 on p. 203, graph 16 on p. 204 and literature 1, 2, 12, 30, 43, 47, 54, 58, 76, 86, 89, 98, 99). In most cases the fruits were smaller, however, and the total yield was less, but more branched first clusters having more fruits than single ones were found (graph 2 on p. 180, table 16 on p. 201 and literature 2, 4, 43). Some workers state they obtained even a higher total yield but in most of such cases the planting had been rather late (43, 55, 76).

With extra light also used after transplanting the yield was very much earlier and the fruits were much larger too (graph 16 on p. 204 and table 18 on p. 203).

3.5. *Carbohydrates*

MURNEEK (62) found after some cloudy days, hence at a low light intensity, a

was nearly always found at higher temperatures. In combination with the above mentioned work it is to be expected that transport of carbohydrates will be faster at higher temperatures, like the growth is.

On the contrary it has to be accepted that at lower temperatures transport goes on at a relatively greater rate than growth (32) and as a result of this the carbohydrates will be higher throughout the plant at lower than at higher temperatures. In connection with this at lower temperatures the balance between vegetative and generative growth shifts to the generative side in comparison with higher temperatures.

6. GROWTH, PHOTOSYNTHESIS AND RESPIRATION

Photosynthesis carried on during daytime must be enough for growth and respiration day and night.

With good light, as found in summer, a rather high temperature during daytime will be the best for photosynthesis (14) and will induce fast growth and a heavy respiration. If the night temperature is high too, growth is less than at a somewhat lower night temperature, presumably as a result of loss by heavy respiration (p. 185). On the other hand at lower night temperatures compared with higher ones growth and respiration are retarded during night, so less material is needed for these and more carbohydrates will be present, the plant will show thicker stems and leaves, the clusters will be better developed, the root system is heavier, the yield is higher but later (pp. 183, 192, 193 and 195). A night temperature lower than the day temperature was advised even as early as the 19th century and throughout the years (7, 29, 36, 61, 84, 91).

If light is less strong, as in winter time, a higher day temperature will not give a higher photosynthesis (14), while respiration and in many cases growth are still larger (pp. 193, 195 and 206). In these cases very thin leaves and stems are found and the clusters are poorly developed; carbohydrates are low. With a lower day temperature growth and respiration are less, providing a better balance between photosynthesis on one hand and growth and respiration on the other hand. Stems and leaves are thicker and clusters are better (table 10 on p. 196, p. 207). A night temperature lower than the day temperature is at least as important if not more so under poor light conditions than under good light conditions (pp. 205-207).

This balance between photosynthesis on one hand and growth and respiration on the other can also be expressed as a balance between light and temperature. The ratio light/temperature is very important and with lower light the same tendency is found as with higher temperatures.

Both have the following result on plant growth:

- a) Vegetative growth: thinner stems with less mean weight of 1 cm, more pith and less xylem and phloem; lighter leaf colour and weight of 1 cm² leaf area, lower percentage of dry matter of the leaves; root system relatively lighter.
- b) Generative growth: clusters smaller and less heavy, with less buds and fruits, smaller fruits.
- c) Carbohydrates: less starch and sugars, less anthocyanin.
- d) Balance between vegetative and generative growth: shifting towards the vegetative side.

All plant parts are thinner, feebler and less sturdy and this will be the result

of less carbohydrates available for development. LAWRENCE (43) has already mentioned this relation between temperature and light for small plants.

7. GROWTH, PHOTOSYNTHESIS AND TRANSPORT OF CARBOHYDRATES

With good light photosynthesis will be higher at higher than at lower temperatures. This will result in a larger difference between the carbohydrates in the leaves and in the other parts of the plant, consequently a faster transport can be assumed. Also the growth is faster. In the summer experiment the decrease in dry weight of leaf disks was mainly from noon till 8 P.M., hence during the second half of the light period (graph 11 on p. 191).

If light conditions are bad and photosynthesis much reduced, the transport will be retarded because the gradient will be less. In winter and in artificially lighted rooms the decrease in dry weight of the leaf disks is found during the night (graph 13 on p. 194, table 13 on p. 199).

GOODALL (27, 28) found in seedlings of about 25 cm height the biggest transport in the afternoon in summer and in the evening and night during winter.

8. GROWTH, RESPIRATION AND TRANSPORT OF CARBOHYDRATES

At higher temperatures carbohydrates are less, caused by the faster growth and respiration. In the case where the night temperature is relatively high, the respiration of the leaves can be so great, that there is not enough material left for the fast growth that would be expected at that high temperature and consequently growth is less than at lower night temperatures (table 3 on p. 185) and transport will be less too. The fact that the transport is less in such cases could give the wrong impression that transport in general is less at higher temperatures, which is not true. The cause of the smaller transport is not the higher night temperature, but the lack of material for transport and growth (see treatment 8 in table 3 on p. 185). In this connection especially the fact that the night temperature is of so great importance is because during the night there is no high photosynthesis to counteract the high respiration. It is clear that generative growth will be worse at such high night temperatures (graph 4 on p. 183, table 5 on p. 187, table 8 on p. 193).

HEWITT and CURTIS (32) found a strong increase of respired sugars at higher temperatures, a decrease in the amount of transported sugars. This could again lead to the wrong conclusion that transport in general is lower at higher temperatures. At higher temperatures the carbohydrates in the leaves were less, caused by a faster transport in connection with faster growth to a certain point. At still higher temperatures, however, the respiration was so high that the material for faster growth and transport was lacking and both will be less than at lower temperatures: the respiration is relatively too great.

BUSHNELL (19) working with potatoes, had about the same results. The carbohydrates used for respiration at 20–23–26–29 °C were 54–64–81–94 % respectively of the total carbohydrates which disappeared from the leaves during the night. For growth and transport there remained only 46–36–19–6 % respectively. Plants at higher temperatures had a lower carbohydrate content. Tuber growth was worse with higher temperatures.

Instead of tuber growth, in tomatoes the generative growth has to be considered. At higher (night) temperatures clusters are smaller and the yield is smaller.

A very characteristic passage of the work of BLACKMAN (8 p. 293) may be cited here:

'To take the hypothetical case that translocation could just bring in, per unit-time, enough carbonaceous material for the growth at the optimal temperature *plus* the respiration at the same temperature. Then, as the temperature rose further and the respiration increased *faster and faster*, so necessarily there would be *less and less* carbon material available for growth'.

At lower temperatures on the other hand transport will be retarded relatively less than respiration and growth, and carbohydrates will increase (compare p. 214).

9. GROWTH, PHOTOSYNTHESIS, RESPIRATION AND TRANSPORT OF CARBOHYDRATES

During the light period photosynthesis takes place, while during the light and dark period respiration and growth go on. To make growth possible transport of material from the leaves formed by photosynthesis is necessary.

Studying the dry weight changes of leaf disks during 24 hours (p. 190) may give a deeper understanding of what is going on. Table 20 gives the relative weight with intervals of 4 hours during 24 hours for the summer (pp. 183–192) and winter (pp. 192–194) experiment, and for the experiment in the artificially lighted rooms with 16 and 8 hours light (p. 199). Besides that the mean dry weight in mg of 26 cm² leaf area is given.

TABLE 20

Dry weight of leaf disks with intervals of 4 hours during 24 hours expressed in percentages of the minimum value and mean dry weight of 26 cm² leaf disks in mg at different light energies

Time in hours	0	4	8	12	16	20	24	Mean dry weight of 26 cm ² leaf area
Summer	100	102	111	111	107	103	100	85.8
Winter	109	100	100	109	112	109	109	43.8
16 hours artificial light	100	100	102	104	112	100	100	51.5
8 hours artificial light	100	103	109	100	100	100	100	31.6
	<i>light period</i>							

It is clear that with more light the dry weight of a certain leaf area is heavier. This may be considered as an adaptation to weak light so that with less light the same material will be spread over a larger area. A thick leaf with feeble light will be uneconomical because the light will not penetrate far enough into the leaf to give as much photosynthesis as could be made with the same thickness of leaf with more light.

As far as the course of the dry weight during 24 hours is concerned, the data show that this increases during daytime, decreases during the night. The differences between lowest and highest values are 9–12%. This is the result of photosynthesis for the increase on one hand and respiration and transport necessary for growth on the other hand. As soon as enough light for photosynthesis comes on the leaves they will increase in weight. In all cases where the light was weak, the highest value for the leaf disks is found at the end of the light period. This shows that with rather weak light it is advisable to have light

on the plants as long as possible, provided that it is not longer than 18 hours a day (compare p. 210).

In summer, however, with strong light giving a good yield, the highest value (111 %) is found rather early in the light period instead of at the end. It may be concluded that after the dry weight has increased to a certain level by photosynthesis transport starts, or, if transport began earlier, it increases to a level as high or higher than photosynthesis. The first assumption is more acceptable. Graph 12 on page 191 shows that sucrose, in which form the transport takes place presumably, is not high in the morning but in the afternoon, hence in the same time that the dry weight decreases fast. It is low in the morning, when photosynthesis but not much transport is presumed (92, 96).

What is found here is the apparent photosynthesis, which is lower at weaker light because the 100 % value is lower then. Consequently the produced material is less with feebler light (table 11 on p. 197, graph 18b on p. 207). In such cases with less light the balance between vegetative and generative growth shifts to the vegetative side (graph 18f on p. 207).

In the artificially lighted rooms a steady increase in weight of the leaf disks during the light period is found and a sharp decrease in the first four hours of the dark period. While in the 16 hours treatment the dry weight increases to 112 %, in the 8 hours treatment this is only to 109 %; the 100 % being about 5/3 times as heavy in the first case. It is not surprising that in the 16 hours treatment stems and roots are more than twice as heavy as in the 8 hours treatment.

BOLAS *et al.* (15, 16, 17) and GOODALL (28), who worked with plants of about 25 cm height and who measured the apparent photosynthesis and determined the changes in dry weight of different plant parts, showed that in summer most of the transport took place during the afternoon and some in the evening. In winter, with weaker light, however, most of the transport took place during the night. So this is in good agreement with the findings described above.

The percentages of dry matter in the same leaf disks (see p. 216) are given in table 21. In the summer experiment with normal light this was $2.4 \pm 0.37\%$ higher than in the winter experiment, while with the light reduced from 1 L to $\frac{2}{3}$ L (p. 205) the difference was $1.0 \pm 0.26\%$. With less light relatively more water is found not only in the leaves, but also in the other parts of the plant (table 15 on p. 200 and literature 14, 57, 65).

TABLE 21

Percentages of dry matter in leaf disks with intervals of 4 hours during 24 hours at different light energies

Time in hours	0	4	8	12	16	20	24	Mean
Summer	12.7	12.8	14.0	14.0	14.0	13.6	12.7	13.5
Winter	10.7	10.4	10.1	12.0	11.8	11.0	10.7	11.0
16 hours artificial light	10.8	11.1	11.6	11.4	11.8	10.9	10.8	11.3
8 hours artificial light	10.7	9.7	10.5	10.7	11.0	10.7	10.6	10.6
	<i>light period</i>							

The course of the dry weight percentages shows a great conformity with the course of the actual dry weights (table 20 on p. 216), giving more water in the

plant at the time that the dry weights are low. The treatment of 8 hours artificial light forms an exception. MELVILLE (57) found the same and assumed that the high water content during the night is the result of loss of material by respiration and transport, the lower water content during daytime the result of faster increase by photosynthesis than decrease by other means. Leaves with a high water content are pale green, thin and have less chlorophyll. No anthocyanin is found in the stems of such plants; low water content was connected with dark green, thick leaves and anthocyanin in the stem.

On page 201 it was shown that the chlorophyll content is not different at different light energies when calculated on a dry weight base. It, however, runs parallel to light energy when calculated on leaf area base (80).

At high light intensity a rather high temperature will give optimum photosynthesis, notwithstanding this, a lower yield was found at higher temperatures probably as a result of the fast vegetative growth and respiration at those high temperatures.

If light intensity is less, the optimum temperature for photosynthesis is lower and when the temperature is high the apparent photosynthesis is lower than at lower temperature. As the total light energy becomes less, the maintenance of a good temperature becomes increasingly more important (compare summer experiment on pp. 183-192 with experiment with reduced light intensity in winter on pp. 205-207). The lower the temperature the less relative disadvantage the plant has from light reduction and the less the generative growth will be decreased.

If, however, light energy is very low, as it is in the Netherlands during the darkest time of the year (compare graph 14 on p. 196), temperature that would be low enough for a good cluster growth is too low for growth at all and in such cases supplementary light is necessary. If light energy is somewhat more, good but slow growth, also cluster growth can take place, but still the temperature will be too low for normal fruit set (p. 209).

Light is increasing every day in spring, and so it is advised to get, by maintaining a low temperature, a good growth of the first cluster in early spring. Some time before flowering temperature has to be raised in the right balance to the higher light energy to get normal flowers and fruit growth. This regulation requires a great deal of growers experience and even then it is very difficult to get a good cluster with normal fruits in a spring crop.

10. ADDITIONAL REMARKS

In many cases fairly constant experimental conditions were available and the influences of different temperatures and/or light energies on the growth were studied. In normal growing temperature and light are changing continuously, but it can be expected that the influences found in this work for longer times of exposure will give a deeper understanding of what to do in so far as regulation of temperature and/or light is possible.

The discussions, referring to the tomato plant, certainly can be applied to a great number of other plants, with some slight changes.

SUMMARY

I. To obtain an early crop of tomatoes it is necessary to raise the seedlings in the darkest time of the year when the light energy is too low for good growth. A good understanding of light influences on growth could help the early tomato growing. It is impossible to study the effect of light without paying attention to temperature. Hence temperature and/or light influences on growth were studied.

II. 1. Experiments were carried out in:

- a) the Earhart Plant Research Laboratory of the California Institute of Technology in Pasadena, California, U.S.A., where rooms with constant temperature and with natural or artificial light are available;
- b) heated greenhouses of the Horticultural Laboratory of the Agricultural University of the Netherlands, where strict temperature control was impossible and natural greenhouse light was used most of the time, sometimes supplemented during the darkest time of the year by artificial light.

II. 2. Under good light conditions at higher day or night temperatures or at higher mean temperatures in comparison to lower ones in general the following results were obtained: faster stem growth, faster growth of the fruits, earlier fruit yield, less fruit capacity, less number of fruits, less weight and length of clusters, lower fruit yield, and less heavy roots, stems and leaves. Dry weights of leaf disks showed a rise during the first half of the light period and a decrease during the second half of this period. The optimum temperatures for moderate growth and a high fruit yield were 20–23 °C during the day and 11–17 °C during the night. The night temperature had to be at least 6 °C lower than the day temperature.

Six varieties were used and these only showed minor differences in reaction to temperature.

If light intensities were lower, as in winter and in the artificially lighted rooms, temperature effects were less pronounced, because small differences in light intensity had big influences. Under weak light dry weights of leaf disks rose during the whole light exposure and decreased during the dark period.

II. 3. Light influences were studied by supplying different light intensities or day lengths. In both cases less light resulted in less total dry weight formed in the same time, thinner leaf blades, while the leaf area was less reduced than the leaf weight, paler green colour but relatively the same chlorophyll content, less dry matter. The cluster is the first thing to be considerably reduced by light reduction and consequently also the yield.

With extra artificial light in winter before planting faster growth and sturdier plants were found which flowered and fruited earlier; the total yield, however, was less than in the controls. More branched first clusters were found.

II. 4. If light intensity is relatively low, at 23 °C no fruit yield was found, at 17 °C some fruits were harvested. With weak light, temperature becomes too high at a lower level.

The lower the light, the more important the maintenance of the correct day temperature and a night temperature considerably lower than the day temperature.

III. The influence of different temperatures and/or light conditions on plant growth are discussed in connection with the influence which temperature and/or light might have on photosynthesis, respiration and transport of carbohydrates.

The similar effects of a higher temperature in comparison to a lower one and

of a bad light condition to a better one will be the result of lack of carbohydrates for sturdy growth.

Emphasis is laid on the balance between vegetative and generative growth, which is strongly influenced by the ratio light/temperature, which in itself determines the balance between photosynthesis on the one hand and growth and respiration on the other.

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SAMENVATTING

TEMPERATUUR, LICHT EN DE TOMAAT

I. Voor het verkrijgen van een vroege tomatenoogst moeten de jonge planten in de donkerste tijd van het jaar worden geteeld, als het licht te zwak is voor goede groei. Een goed begrip van de invloed van het licht op de groei zou zijn nut kunnen hebben voor de vroege tomatenteelt. Het is echter onmogelijk de invloed van licht te bestuderen zonder de temperatuur er bij te betrekken. Daarom is de invloed van temperatuur en/of licht op de groei nagegaan.

II. 1. Proeven werden gedaan in:

- a) het 'Earhart Plant Research' Laboratorium in het 'California Institute of Technology' in Pasadena, Californië, U.S.A., waar ruimten met constante temperatuur en met natuurlijk licht of kunstlicht aanwezig zijn;
- b) de kassen van het Laboratorium voor Tuinbouwplantenteelt van de Landbouwhogeschool te Wageningen, waar een nauwkeurige temperatuurregeling niet mogelijk was, terwijl van het natuurlijke kaslicht gebruik werd gemaakt, soms in de donkerste tijd van het jaar aangevuld door kunstlicht.

II. 2. Bij goed licht werd bij een hogere dag-, nacht- of gemiddelde temperatuur, in vergelijking met een lagere, gevonden: snellere stengelgroei en vruchtgroei, vroegere oogst, minder knoppen per tros, minder vruchten, lichtere en kortere trossen, lagere vruchtenoogst en lichter wortelstelsel, lichtere stengels en bladeren. Drooggewichten van bladstukjes vertoonden een stijging gedurende de eerste helft van de lichtperiode en een daling in de tweede helft. De optimum temperaturen voor een matig snelle groei en een hoge vruchtenoogst waren: 20–23 °C dag en 11–17 °C nacht. De nachttemperatuur moet minstens 6 °C lager zijn dan de dagtemperatuur.

Zes rassen werden gebruikt en deze vertoonden slechts geringe verschillen in reactie op de temperatuur.

Bij lagere lichtintensiteiten, zoals in de winter en in kunstlichtkamers, waren de invloeden van de temperatuur veel minder uitgesproken, daar kleine verschillen in lichtintensiteit relatief grote invloed hadden. Bij zwak licht ver-

toonden drooggewichten van bladstukjes een stijging gedurende de gehele lichtperiode en een daling gedurende de nacht.

II. 3. Invloed van het licht werd nagegaan door het geven van verschillende intensiteiten of daglengten. In beide gevallen betekende minder licht een geringere drooggewichtsproductie in dezelfde tijd; dunnere bladeren, terwijl de bladoppervlakte minder afnam dan het gewicht; meer bleekgroene bladeren, maar verhoudingsgewijs hetzelfde chlorophylgehalte; minder drogestofgehalte. De tros en dus ook de opbrengst wordt door vermindering van licht het sterkst beïnvloed.

Bij gebruik van extra kunstlicht in de winter vóór het uitplanten, werden een snellere groei en steviger planten verkregen, die eerder bloeiden en rijpe vruchten gaven; de totale oogst was echter minder dan van de contrôles. Meer vertakte trossen werden gevonden als gevolg van de extra belichting.

II. 4. Bij een betrekkelijk lage lichtintensiteit werden bij 23 °C geen vruchten gevormd, wel bij 17 °C. Bij zwak licht is de temperatuur spoedig te hoog.

Hoe minder licht, des te belangrijker om een goede dagtemperatuur aan te houden en te zorgen voor een nachttemperatuur lager dan de dagtemperatuur.

III. De invloeden van verschillende temperaturen en/of lichthoeveelheden op de groei van de plant zijn besproken in verband met de invloeden die temperatuur en/of licht hebben op fotosynthese, ademhaling en vervoer van koolhydraten.

De overeenkomstige invloeden van hogere temperatuur en lagere lichtintensiteit zullen voortvloeien uit een gebrek aan koolhydraten voor goede groei.

De nadruk wordt gelegd op het evenwicht tussen vegetatieve en generatieve groei, dat sterk beïnvloed wordt door de verhouding licht/temperatuur, welke laatste op zijn beurt het evenwicht tussen fotosynthese aan de ene kant en groei en ademhaling aan de andere kant bepaalt.

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a: Plants sown on October 8, photographed on December 12



b: Plants sown on November 14, photographed on January 12

PHOTO 2 a and b. Left two plants received extra light, a total of 15 hours a day; right two plants normal day light only (compare p. 202)

decrease in sugars and starch and an increase in nitrates in the neighbourhood of the tips; after sunny days the reverse was true. With only three hours light a day starch and sugars were abnormally low.

MITCHELL (60) found less sugars and starch in plants receiving less light.

HOWLETT (34) found a positive correlation between the amount of starch near a cluster and the number of buds on that cluster that opened. In winter without extra light a high percentage of nitrates in leaves and stems was found; starch was never found.

Hence with low light energy less carbohydrates are to be expected in the plants.

3.6. *Balance between vegetative and generative growth*

GOODALL (25, 26) noted that the number of leaves formed before the first cluster can vary widely, probably from 6 leaves up to 15 under more or less normal light conditions. He thought that the sturdiest plants had the smallest number of leaves under the first cluster.

The more leaves that were removed in a very young stage, the more that were initiated before the initiation of the first cluster. With reduced light also, more leaves were initiated first (102).

Full grown leaves are necessary for fruit set (49). It is clear that the largest part of the material necessary for fruit growth has to be made by the leaves, so it is quite reasonable that without leaves no fruit growth of any significance can take place. The more big leaves the better the fruit set and fruit growth (49). Pinching off part of the leaves gave less fruit production (63). More leaves will mean more photosynthesis, hence more carbohydrates for fruit growth. It is not surprising that less light has the same result as less leaves, namely more leaves for the same amount of fruits (31, 70), with less light the cluster growth is less pronounced (table 11 on p. 197, table 12 on p. 198 and graph 15e on p. 199, p. 201 and literature 78).

Hence the lower the light energy the less the generative growth.

4. GROWTH AND RESPIRATION

4.1. *Introduction*

Respiration has to be considered as a kind of combustion process. Sugars are burned and carbonic acid and water are formed, resulting in an apparent loss. By this combustion the energy is made to build material necessary for growth and maintenance of the plant life (21). Respiration goes on day and night as long as the organism lives. The intensity, however, is strongly influenced by temperature: normally a higher temperature will be connected with a higher respiration too. BUSHNELL (19) found a heavier loss of sugars by respiration in the leaves of potatoes at higher temperatures, HEWITT and CURTIS (32) a heavier loss of dry weight in tomato leaves at higher temperatures in a range of 4–40 °C.

Hence at high temperatures normally the loss by respiration is larger than at lower temperatures (87). During a night with low temperatures relatively less will be lost by respiration compared with a night at higher temperatures.

4.2. *Vegetative growth*

In connection with the fast growth found at higher temperatures compared with lower ones it can be expected that at those high temperatures an intenser respiration takes place and consequently a greater loss is found through res-

piration. For fast growth and fast respiration a large amount of material (sugars) will be used at high temperatures, much more than for the slower growth and less intense respiration at lower temperatures.

4.3. *Generative growth*

That lower or higher respiration can be an important factor in fruit yield was found by KLINKER and SWEET (38). Their work shows that the best yielding varieties had a lower respiration than the other ones.

4.4. *Carbohydrates*

As a result of less growth and respiration at lower temperatures an accumulation of carbohydrates takes place (48). Sugar determinations showed that the respired material is mostly starch and sugars (32). During the night a decrease of sugars and a decrease of sucrose sometimes to $\frac{1}{3}$ of the value during daytime was found by ARTHUR *et al* (3). In our summer experiment it was found that compared with the highest amount of sucrose in the leaves the lowest point dropped to about $\frac{1}{4}$. The total sugars showed the same trend but less pronounced (graph 12 on p. 191). Of course this disappearance of the sugars is not only the result of respiration.

4.5. *Balance between vegetative and generative growth*

On account of the bigger amount of material being used for growth and respiration at higher temperatures compared with lower ones and the smaller amount of carbohydrates at higher temperatures, less material will be left for good cluster growth. At higher temperature the balance between vegetative and generative growth shifts to the vegetative side. At lower night temperatures larger clusters and a better fruit set were found (91). GOODALL (25, 26) found that tomato plants from old seeds or from seeds kept at a relatively high temperature made more leaves before cluster initiation than plants from younger seeds or from seeds kept at normal temperature, respectively. Both may be the result of more loss of material by respiration during the storage of the seed. More leaves are necessary to restore the level necessary for cluster initiation.

5. GROWTH AND TRANSPORT OF CARBOHYDRATES

Because photosynthesis takes place mainly in the leaves and not in the growing points, transport of carbohydrates from the leaves to the growing points is necessary to make growth possible. This transport presumably will be in the form of sucrose (18, 92, 96).

Temperature influence on this transport was studied in two ways:

a) As a loss of dry weight of leaves or leaf parts in the dark, after the loss through respiration has been deducted. At higher temperatures more transport was found with a maximum between 20° and 30 °C (22). In another experiment it was found that transport at 30 °C was slightly more than at 20 °C, at 40 °C much lower, however (32).

b) By measuring the growth that can take place only after transport. Plants with one leaf left on the stem, which were fed by means of that leaf in the dark with sucrose showed faster growth at higher temperature in the range 12–18–24 °C, but 30 °C gave a slightly slower growth than 24 °C (13), however.

In our work it was found that if the light intensity was good a faster growth

the glass will take away one third to one half of the light intensity. It is not surprising then that the light energy which reaches the plants in winter, especially between the time indicated by the vertical broken lines in graph 14, is too low for normal growth of the tomato, a plant that originally came from the Tropics.

3.2. Differences in light energy

3.2.1. Introduction

In the chapter about temperature the results of the differences in light energy between the summer and the winter experiment have already been discussed. There, however, the effect of light energy was not directly investigated.

In other experiments, however, the amount of light energy the plants received between two dark periods (24 hour-cycles) was varied:

- a) by reducing the light intensity, or
- b) by shortening the length of light exposure.

Experiments using the variety Tuckqueen were done in the greenhouses as well as in the artificially lighted rooms of the Earhart Plant Research Laboratory.

In the greenhouse the normal light intensity was reduced by cloth.

In the artificially lighted rooms the amount of light energy was varied in two ways:

- a) by putting the plants closer to or further from the lamps, or
- b) by putting the plants for a shorter or longer period under a constant light intensity. The amount of light received was then proportional to the day length.

3.2.2. Reduced light intensity

Two experiments were carried out with reduced light intensity. One (experiment VI) was during the months September and October in the greenhouse at normal light intensity (1 L), $\frac{1}{3}$ L and $\frac{1}{9}$ L. The day temperature was 23 °C, the night temperature 17 °C. The other (experiment VII) was in an artificially lighted room at a constant temperature of 17 °C with 16 hours light a day. The treatments were 1 L (= about 10,000 lux), $\frac{1}{2}$ L and $\frac{1}{4}$ L.

After about 55 days dry weights and lengths of the different parts were determined. The most important results are found in table 11, where the values for 1 L are expressed as 100 and the values for the reduced light treatments are expressed as percentages of these.

TABLE 11. A comparison of plants grown at different light intensities

Character \ Light intensity	Greenhouse			Artificial-light room		
	1 L	$\frac{1}{3}$ L	$\frac{1}{9}$ L	1 L	$\frac{1}{2}$ L	$\frac{1}{4}$ L
1 Dry weight (same values for whole plants, stems, roots or leaves)	100	36	6	100	44	15
2 Leaf blade dry weight (\pm 30 cm ²)	100	64	42	100	72	51
3 Surface area of leaves	100	59	13	100	57	26
4 Stem length	100	94	54	100	107	75
5 Dry weight of 1 cm stem	100	37	12	100	45	21
6 Height of the first cluster	100	135	—	100	125	—
7 Fresh weight of the first cluster	100	3	—	100	70	—
8 Percentage dry matter of the leaf blades	100	95	80	100	87	76