THE INFLUENCE OF SOME ENVIRONMENTAL FACTORS ON GROWTH AND DEVELOPMENT OF *SESAMUM INDICUM* L.

K. W. SMILDE

THE INFLUENCE OF SOME ENVIRONMENTAL
FACTORS ON GROWTH AND DEVELOPMENT
OF *SESAMUM INDICUM* L.

(MET EEN SAMENVATTING IN HET NEDERLANDS)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWKUNDE
OP GEZAG VAN DE WND. RECTOR MAGNIFICUS IR. W. F. EIJSVOOGEL,
HOOGLERAAR IN DE HYDRAULICA, DE BEVLOEIÏNG,
DE WEG- EN WATERBOUWKUNDE EN DE BOSBOUWARCHITECTUUR,
TE VERDEDIGEN TEGEN DE BEDENKINGEN
VAN EEN COMMISSIE UIT DE SENAAT
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP VRIJDAG 17 JUNI 1960 TE 16 UUR

DOOR

K. W. SMILDE

STELLINGEN

I

Sesamum indicum vertoont geen dagelijkse thermoperiodiciteit.
Dit proefschrift.

II

Om een juist inzicht te verkrijgen in de fotoperiodieke reactie van de plant is het noodzakelijk zowel het aantal dagen tot de bloeiinitiatie, als het aantal bladeren dat aangelegd wordt alvorens bloemknopaanleg optreedt, te bepalen bij verschillende fotoperioden.

R. VAN DER VEEN und G. MEYER, Licht und Pflanzen. Eindhoven, 1958.
Dit proefschrift.

III

Consumptie van sesamzaad of sesammeel dient gepropageerd te worden in gebieden waar de bevolking om economische redenen aangewezen is op plant-aardige eiwitten als eiwitvoeding.

IV

Het verschil in oliegehalte van lijnzaad uit tropische en uit gematigde streken dient ten dele toegeschreven te worden aan in de cultuurgebieden bestaande verschillen in daglengte.

E. KURNIK, Kiserl. Közl. 50, 1956: 57–79.

V

Het gebruik van de term „vernalizatie" voor blootstelling van planten aan andere dan lage temperaturen, of de uitwerking van een dergelijke behandeling in de plant, geeft aanleiding tot verwarring.

VI

De fotoperiodieke reacties van Xanthium pennsylvanicum en Kalanchoë blossfeldiana in van 24 uur afwijkende licht en donker cycli kunnen niet op bevredigende wijze verklaard worden met Bünnings theorie der endogene ritmen.

W. W. SCHWABE, Physiol. Plant. 8, 1955: 263–278.

K. W. SMILDE,
Wageningen, april 1960

VII

De voortdurende dreiging van introductie van de Zuidamerikaanse blad-
ziekte (Dothidella uleï) in de rubbercultuur van Z.O.-Azië maakt het noodzake-
lijk de uit Latijns Amerika geïmporteerde resistente Hevea typen zo snel moge-
lijk in cultuur te brengen.

C. W. BROOKSON, J. Rubb. Res. Inst. Malaya 14,
1956: 423–447.
R. D. RANDS and L. G. POLHAMUS, Circ. U.S.
Dept. Agric. 976, 1955.

VIII

Toepassing van premunitie tegen de „swollen shoot" ziekte van cacao dient
beperkt te blijven tot die gebieden, die anders voor de cacaocultuur verloren
gaan.

J. M. THRESH, Tech. Bull. W. Afric. Cocoa Res.
Inst. 4, 1958.
J. M. THRESH and T. W. TINSLEY, Tech. Bull. W.
Afric. Cocoa Res. Inst. 7, 1959.

IX

Verkorting van de studieduur zou bevorderd kunnen worden door de studie-
en exameneisen scherper te omlijnen, en deze voor elk vak te doen beoordelen
door de gezamenlijke hoogleraren binnen de studierichting.

H. J. WOLTJER, Universiteit en Hogeschool 5,
1959: 301–309.

VOORWOORD

Aan allen die bijgedragen hebben tot het verschijnen van dit proefschrift wil ik op deze plaats mijn dank betuigen.

Hooggeleerde COOLHAAS, hooggeleerde promotor, het door U in mij gestelde vertrouwen en de vrijheid die U mij steeds in het onderzoek hebt toegestaan, heb ik zeer gewaardeerd. Verder ben ik U zeer erkentelijk voor de door U in mijn onderzoek getoonde belangstelling en voor Uw critische opmerkingen bij het doornemen van dit proefschrift.

Zeergeleerde Mevrouw FRAHM-LELIVELD, voor Uw heldere suggesties bij de beoordeling van dit proefschrift ben ik U zeer erkentelijk.

Weledelgestrenge BOLHUIS, Uw praktische opmerkingen, steunend op Uw ervaring, en de door U verleende bemiddeling bij het verkrijgen van zaaizaad uit India, zijn voor mij zeer waardevol geweest.

Weledelgestrenge BEST, veel heb ik geleerd van Uw methode van onderzoek.

Zeergeleerde KEULEMANS, Uw collegiale hulp heeft mijn werk aanmerkelijk verlicht.

Weledelgestrenge BEKENDAM, in U zal ik een goede collega missen.

Zonder U, studentenassistenten, zou de uitvoering van proeven onmogelijk zijn geweest; met dankbaarheid zie ik terug op Uw veelal voortreffelijke hulp, en hartelijke samenwerking.

Geachte MEULENKAMP, Uw medewerking bij de uitvoering van proeven verdient alle lof. Geachte BOEKELMAN, Uw toewijding en nauwgezetheid in het tekenwerk stel ik op hoge prijs. Voorts dank ik alle anderen die verbonden zijn aan het Laboratorium voor Tropische Landbouwplantenteelt voor hun samenwerking.

Weledelgestrenge TERGAST, dank zij Uw hulp kon ik interessante Birmese sesamvariëteiten verkrijgen, waarvoor ik U oprecht dankbaar ben.

Geachte BERENDS, U ben ik zeer erkentelijk voor de prettige wijze waarop U mij geholpen heeft bij het corrigeren van de tekst.

Weledelgestrenge SZTEYN, U dank ik voor het vertalen van Russische tekst.

I am much indebted to Mr. KINMAN for his co-operation in procuring sesame seeds and for his interest in my investigations.

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(met een samenvatting in het Nederlands)

by

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(Received/Ontvangen 22.2.'60)

CONTENTS

CHAPTER I

GENERAL REMARKS

I-1. INTRODUCTION

Sesame (*Sesamum indicum* L. or *Sesamum orientale* L.) is the first oilseed crop cultivated by man. Other names are: til, benne, gingelly and ajonjoli.

HERODOTUS (484–425 b. Chr.) already mentioned the existence of its cultivation in India (see 96). Now the crop is widespread in tropical and sub-tropical regions, especially in India and China, where it is considered as one of the most important oil crops.

The average world production per year from 1952 to 1955 was 1.780.000 tons on 5.300.000 ha (3,5). The world trade is small, only about 10% of the total production (4).

In the western hemisphere the expansion of the culture was hampered because this crop is not adapted to completely mechanized harvest, owing to the dehiscence of the capsules at maturity. Since the discovery of a type of which the capsules did not open at maturity by LANGHAM in 1943, non-shattering varieties have been produced. These indehiscent types can be harvested by machines.

In the United States sesame has only been produced commercially since 1950, but the area in this country and in Latin America is steadily increasing.

Sesame produces more oil per ha. than any other annual edible oilseed crop; yields of over 2200 kg./ha. of seed (about 1100 kg. of oil) is possible (9). In Latin America the oil is considered as the "Queen of the vegetable oils", because of its keeping quality.

The development of non-shattering varieties opens the way for sesame to become one of the most important annual edible oilseed crops (43).

Sesame may be cultivated in several new regions. In consequence research is necessary to discover the optimal environmental conditions for growth and development.

I-2. AIM OF THE INVESTIGATION

Little is known about the physiology of sesame. Most work done in India, Japan, Venezuela and the U.S.A. in recent years concerns the genetics and the breeding of improved varieties.

One of the most fundamental problems, the choice of suitable climatic conditions, has not yet been studied thoroughly. "It is more than probable that sesame has been grown in many unsuitable areas in the past" (43). At present several new varieties are not adapted to the region in which they are cultivated. In Sudan indehiscent varieties imported from the U.S.A. were inferior to local varieties, because they were not adapted to the Sudanese conditions with respect to their photoperiodic requirements (2). A similar case is mentioned by HAARER (43).

The aim of the investigations is to study the influence of light and temperature on the vegetative and reproductive development of sesame. With regard to the light factor the influence of the length and the composition of the photoperiod was studied. The investigations on the temperature included the effect of constant temperatures and different day and night temperatures.

In Chapter III the experiments on the vegetative phase, including germination, stem growth and leaf production, are described. Chapter IV deals with the experiments on the reproductive phase, including floral initiation, flowering and fruit setting. In Chapter V the relation between vegetative and reproductive development is discussed, and the influence of fruit set on flowering is taken into account.

<div align="center">CHAPTER II</div>

MATERIAL AND METHODS

II-1. PLANT MATERIAL

Sesamum indicum L. belongs to the family of the Pedaliaceae, which is related to the Bignoniaceae. Sesame is an erect annual plant; depending on the variety and the conditions of growth, the height varies from 1 to $2\frac{1}{4}$ m. (3 to 8 ft), and the growth cycle from $2\frac{1}{2}$ to 5 months.

Some varieties produce many branches, others are not branched.

Flowering sets in about six weeks after sowing; the date of flowering, however, is dependent on the environmental conditions.

One to three flowers are borne in each leaf axil, and develop into fruits. Flowers open in acropetal succession; if two or three flowers occur in the axils, the central buds open first, a fairly long time before the lateral buds.

Flowering and stem growth continue until maturity. Thus the same plant can bear seed capsules, flowers and flower buds. The capsules of dehiscent varieties open at maturity, those of indehiscent varieties remain closed. When flowering ceases and most leaves are shed, the plants can be harvested.

In the present experiments varieties from the U.S.A., India, Burma, Indonesia and Nigeria were used, viz.:

U.S.A.:   Early Russian,
          Nebraska 1119-3 (N 1119-3),
          Margo: a Kansas-10 variety, obtained by selection from a Syrian
                strain,
          Dulce: Rio × Margo, with Rio as non-shattering parent,
          Venezuela-51: a selection from a Chinese strain, obtained in
                Venezuela.

India: N.P.-6: Indian Agric. Res. Inst. New Delhi,
          TMV-2: Madras,
          No. 41: Madhya Pradesh,
          Sesamum 85 (S 85): Bombay,
          T 10: Kanpur, U.P.

Burma: Judium,
          Hnan Yin,
          Boke Htaung,
          "Mountain variety".

Indonesia: Stamboom 54: Bogor.

Nigeria: Botanist 055.

The choice of varieties in the experiments was restricted in view of their growth and production capacities in the different environments. Under greenhouse conditions at Wageningen the U.S.A. varieties Early Russian, Dulce, Venezuela-51, Margo and N 1119-3 were most suited to test both vegetative growth and fruit production. Early Russian is characterized by one flower in each leaf axil, whereas Dulce, Venezuela-51, Margo and N 1119-3 have one to three flowers in each leaf axil. Dulce was preferred to Margo, owing to its quality of indehiscent seed capsules. N 1119-3 was not used in greenhouse experiments, as this variety bore too great a similarity to Margo.

The fruit production of varieties originating from tropical regions, viz. India, Burma, Indonesia and Nigeria was not satisfactory. For that reason the varieties N.P.-6, TMV-2, 41, S 85, T 10 (India); Judium, Hnan Yin, Boke Htaung, Mountain variety (Burma); Stamboom 54 (Indonesia), and Botanist 055 (Nigeria) were mainly used to investigate their photoperiodic response, whereas some observations on vegetative growth were also made.

The experiments on vegetative growth and floral initiation under controlled temperature conditions (controlled environment rooms), were started in 1957 when only the U.S.A. varieties Early Russian, N 1119-3, Margo, Venezuela-51; the Indian varieties N.P.-6, TMV-2 and 41 were available. In the course of 1958 more varieties were obtained from several experimental stations. Therefore in the 1958 greenhouse experiments some new varieties could be introduced; the dehiscent Margo was replaced by the indehiscent Dulce, which is closely related to Margo.

II-2. DESCRIPTION OF THE EXPERIMENTAL ROOMS

II-2-1. *Controlled environment rooms.* In these rooms light, temperature and humidity were controllable. The light source consisted of a removable frame, which could be moved upwards and downwards, with twenty-four 40 W Philips TLF 55 daylight fluorescent tubes. An intensity of 50.000 erg. sec.$^{-1}$cm^{-2} was measured at plant level, 5 cm. from the lamps.[1]) Temperature was controlled by a thermostate between 20° and 35 °C within 1 °C. Long-day conditions

[1]) 3.64 erg.sec.$^{-1}$cm^{-2} = 1 lux = 0.093 ft.c. for fluorescent light Philips TL 55.

consisted of a 10-hour high intensity light period, supplemented by 7 hours of weak light from one TLF 55 lamp, with a light intensity of 1500 erg.sec.$^{-1}$cm^{-2} at plant level.

II-2-2. *Cabinets*. In these cabinets only light and temperature were controllable. The light source consisted of sixteen TLF 55 lamps, with an intensity of 40.000 erg.sec.$^{-1}$cm^{-2} at plant level, 5 cm. from the lamps. Temperature was controlled between 15° and 35°C within 2°C. Humidity varied between 40% and 70%. Under long-day conditions additional light from one TLF 55 lamp was given, with an intensity of 1500 erg.sec.$^{-1}$cm^{-2} at plant level. For a detailed description, see FORTANIER (39).

II-2-3. *Greenhouses*. The two greenhouses used for the experiments will be mentioned the A- and C-greenhouse. In the A-greenhouse plants were grown in eight trucks, placed by twos in the four compartments of a shed during the dark period. Supplemental weak light, extending the daylight period, was given in the compartments with TLF 55 lamps; the light intensity at plant level, 1 m. from the lamps, was 500 or 2000 erg.sec.$^{-1}$cm^{-2} according to the conditions required in the different experiments.

In the C-greenhouse plants were similarly grown in sixteen trucks placed by fours in the four compartments of a large shed. The intensity of supplemental light from two TLF 55 lamps was 2000 erg.sec.$^{-1}$cm^{-2} at plant level, 1 m. from the lamps.

Some experiments in this greenhouse were carried out in concrete containers under frames which could be covered by black cloth. The intensity of supplemental light from one TLF 55
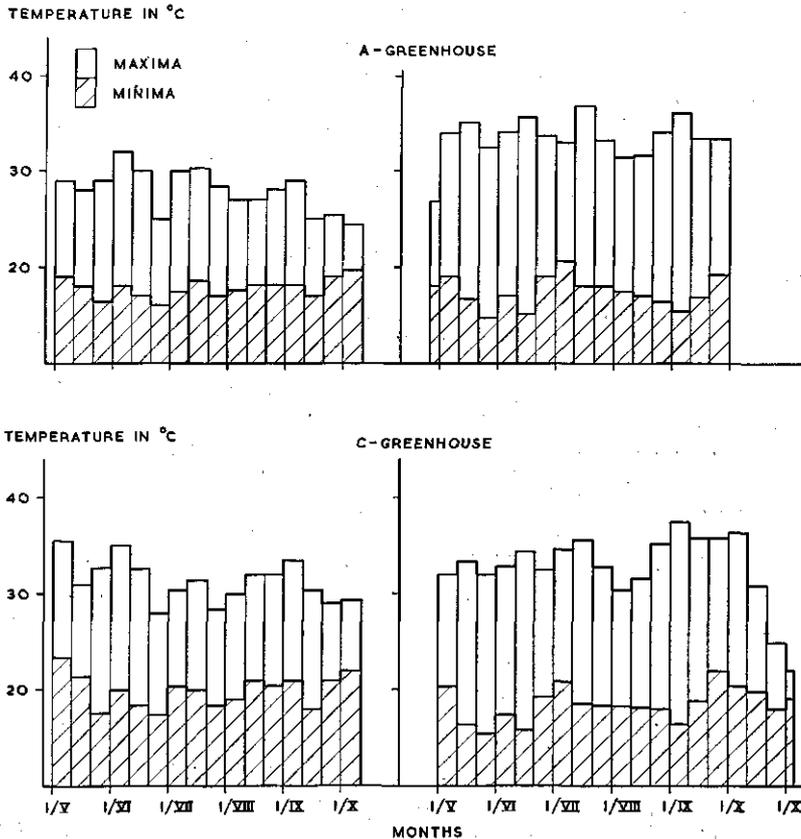
GRAPH 1. Maximum and minimum temperatures per 10 days; to the left 1958, to the right 1959.

lamp was 250 erg.sec.$^{-1}$cm^{-2} at plant level, 1 m. from the lamp. See also KEULEMANS (52) for more details.

Usually the trucks were moved outside at 7 a.m., when the cloth was also removed from the frames.

In the greenhouses the temperature was not controllable. Minimum temperatures could be kept above 15°C by heating. Temperature and humidity were recorded automatically by a thermo-hydrograph at 30 cm. from the soil.

Humidity varied between 50% and 95% in both greenhouses; the temperatures are recorded in graph 1.

The average radiation energy of the natural daylight at Wageningen is shown in graph 2; in the greenhouses, however, a loss of about 35% occurs.[1])

The relative spectral energy distribution of TLF 55 daylight fluorescent tubes is described by Philips' light catalogue 1958.

LIGHT ENERGY IN CAL. CM.$^{-2}$ DAY^{-1}
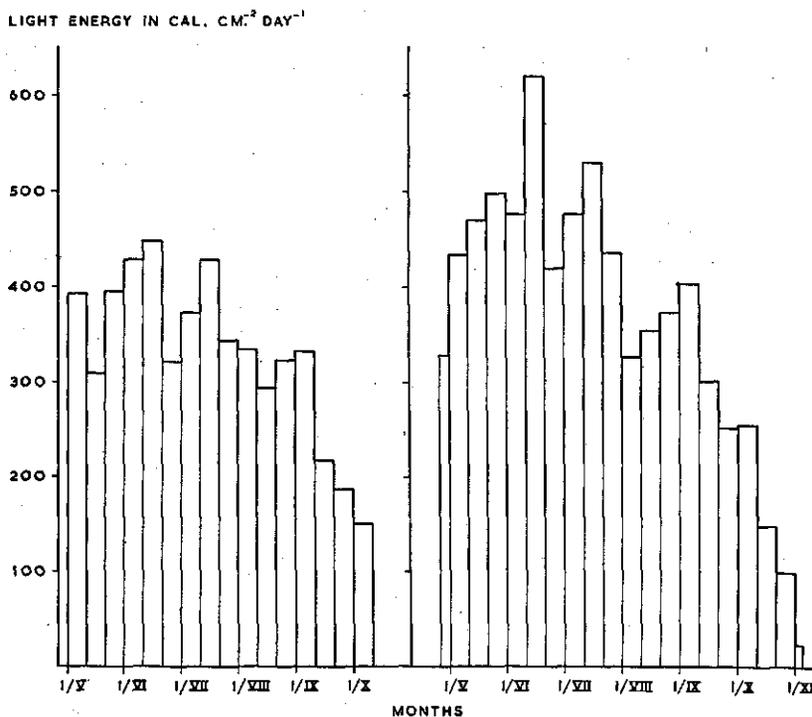
GRAPH 2. Energy of daylight in cal. day^{-1} cm^{-2} per 10 days at Wageningen; to the left 1958, to the right 1959.

II-3. GROWTH CONDITIONS

The seeds were pre-germinated at 32°C for 24 hours and sown in pots at a depth of about 1.5 cm. During the first week after sowing temperature was kept at 30°C, and at seedling emergence a photoperiod of 17 hours was given to prevent short-day induction. After this first week the treatment was started with five uniform plants left in each pot. The same treatment was used in the greenhouse experiments, but in this case the one-week-old seedlings were planted out.

[1]) 1 cal. day^{-1}cm^{-2} = 486 erg.sec.$^{-1}$cm^{-2}

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A light sandy soil, thoroughly mixed with leaf-mould, farmyard manure, compost and some peat, was used.

In the controlled environment rooms the earthen pots (contents 4 litres) were placed in dishes.

In the greenhouses plants were grown either in pots dug in the soil or in soil without pots; after thinning two plants were left in each pot and the plant spacings varied between 21 cm. and 14 cm. For the plants grown without pots the spacing in the row was 20 cm., between the rows 14 cm. Each variety was planted in rows, the rows running in a north-south direction.

As sesame is not tolerant to excessive moisture and "wet feet", water was distributed carefully. Hoeing was necessary to secure good soil aeration. The expected advantage from growing in pots, to avoid water being directly applied to the pots by watering between them, was not attained. As this system required too much labour it was abandoned in the second year experiments.

High humidity on cold and rainy days favoured fusarium wilt, caused by *Fusarium oxysporum sesami*. The spraying of parathion was sometimes necessary to destroy aphids or mites.

Plants grown in conditions of artificial light only remained small, were not branched, possessed short internodes, whereas flowering and fruit set were very poor. This must have been caused by shortage of carbohydrates owing to the relatively low light intensity and consequently limited the experiments on flowering and fruit set under controlled temperature conditions. There was no improvement when the TLF 55 lamps were replaced by TL 33 lamps, which radiate 10,5 % more yellow and 0,5 % more red light. Flowering and fruit set were also poor when the light source consisted of two high pressure mercury vapour lamps (Philips HO 2000, 450 W) and one incandescent lamp (150 W), with a total light intensity of 90.000 erg.sec.$^{-1}$cm^{-2} at plant level.

II-4. OBSERVATIONS

Stem length was measured from the cotyledons to the top.

The number of leaves counted does not include cotyledons and unexpanded leaves. Branches shorter than 4 cm. were not taken into account.

The decussate leaves were numbered from the base upwards. The pair of leaves formed after the cotyledons will be indicated as first pair and the corresponding node as first node.

In order to determine the date of floral initiation growing-points were dissected in boiling chloral hydrate (CCl$_3$COH.H$_2$O) and examined under a microscope with sixtyfold magnification for the presence of floral primordia. Then the position of the first floral primordium was determined by verifying the position of the macroscopically visible flower buds on the plants left. When working with uniform plants, dissecting a total of four or five growing-points on successive days was sufficient. Under conditions of more than sixteen hours of light daily, plants were less uniform so that more growing-points had to be dissected.

The mean number of days until floral initiation and flowering is rounded off to a whole number. Opening of the first flower of a plant was the criterion of flowering.

Meded. Landbouwhogeschool, Wageningen 60 (5), 1-70 (1960)

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EXPERIMENTS ON THE VEGETATIVE DEVELOPMENT

III-1. GERMINATION

III-1-1. *General.* The rate of germination is of great importance with respect to further development. Influence of temperature and light on germination is discussed below. The small seeds consist of the embryo, the cotyledons and the rootlet of which are discernable within the seedcoat.

III-1-2. *Temperature.* Germination was tested at temperatures of 20°, 24°, 27°, 30°, 33° and 35°C in a germinator. About 50 seeds of the variety Botanist 055 were sown on moist sand. Continuous light was given from two TLF 55 lamps, with an intensity of 8000 erg.sec.$^{-1}$cm^{-2}.

At 35°C, 80% to 90% of the seeds showed the rootlet after 17 hours; after about 30 hours hypocotyls began to elongate and 18 hours later the cotyledons penetrated the seedcoat and expanded. At that time the length of the hypocotyls was 3 to 5 mm.

At 20°C germination was much slower; the rootlet appeared after 54 hours and after about 90 hours expansion of cotyledons started and a hypocotyl length of 2 mm. was measured.

Not much difference was found between 33° and 35°C, whereas germination and expansion of cotyledons at 30°C and lower temperatures was slower.

As regards temperatures beyond this range, at 15°C only 70% of the seeds had germinated after 10 days and 50% after 5 days; at 39°C, however, germination was not much delayed compared with 35°C.

III-1-3. *Vernalization.* Seeds of the varieties TMV-2 and N.P.-6 were vernalized in dark for 5, 10, 15, 20 and 25 days in a refrigerator at 3° to 5°C. The swollen seeds used for vernalization had been pre-germinated for 15 hours at 30°C on moist filter paper in Petri-dishes. Each treatment included 1 Petri-dish with 300 seeds.

The treated seeds and the controls (only pre-germinated) were sown simultaneously in pots in a controlled environment room. After one week the controls were completely, the seeds of both varieties vernalized for 5 days only partly emerged.

Now ten seedlings of each of these groups were placed under short-day conditions, consisting of 10 hours of light; a similar number was placed under long-day conditions, consisting of 10 hours of light supplemented by 7 hours of weak light (see p. 4). The temperature in both controlled environment rooms was 28°C; humidity was 60% to 70%. The time between sowing and floral initiation, and the position of the node of the first flower bud were examined. The experiment was terminated 60 days after sowing. Seeds vernalized for more than 5 days were not considered, because emergence was too poor. Only a few N.P.-6 seeds vernalized for more than 5 days appeared; emergence of the seeds vernalized for 25 days was somewhat better. TMV-2 seeds vernalized for more than 5 days did not emerge at all. The results are given in table 1.

Under short-day conditions floral initiation in the vernalized plants was 3 to 6 days later compared with the controls, for N.P.-6 and TMV-2 respectively; the position of the flower bud on the stem was correspondingly higher.

TABLE 1. Effect of vernalization on the number of days to floral initiation and node position of the first flower bud under short-day and long-day conditions.

	N.P.-6				TMV-2			
	Short-day		Long-day		Short-day		Long-day	
	Control	Vernalized	Control	Vernalized	Control	Vernalized	Control	Vernalized
Days to floral initiation	18	21	36	43	18	24	54	53
Average node number of the first flower bud	3.0	3.7	6.0	8.0	3.0	4.0	9.0	8.7
Number of plants	8	7	8	9	9	5	2	3

Under long-day conditions floral initiation in the control N.P.-6 was 7 days earlier than in the vernalized plants; no difference in this respect was shown by TMV-2. In the latter case the number of plants examined was small, as most plants of both treatments were still in the vegetative stage when the experiment had to be terminated.

The conclusion seems justified that vernalization has little effect on, or delays, floral initiation; the effect of the photoperiod is predominant.

III-1-4. *Light*. At temperatures varying from 20° to 35°C the germination rate was constant under the following conditions: continuous light, continuous darkness, and 12 hours light + 12 hours darkness; light was given from two TLF 55 lamps, with an intensity of 8000 erg.sec.$^{-1}$cm^{-2}.

In the dark the hypocotyls were more elongated than in the light, and the cotyledons had a yellow colour.

III-1-5. *Discussion*. Not only in the variety Botanist 055 but also in several other sesame varieties an optimum germination temperature of 32°-35°C was found. This temperature is also mentioned in literature (96).

MIROSHNICHENKO (71) investigated the germination of sesame seeds at various temperatures; at 25°-35°C seeds germinated after 12 to 20 hours, at 20°C after 35 to 40 hours and at 16°C after 7 to 9 days. This is in accordance with the above mentioned results.

These high germination temperatures mean in practice that sesame should not be sown at soil temperatures below 24°C (53).

MIROSHNICHENKO found that emergence is improved and the germination rate increased by vernalization for 1 to 2 days at 24°-26°C.

In the present experiments seeds were always pre-germinated to avoid poor emergence; this is important when seeds are used that are more than one year old.

Vernalization proved to be detrimental to germination, especially when the plants were treated for more than 5 days. Moreover in the material vernalized for 5 days flowers were not initiated earlier. According to CHAKRAVARTI (28, 29) pre-chilling of sesame seeds does not markedly shorten the vegetative period.

Perhaps vernalization at higher temperatures will give better results. In cotton an increase in earliness varying from 1 to 6 days was found by vernalization at 10°-12°C (7, 55). Is it, however, a moot point whether this has to be looked upon as vernalization. Soaking of seeds at temperatures of 24°-26°C should not be called vernalization.

Germination was not affected by the different conditions of light applied (p. 8).

III-2-1. *Temperature*. The influence of temperature on stem elongation and leaf production was investigated in the controlled environment rooms. The daily light period was 12 hours and the humidity varied between 60% and 70%. The following combinations of day and night temperatures were applied: 21°–21°C, 21°–27°C, 27°–21°C, 27°–27°C, 21°–33°C, 33°–21°C and 33°–33°C, in each case the day temperature being mentioned first. The experiment was done with fifteen to twenty plants of the varieties Early Russian and Margo per treatment. Stem length and number of leaves were recorded at eight weekly intervals. The results on the stem length are shown in graph 3; the leaf production is discussed on p. 17.

STEM LENGTH IN MM
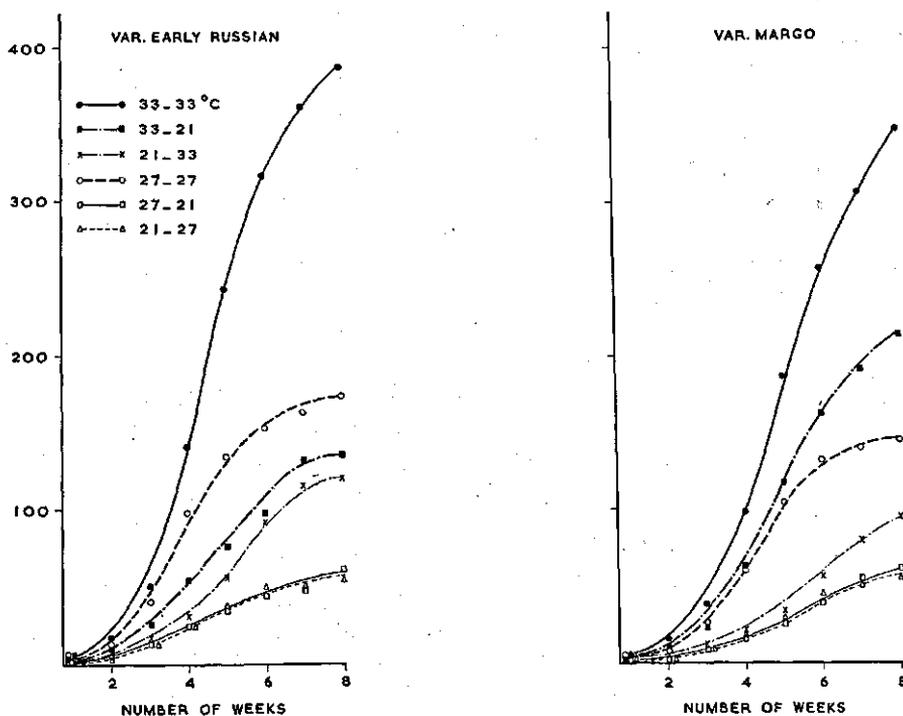
GRAPH 3. Stem growth at different temperatures.

Of the temperature combinations tested a constant temperature of 33°C proved to be optimal for stem growth in both varieties, whereas a constant temperature of 21°C was too low for normal growth under the experimental conditions mentioned above. Growth conditions improved as the average temperature was raised to 24°C (27°–21°C, or 21°–27°C), but it made no difference whether the lowest temperature was given in the light or in the dark period. The adverse effect of the low day (night) temperature could be compensated for by the higher night (day) temperature.

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At an average temperature of 27 °C the varieties behaved differently. In Margo growth was most vigorous at 33°–21 °C; apparently this variety preferred the alternation of day and night temperature to a constant temperature of 27 °C, although this is hardly reconcilable with the fact that 33°–33 °C in turn proved to be more favourable than 33°–21 °C. The 21°–33 °C combination induced a poorer growth as compared with 27°–27 °C and 33°–21 °C. In Early Russian, however, the results of the 33°–21 °C and 27°–27 °C treatments were not significantly different, and the same is true for the 33°–21 °C and 21°–33 °C treatments; a significant difference was only found between 27°–27 °C and 21°–33 °C, the constant temperature being most favourable.

III-2-2. *Light.* The experiments on the influence of the photoperiod on stem growth were started on June 19, 1958. Stem length was measured twice a week.

In the A-greenhouse a 10-hour photoperiod of natural daylight was prolonged by 0, 3, 6, 10 or 14 hours of artificial light with an intensity of 500 erg.sec.$^{-1}$cm^{-2}, see also p. 31. The following notation will be used: 10, 10 + 3, 10 + 6, 10 + 10 and 10 + 14 hours. In each treatment ten plants of the varieties Early Russian, Dulce, Venezuela-51, S 85 and Boke Htaung were used. The results of some varieties are shown in graph 4, 5. There is a great similarity between the curves for Early Russian and Boke Htaung on the one hand and between Venezuela-51, Dulce and S 85 on the other.

In the early stages of growth there was no great difference in the height of the plants, the plants at the longest photoperiods being somewhat shorter. Plants ceased growth earlier as the photoperiod became shorter and finally the tallest plants occurred at the longest photoperiods. This was found in all five varieties tested, but in Early Russian the differences between 10, 10 + 3 and 10 + 6 hours were not significant.

At first the stems grew slowly, later rapidly and then retarded their growth again, showing sigmoid curves. The curves for the growth rates are parabolic in shape. The longer the photoperiod, the later the date at which the maxima of the growth rates were attained. Early Russian has about identical curves for 10, 10 + 3 and 10 + 6 hours.

At the same time the influence of different periods of daylight without additional light was investigated. This included photoperiods of 5, 7, 8½ and 11½ hours in the C-greenhouse, and 13 hours in the A-greenhouse. In this experiment the varieties Early Russian, Dulce and Venezuela-51 were observed. From graph 6 it appears that right from the beginning, plants were shorter as the period of daylight was further reduced. At first the differences between 10, 11½ and 13 hours were slight, but finally the 13-hour plants grew tallest. Early Russian was somewhat irregular since at 10 hours the plants were taller than at 11½ hours.

The curves for the growth rates show a parabolic shape, except at the 5-hour photoperiod. Early Russian attained its maximum growth soonest at a photoperiod of 11½ to 13 hours, Dulce and Venezuela-51 at a photoperiod of 10 to 11½ hours. The height of the maxima diminished with decreasing length of the photoperiod.

Growth was also observed at photoperiods of the same duration but consisting of different periods of daylight. In the C-greenhouse different 7-hour photoperiods were applied, namely 5 + 2, 6 + 1 and 7 hours; the intensity of the supplemental light was 250 erg.sec.$^{-1}$cm^{-2}. Growth became poorer as the part of the photoperiod consisting of artificial light increased. Generally no

STEM GROWTH IN MM PER DAY

VAR. EARLY RUSSIAN

LENGTH OF STEM IN MM
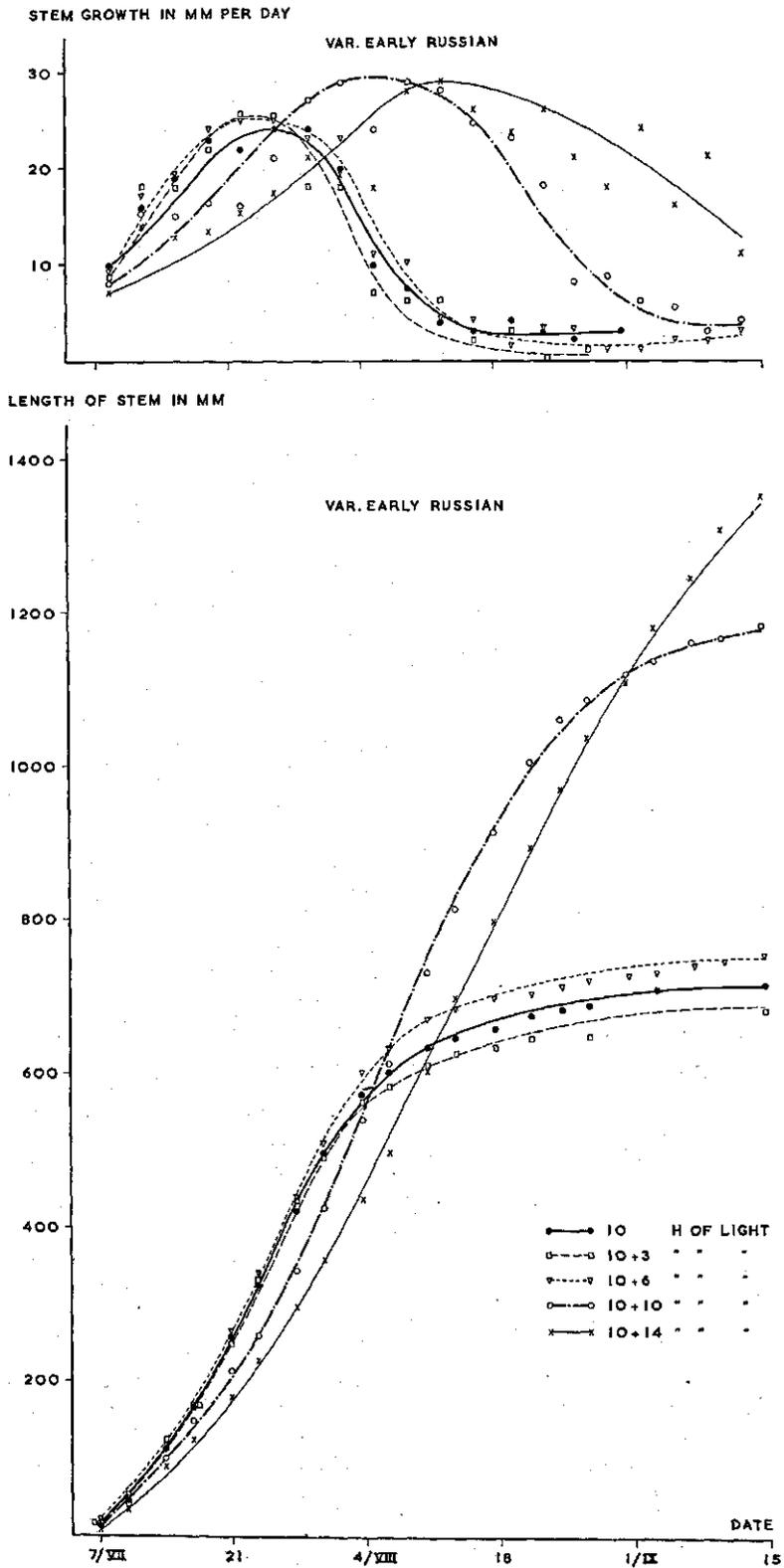
VAR. EARLY RUSSIAN

GRAPH 4. Average rate of stem growth (above) and stem growth (below) at different photo-
periods for variety Early Russian; basic illumination 10 hours.

STEM GROWTH IN MM PER DAY

VAR. VENEZUELA 51

LENGTH OF STEM IN MM
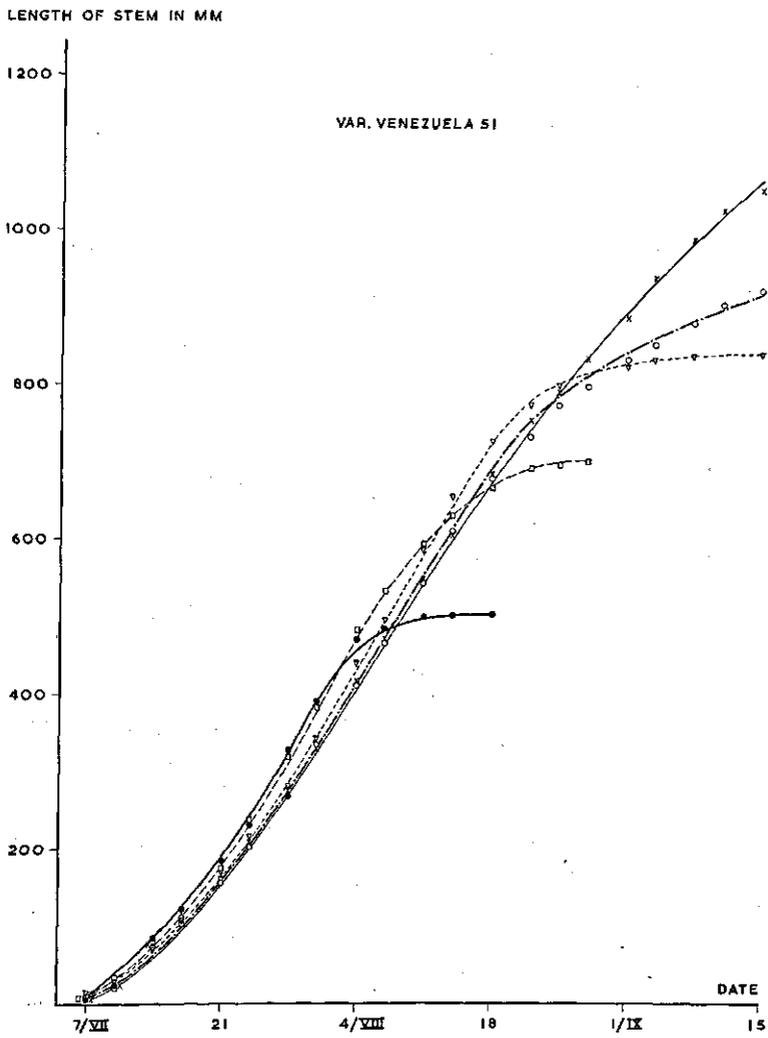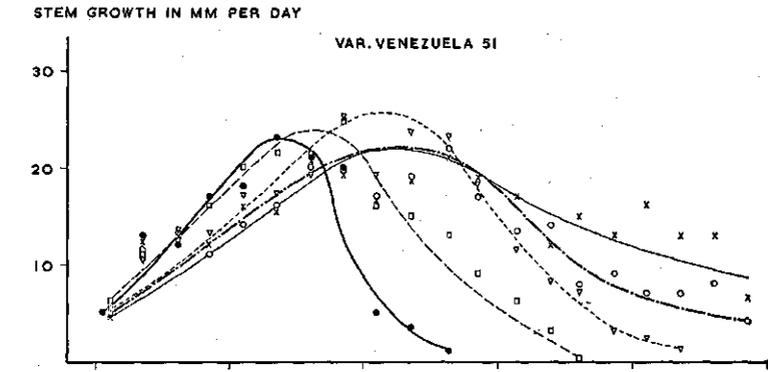
VAR. VENEZUELA 51

GRAPH 5. Average rate of stem growth (above) and stem growth (below) at different photo-periods for variety Venezuela-51; basic illumination 10 hours, legend as in graph 4.

STEM GROWTH IN MM PER DAY

VAR. EARLY RUSSIAN

LENGTH OF STEM IN MM
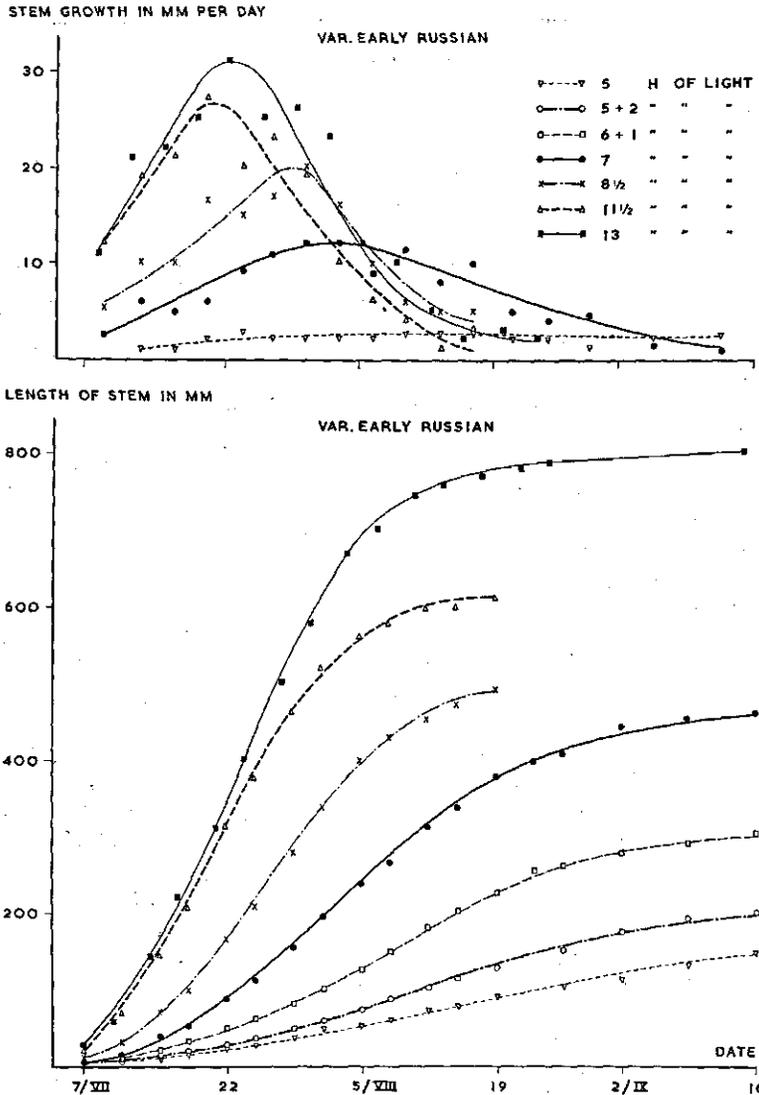
VAR. EARLY RUSSIAN

GRAPH 6. Average rate of stem growth (above) and stem growth (below) at different photo-periods for variety Early Russian; different basic illuminations.

significant differences were found between 10 and 13 hours of daylight at photoperiods of the same duration, see table 2.

The data on Early Russian were somewhat conflicting because no difference was found between $10+14$ and $13+11$ hours, whereas at photoperiods of 20 and 13 hours the plants having received 13 hours of daylight were tallest.

In an experiment started in the C-greenhouse on April 23, 1959, the following photoperiods were given: 6, $6+4$, $6+7$, $6+14$, 8, $8+2$, $8+8$, $8+12$, 10, $10+3$, $10+6$, $10+10$ and 13 hours; the intensity of the additional light was 2000 erg.sec.$^{-1}$cm^{-2}, see also p. 34. The final length of the stem in Early Russian,

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TABLE 2. Maximum stem length in mm. at photoperiods of different composition.

	10 + 3 hours	13 hours	10 + 10 hours	13 + 7 hours	10 + 14 hours	13 + 11 hours
Early Russian	688 ± 39*	804 ± 38	1193 ± 73	1384 ± 58	1398 ± 38	1375 ± 58
Dulce	741 ± 69	754 ± 77	1088 ± 69	1082 ± 35	–	–
Venezuela-51	716 ± 68	698 ± 30	951 ± 58	984 ± 58	1103 ± 56	1092 ± 40

* Standard error of mean

Dulce and Venezuela-51 was measured, and the dry weight of 10 cm. of the stem just above the cotyledons, was determined in Early Russian and Dulce, see table 3.

At each basic illumination period, i.e. 6, 8 and 10 hours of daylight, the length of the stem increased as the photoperiod became longer. A similar tendency appeared at the photoperiods consisting of daylight only, although in Dulce and Venezuela-51 the difference between 8 and 10 hours was slight.

At photoperiods of the same duration no general rule could be established for the effect of the basic illumination period of daylight. In Early Russian the effect of substituting daylight for artificial light was different at varying photoperiods. In Dulce and Venezuela-51 the replacement of a 10-hour daylight period by a 6-, or 8-hour basic illumination induced an increase in stem length, except in the 20-hour treatments of Venezuela-51.

A positive correlation existed between stem length and dry weight of 10 cm. of the stem; the coefficients were 0.96 and 0.87 for Early Russian and Dulce respectively. Hence the dry weight increased as the photoperiod became longer.

At photoperiods of equal length the composition was found to be important. Generally the dry weight increased with an increase in the part of the photoperiod consisting of daylight. In Early Russian, however, no significant difference was found between 6 + 14 and 8 + 12 hours. In Dulce no essential differences existed between basic illumination periods of 8 and 10 hours of daylight at photoperiods of the same length.

In an experiment started in the A-greenhouse, on April 21, 1959, the vege-

TABLE 3. Final length of stem, and dry weight in grammes of 10 cm. of the stem at different photoperiods.

Photoperiod in hours	Early Russian		Dulce		Venezuela-51
	Length of stem (in mm)	Dry weight in g.	Length of stem (in mm)	Dry weight in g.	Length of stem (in mm)
6	411	0.11	395	0.14	383
6 + 4	491	0.12	602	0.25	613
6 + 7	587	0.14	749	0.40	878
6 + 14	1598	0.74	1304	0.86	1154
8	602	0.31	478	0.33	572
8 + 2	726	0.32	609	0.46	717
8 + 8	755	0.27	956	0.70	1101
8 + 12	1453	0.69	1201	1.26	1216
10	675	0.38	491	0.39	575
10 + 3	775	0.39	582	0.54	713
10 + 6	886	0.42	864	0.73	981
10 + 10	1484	0.84	1050	1.24	1246
13	771	0.42	543	0.47	661

tative development of 9 varieties was observed at photoperiods of 10, 10 + 3, 10 + 6 and 10 + 10 hours. The intensity of the additional light was 2000 erg. sec.$^{-1}$cm^{-2}, see also p. 36. At the moment of flowering the length of the stem, number of leaves and dry weight of parts above ground were determined, see table 4.

TABLE 4. Length of stem, number of leaves, and dry weight of stem + leaves at different photoperiods, as determined at the onset of flowering.

a. Number of days to flowering

Photoperiod in hours	Bot. 055	Hnan Yin	Judium	Stamb. 54	T 10	TMV-2	N.P.-6	41	Burmese mount. var.
10	40	37	32	44	33	36	32	32	16
10 + 3	48	40	34	48	32	42	32	34	30
10 + 6	58	52	49	64	46	53	38	53	49
10 + 10	67	57	54	106	85	61	57	70	110
10 + 10; at night 25°–35°C	72	90	62	–	81	71	57	63	–

b. Stem length in mm

Photoperiod in hours	Bot. 055	Hnan Yin	Judium	Stamb. 54	T 10	TMV-2	N.P.-6	41	Burmese mount. var.
10	444	391	285	571	260	307	239	246	300
10 + 3	748	554	362	709	312	448	267	314	581
10 + 6	963	874	793	982	595	694	491	553	1113
10 + 10	811	763	696	1321	1062	818	771	740	1340
10 + 10; at night 25°–35°C	1084	1328	901	–	1117	907	788	713	–

c. Number of leaves

Photoperiod in hours	Bot. 055	Hnan Yin	Judium	Stamb. 54	T 10	TMV-2	N.P.-6	41	Burmese mount. var.
10	10.9	18.4	15.6	23.4	16.3	16.2	14.0	17.1	22.3
10 + 3	27.6	22.4	16.8	28.3	17.4	19.7	14.9	20.8	37.5
10 + 6	33.3	29.8	27.8	38.0	25.0	26.0	21.0	30.9	78.3
10 + 10	39.2	31.4	31.4	55.8	50.6	33.1	35.1	39.2	78.7
10 + 10; at night 25°–35°C	48.8	53.2	42.8	–	52.4	44.3	42.2	40.2	–

d. Dry weight of parts above ground in g

Photoperiod in hours	Bot. 055	Hnan Yin	Judium	Stamb. 54	T 10	TMV-2	N.P.-6	41	Burmese mount. var.
10	1.90	1.37	0.57	2.53	0.63	0.89	0.61	0.75	1.22
10 + 3	5.48	2.68	0.94	2.12	0.81	1.69	0.82	1.29	6.61
10 + 6	9.35	5.55	3.40	10.21	2.83	4.57	2.92	5.85	27.87
10 + 10	12.30	7.05	4.39	30.34	17.07	6.56	9.59	12.95	35.01
10 + 10; at night 25°–35°C	21.80	27.49	9.73	–	21.10	15.75	15.11	17.14	–

The increase in the number of days to flowering by extension of the daylight period with artificial light, was accompanied by an increase in length of stem, number of leaves and dry weight of above-ground parts. These three aspects of growth appeared to be closely interconnected. Botanist 055, Judium and Hnan Yin seemed to deviate from this rule because at the beginning of flowering the tallest plants were found at a photoperiod of 10 + 6 hours. It may be predicted, however, that the plants eventually attain the greatest height at the longest photoperiod.

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III-3. LEAF PRODUCTION

III-3-1. *Temperature.* In the experiment described above the influence of the night temperature was investigated at a photoperiod of $10+10$ hours, see table 4. Night temperatures above 25°C (25°–35°C) were compared with night temperatures varying from 15° to 20°C. The effect on floral initiation and flowering is described in Chapter IV, p. 28, whereas the effect on the vegetative development is discussed in this section.

The values for number of leaves, length of stem and dry weight of above-ground parts, as determined at the beginning of flowering, were greatest at night temperatures ranging from 25° to 35°C. The results of the two temperature treatments are, however, not fully comparable, since the dates of flowering were different. Nevertheless in N.P.-6, 41 and T 10, where flowering was not delayed by night temperatures above 25°C, the differences in dry weight of above-ground parts were obvious. Doubtlessly in these varieties, and in all probability also in the other varieties tested, growth was favoured by night temperatures maintained above 25°C (cf. p. 29).

The influence of controlled temperatures on leaf production was investigated in the controlled environment rooms, see p. 10. Stem growth and leaf production were fairly well correlated. The greatest numbers of leaves occurred in the 33°–33°C treatment in both varieties, whereas leaf production at a constant temperature of 21°C was very low. The numbers of leaves were almost equal at 27°–21°C and 21°–27°C. In contrast to the data found on stem growth in both Margo and Early Russian, no significant differences occurred between 33°–21°C, 27°–27°C and 21°–33°C in numbers of leaves. The results are shown in graph 7.

NUMBER OF LEAVES
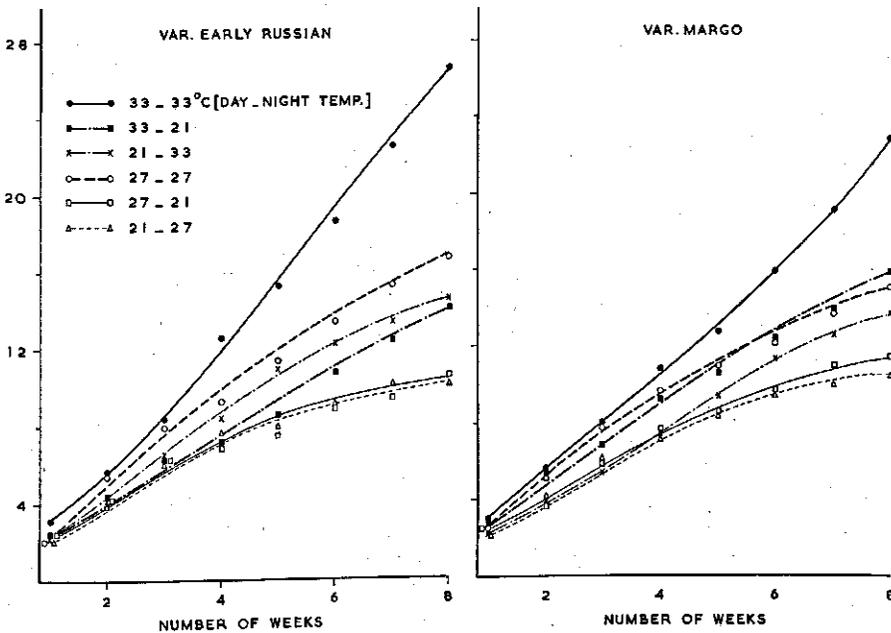
GRAPH 7. Leaf production at different temperature combinations.

NUMBER OF LEAVES

VAR. EARLY RUSSIAN

- ●——● 10   H OF LIGHT
- □----□ 10+3   "   "   "
- ▼----▼ 10+6   "   "   "
- ○—·—○ 10+10 "   "   "

40

32

24

16

8

7/VII   21   4/VIII   18

DATE
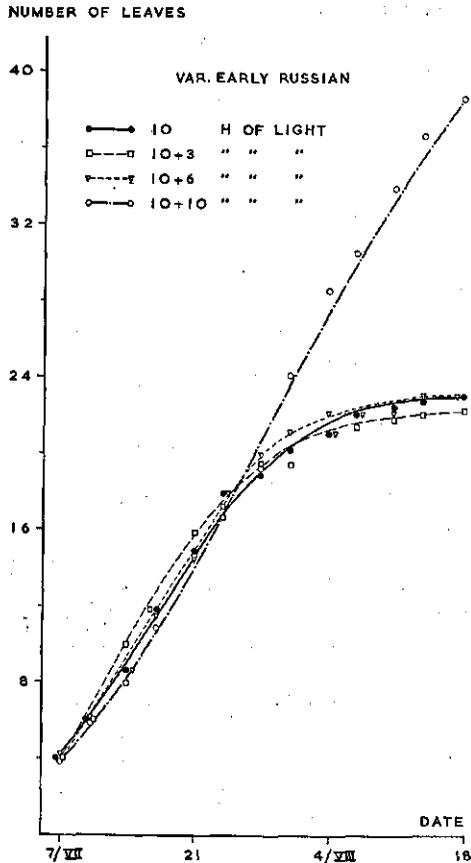
GRAPH 8. Leaf production at different photo-
periods; basic illumination 10 hours.

III-3-2. *Light.* In the experiment started on June 19th, 1958, (see p. 11) the production of leaves was observed in the varieties Early Russian, Dulce, Venezuela-51, S 85 and Boke Htaung. The photoperiods were 10, 10+3, 10+6, 10+10, 10+14 and 13 hours in the A-greenhouse and 5, 6+1, 7, $8\frac{1}{2}$ and $11\frac{1}{2}$ hours in the C-greenhouse. In S 85 and Boke Htaung the illumination periods of 7, $8\frac{1}{2}$ and $11\frac{1}{2}$ hours had to be omitted. The results of Early Russian are shown in graph 8, 9.

The curves representing the production of leaves closely resemble the curves for stem growth (see p. 12). The counting of leaves was discontinued when the plants at 10+10 and 10+14 hours were still producing leaves. From graph 8 it is evident, however, that the plants at these photoperiods will eventually produce the greatest number of leaves. The 10+14-hour curve was omitted in graph 8, as it was almost identical with the 10+10-hour curve. In Early Russian the differences between 10, 10+3, and 10+6 hours were slight, whereas at a photoperiod of 10 hours more leaves were produced that at $11\frac{1}{2}$ hours. This is in accordance with the data on stem length.

A close correlation was found between final length of the stem and total number of leaves; the correlation coefficients calculated for Early Russian, Dulce and Venezuela-51 were 0.97, 0.91 and 0.88 respectively. Thus the number of leaves became higher as the photoperiod increased. This was found both in the range of 10 to 10+14 hours, and of 5 to 13 hours.

The results of the experiment started in the C-greenhouse on April 23, 1959, (see p. 15) will have to be discussed in more detail. At photoperiods of 6, 6+4, 6+7, 6+14, 8, 8+2, 8+8, 8+12, 10, 10+3, 10+6, 10+10, and 13 hours the final number of leaves was counted in Early Russian, Dulce and Venezuela-51, see table 5. The leaf area of one leaf of the third node was calculated for Early Russian and Dulce by multiplying the maximum length by the maximum width, see table 5.

The number of leaves increased as the photoperiod became longer, independent of its composition. In Early Russian, however, no significant differences appeared between photoperiods of 6, 6+4 and 6+7 hours. At photoperiods of equal duration but of different composition the effect of the basic illumination

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was not quite clear. Generally the highest number of leaves was found at the greatest length of the stem, and conversely. As a matter of fact, in the whole range of photoperiods a positive correlation existed between length of stem and number of leaves. The correlation coefficients calculated were 0.99, 0.98 and 0.94 for Early Russian, Dulce and Venezuela-51 respectively.

The area of the leaf of the third node increased as the photoperiod became longer, whether consisting of daylight only, or of daylight and artificial light. At photoperiods of the same duration but differing in composition the largest leaf area was found at the longest period of daylight.

NUMBER OF LEAVES
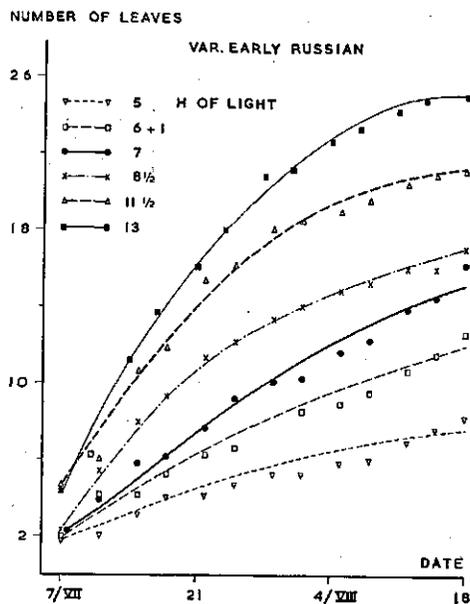
GRAPH 9. Leaf production at different photoperiods; different basic illuminations.

III-3-3. *Discussion.* Under conditions of artificial light only, an average temperature of at least 24°C was required for elongation of the stem and production of leaves, whereas of the temperatures investigated 33°C was optimal (p. 17). The harmful effect of low night temperatures was compensated for by high day temperatures and conversely. Under conditions of natural daylight the dry weight of the above-ground parts, length of the stem and number of leaves increased when night temperatures were maintained above 25°C (p. 17).

In literature only a few data are available on the effect of temperature on growth of sesame. KINMAN (53) reports that growth and fruiting are favoured

TABLE 5. Total number of leaves, size in mm. of one leaf of the 3rd node and area (max. length × max. width) in cm², at different photoperiods. Averages of 20 plants.

Photoperiod in hours	Early Russian			Dulce			Venezuela-51
	Number of leaves	Leaf size in mm.	Area in cm²	Number of leaves	Leaf size in mm.	Area in cm²	Number of leaves
6	20.1	58.5 × 35.8	20.9	23.0	82.9 × 42.2	35.0	18.8
6 + 4	19.2	69.7 × 41.3	28.8	27.9	99.6 × 55.5	55.3	24.1
6 + 7	20.1	76.3 × 44.6	34.0	36.0	99.9 × 55.2	55.1	39.4
6 + 14	81.4	84.4 × 53.7	45.3	67.3	107.0 × 59.3	63.5	53.3
8	25.1	86.1 × 51.0	43.9	26.8	106.1 × 62.9	66.7	28.5
8 + 2	25.4	90.7 × 51.0	46.3	31.0	124.4 × 65.2	81.1	–
8 + 8	27.7	99.3 × 58.4	58.0	52.9	128.1 × 75.6	96.8	55.8
8 + 12	68.0	98.2 × 65.6	64.4	72.8	133.0 × 81.3	108.1	54.6
10	28.9	95.0 × 51.9	49.3	28.3	120.9 × 68.6	82.9	26.6
10 + 3	30.7	101.7 × 60.1	61.1	32.9	133.5 × 77.5	103.5	36.2
10 + 6	35.4	–	–	50.6	146.4 × 96.4	141.1	55.5
10 + 10	67.6	124.2 × 98.3	122.1	65.5	155.0 × 106.0	164.3	56.9
13	34.6	107.5 × 66.5	71.5	33.9	141.3 × 80.4	113.6	31.6

by daily temperatures around 80 °F, whereas growth is retarded by cool temperatures. BALLY (8) mentions a "heat-sum" of 2700 °C in 120 days. In a review article SPRECHER VON BERNEGG (96) points out that large diurnal temperature fluctuations are detrimental to growth. In a date-of-sowing experiment SEN and PAIN (90) found that plants grown in summer and monsoon (India) grew taller and produced more leaves and branches than plants grown in autumn and winter.

In his articles on thermoperiodicity WENT (26, 37, 109, 110, 111, 112) emphasizes the importance of diurnal temperature changes. In tomato, Chili pepper and tobacco, high night temperatures were detrimental to vegetative growth and fruit setting. According to the author this is caused in the first place by a decrease in the transport of sugars from the leaves at high night temperatures, rather than by a stimulated dissimilation. According to PARKER and BORTHWICK (75) in soybean no beneficial effect of low night temperatures was found. FORTANIER (39) pointed out that the phenomenon of thermoperiodicity is less universal than is suggested by WENT. FORTANIER found that dry weight of parts above ground and elongation of stem in peanut were mainly dependent on the average temperature; 32 °C proved to be optimal, whereas great fluctuations in the diurnal temperature were detrimental to the production of dry matter and stem growth. The effect of low day or night temperatures could be counteracted by high night or day temperatures respectively.

As with soybean and peanut, growth in sesame was not favoured by low night temperatures (p. 10 and 17). WENT's theory apparently does not apply to these crops.

The length of stem increased as the photoperiod became longer no matter whether it consisted of daylight only, or of daylight and artificial light (p. 11).

This is in accordance with the data in literature. GHOSH (41) found that length of stem, number of branches and number of leaves and leaf area were reduced by shortening the natural daylength (India) to 7 or 9 hours. SEN and PAIN (90) compared the natural daylength, varying from $10\frac{1}{2}$ to $13\frac{1}{2}$ hours, with a shortened period of daylight (10 hours) and a period of daylight prolonged with artificial light to 14 hours. Generally there was a clear difference between 10 and 14 hours, the tallest plants occurring at the longest photoperiod. The controls (natural daylength) were intermediate in height, more or less depending on season, probably due to seasonal changes in daylength. According to SEN GUPTA and SEN (92) the length of stem at the onset of flowering was greatly reduced by shortening the natural daylength ($13\frac{1}{2}$–$12\frac{1}{2}$ hours) to 10 hours. KURNIK (56) imitated the daylength conditions of 0°, 20°, 30°, 35° and 40° latitude in Hungary (47°) by darkening for certain periods daily. He found that length of stem increased at higher latitudes. ALEKSEEV (1) shortened the natural daylength (Russia, latitude 47°) to 9 hours for 5, 10, 15, 20, 25, 30, 35, 40 days after seedling emergence. An increasing reduction in length of stem was found as more short days were given, and it was maximal if the short-day treatment was continued throughout the experiment. The effect of the first 5 to 10 short days was not clear-cut.

Substitution of daylight for artificial light in the various photoperiodic treatments did not always have a similar effect (see p. 15). At very short photoperiods, 7 hours or less, the daylight period was decisive for stem elongation, and replacement of daylight by artificial light affected stem growth adversely. The data in literature give no information on this point.

The maxima of the growth rates were attained later if the photoperiod was longer or shorter than $11\frac{1}{2}$ hours (p. 11). This is in accordance with ALEKSEEV who found that the maximum rate of stem growth was attained sooner if the natural daylength was shortened to 9 hours.

There was a positive correlation between length of stem and number of leaves (p. 18). This also appears from the data mentioned by GHOSH (41) but is not clearly shown from the data reported by SEN and PAIN (90).

The leaf area increased as photoperiods became longer, independent of their composition. However, substitution of daylight for artificial light induced a decrease in the leaf area (p. 19). A similar relation was found between dry weight of the stem base and photoperiod (p. 15), but in this case replacement of daylight by artificial light did not always have a detrimental effect.

It is clearly demonstrated in table 4 that a delay in flowering was accompanied by a more vigorous vegetative development. This is important with respect to the seed yield, as is shown in Chapter VI.

In literature no data are found on the effect of light conditions on dry weight and leaf area of sesame. Sesame responds to light periods of high intensity, whether or not extended by weak light, in very much the same way as peanut (39), Kalanchoë (45), chrysanthemum (102), sorghum (52) and other plants (113). The effect of light on stem growth, as described for sesame, is even more universal (21, 44, 74, 89, 97, 98, 105).

CHAPTER IV

EXPERIMENTS ON THE REPRODUCTIVE DEVELOPMENT
IV-1. THE JUVENILE PHASE

On June 12th, 1959, an experiment was started in the A-greenhouse in order to determine the stage at which the length of the photoperiod has no effect on floral initiation. The varieties used were 41 and Burmese mountain variety, as these varieties could be subjected to an adequate number of long days without interference of floral initiation.

Immediately after sowing 0, 5, 10, 15 or 20 long days were given. After this treatment each group, consisting of fourteen plants, was placed under short-day conditions. At the same time other groups of plants received 0, 5, 10 or 15 short days immediately after sowing, and this treatment was followed by long-day conditions. The photoperiod was 10 hours in short days and $10 + 10$ hours in long days. The intensity of the additional light was 2000 erg.sec.$^{-1}$cm^{-2}. The results are shown in graph 10.

In variety 41, when given five long days immediately after sowing, floral initiation was delayed by only one day, compared with the conditions of constant short days. Each following cycle of five long days gave a delay in floral initiation of about five days. This means that already five days after sowing, plants responded to a short-day treatment, which resulted in flowers being initiated about five days after the beginning of the treatment.

It also appeared that when more than five short days were given after sowing floral initiation was greatly advanced, compared with the conditions of constant long days.

The accelerating effect of the short-day treatment, however, was much more

NUMBER OF DAYS

LONG DAY, FLORAL INITIATION
"   "   FLOWERING
SHORT DAY, FLORAL INITIATION
"   "   FLOWERING

BURMESE MOUNTAIN VARIETY

VAR. 41

NUMBER OF SHORT [LONG] DAYS
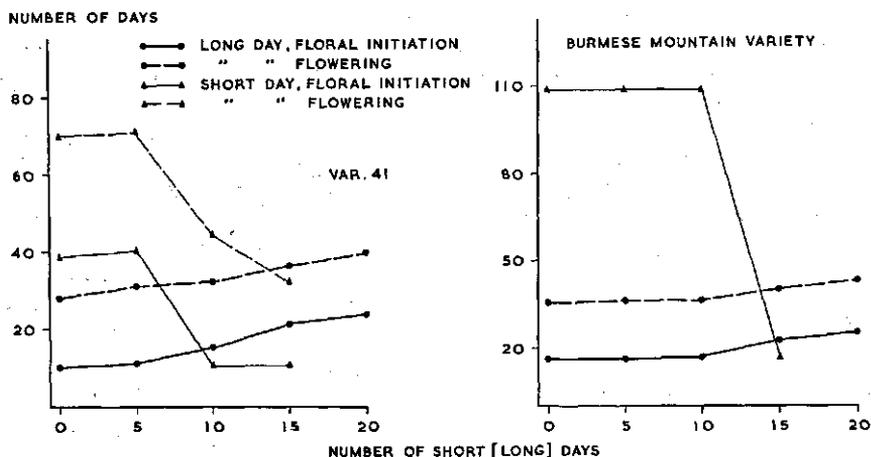
GRAPH 10. Number of days to floral initiation and flowering at different numbers of short or long days, given immediately after sowing, and followed by long-day or short-day conditions respectively.

pronounced than the retarding effect of the long-day treatment.

This result was confirmed by a similar experiment in a controlled environment room at a constant temperature of 27 °C.

In Burmese mountain variety the effect of short photoperiods manifested itself ten days after sowing. Thus the length of the juvenile phase is 10 days, see graph 10.

Something should be said about the number of days to flowering. If short-day conditions were preceded by 0 to 20 long days both floral initiation and flowering took place after the long-day treatment had been terminated. In this experiment the period between floral initiation and flowering proved to be independent of the number of long days given. This was found to be true for both varieties.

If in variety 41 long-day conditions were preceded by 10 to 15 short days floral initiation already occurred during the treatment, but flowering started after it. The period between floral initiation and flowering decreased as the number of short days increased. When only 0 to 10 short days were given before transfer to long-day conditions both floral initiation and flowering occurred under long days, and the period in between was almost constant.

In this experiment which had to be terminated in October owing to low temperatures, flowering could not be induced in Burmese mountain variety under long-day conditions, whether or not preceded by short days.

IV-2. FLORAL INITIATION

IV-2-1. *The transition from the vegetative to the reproductive phase.* In the vegetative stage the leaflets differentiating in the axillary buds of the leaves on the main stem are large in proportion to the size of the bud. Such buds reproduce the main stem or remain dormant (figure 1).

The reproductive stage is characterized by a broadening of the stem apex. This is, with some difficulty, macroscopically discernable. Dissecting and ex-

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amining microscopically is necessary, however. In this stage the leaflets differentiating in the axillary buds are very small in relation to the size of the bud. In this case the small leaves are bracteal leaves and the growing-point develops into a flower bud. The size of these buds is also large in proportion to the size of the growing-point of the main stem (figure 2).

In the vegetative phase the axillary buds are borne in the axils of leaves of a certain age, whereas in the reproductive phase the axillary buds that will develop into flower buds are already borne in the axils of even the youngest leaves.

IV-2-2. *Relation between leaves and induction.* Floral initiation was investigated at different degrees of defoliation in order to determine the number of leaves required for perception of the floral stimulus. The following degrees of defoliation were applied in Dulce:

1. Leaves removed as they appeared, after the development of cotyledons.
2. As in 1, but one leaf on the 1st node left.
3. As in 1, but both leaves on the first node left.
4. As in 1, but both leaves on the 1st and 2nd node left.

This experiment was started in the C-greenhouse on July 1st, 1959. Photoperiods of 10 hours and 10 + 10 hours were given. The intensity of the additional light was 2000 erg.sec.$^{-1}$cm^{-2}. The leaves were removed as soon as possible and every day the newly grown leaves were cut back. Twenty to twenty-four plants. were used in the treatments 3 and 4, and about thirty-five in the treatments 1 and 2.

At the 10-hour photoperiod the four defoliated groups of plants attained the reproductive phase after 15 days just as the non-defoliated control. In each group the first flower bud was found in node number three. The defoliation of group 4 had just been started about this time.

At the photoperiod of 10 + 10 hours group 2, 3 and 4 attained the reproductive phase after 23 days, same as the non-defoliated control. The first flower bud in these groups was found in node number five or six.

Group 1 (completely defoliated but cotyledons left), however, was still in the vegetative phase when the experiment was terminated after 105 days. This reduction of the leaf area by complete defoliation, cotyledons excepted, could not prevent plants from initiating floral primordia if the photoperiod was 10 hours, but did prevent initiation at a 10 + 10-hour photoperiod. Under favour-. able photoperiodic conditions (10 hours) the leaf area that is capable of perceiving the floral stimulus is very small indeed, even the area of two cotyledons· appeared to be sufficient. This is discussed in more detail on p. 39. The relation between leaves and reproductive development is also dealt with in Chapter V.

IV-2-3. *Temperature under artificial light conditions.* The experiments were carried out in controlled environment rooms. At a 10-hour photoperiod four temperature groups were taken into account:

1. Constant temperatures: 21°, 24°, 27°, 30° and 33 °C.
2. The same night temperature (15 °C); different day temperatures: 24°, 27°, 30°, 33°, 36 °C. ·
3. The same night temperature (33 °C); different day ·temperatures: 21°, 24°, 27 °C.
4. The same day temperature (27 °C); different night temperatures: 21°, 24°, 30 °C.
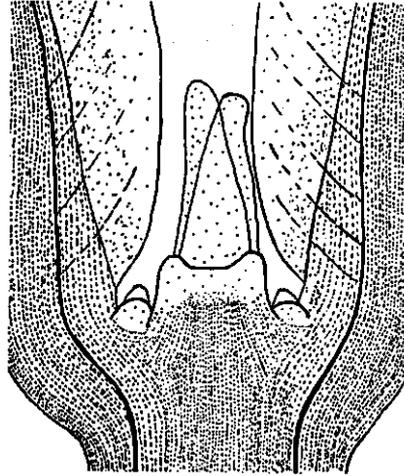
FIG. 1. Vegetative stage. Magnification 270 ×.
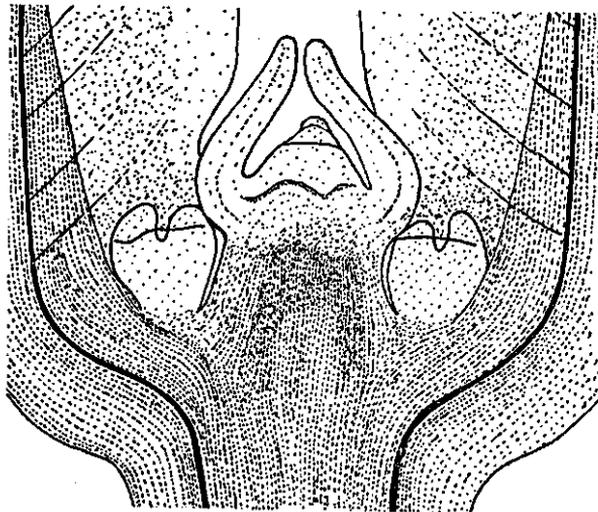
FIG. 2 Reproductive stage. Magnification 270 ×.

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The day temperature was given for 10 hours, the night temperature for 14 hours. The mean temperature is calculated from the formula:

$$\frac{10 \times \text{day temperature} + 14 \times \text{night temperature}}{24}$$

The notation a°–b°C means: a day temperature of a°C combined with a night temperature of b°C.

In this experiment ten plants of each of the varieties Early Russian, N 1119-3, Margo, Venezuela-51, N.P.-6, TMV-2 and Strain 41 were used. The average number of days to floral initiation and the average node number of the first flower bud were determined, see table 6 and 7.

TABLE 6. Number of days to floral initiation at different temperature combinations. Photoperiod 10 hours; temperature in °C.

Temperature			Variety							Average
Day	Night	Mean	Early Russian	N 1119-3	Margo	Venezuela-51	N.P.-6	TMV-2	41	
21	21	21	22	22	24	28	20	21	21	22.6 ± 1.7*
24	24	24	20	18	19	23	16	16	17	18.4 ± 0.9
27	27	27	21	19	19	19	16	16	16	18.0 ± 0.7
30	30	30	23	21	27	28	17	17	17	21.4 ± 1.7
33	33	33	34	36	32	38	24	24	28	30.9 ± 2.0
24	15	18.8	28	–	–	–	25	–	–	26.5
27	15	20.0	21	26	31	31	21	20	23	24.7 ± 1.7
30	15	21.3	17	28	30	31	19	19	20	23.4 ± 2.1
33	15	22.5	19	28	30	36	19	18	20	24.3 ± 2.5
36	15	23.8	18	27	29	36	18	19	18	23.6 ± 2.5
21	33	28.0	26	–	25	27	20	19	20	22.8 ± 1.4
24	33	29.3	37	36	34	35	21	19	17	28.4 ± 3.1
27	33	30.5	34	34	34	35	27	18	22	29.1 ± 2.4
33	33	33	34	36	32	38	24	24	28	30.9 ± 2.0
27	15	20.0	21	26	31	31	21	20	23	24.7 ± 1.7
27	21	23.5	18	21	19	22	17	17	17	18.7 ± 0.7
27	24	25.3	17	17	17	19	16	16	16	16.9 ± 0.4
27	27	27	21	19	19	19	16	16	16	18.0 ± 0.7
27	30	28.8	21	21	22	22	20	20	21	21.0 ± 0.3
27	33	30.5	34	34	34	35	27	18	22	29.1 ± 2.4

* Standard error of mean

At constant temperatures (group 1) floral initiation was earliest at a temperature of 24° to 27°C. In the range of 21° to 24°C floral initiation was advanced, whereas the average node number of the first flower bud remained constant. Partly this should be interpreted as an improvement of the growing conditions. In the range of 27°C to 33°C an increasing number of days to floral initiation was attended by a higher average node number of the first flower bud.

Under conditions of low night temperatures (group 2) no significant differences occurred in the number of days to floral initiation and in the average node

number of the first flower bud. At 24°–15°C the growth of most varieties was very poor and only the data on Early Russian and N.P.-6 were recorded.

Comparison of group 1 and group 2 shows, that floral initiation was retarded by low night temperatures. The extension of the vegetative phase was not reflected in the production of more nodes. Early Russian was not delayed by low night temperatures. The delaying effect of low night temperatures was not found at a day temperature of 33 °C.

Under conditions of high night temperatures (group 3) no significant differences were found between 24°–33 °C, 27°–33 °C and 33°–33 °C in the number of days to floral initiation and the position of the first flower bud. In some cases (TMV-2 and 41) the 33°–33 °C treatment was somewhat later than the other treatments. At 21°–33 °C floral initiation of Early Russian, Margo and Venezuela-51 was essentially advanced by the relatively low day temperature. The highest node of the first flower bud was found at 33°–33 °C.

TABLE 7. Average node number of the first flower bud at different temperature combinations. Photoperiod 10 hours; temperature in °C.

Temperature			Variety							Average
Day	Night	Mean	Early Russian	N 1119-3	Margo	Venezuela-51	N.P.-6	TMV-2	41	
21	21	21	2.9	3.0	2.8	3.0	2.6	2.9	2.5	2.8 ± 0.2
24	24	24	2.9	3.1	2.6	3.0	2.9	3.0	2.3	2.8 ± 0.1
27	27	27	3.5	3.0	3.3	3.0	3.0	3.0	2.2	3.0 ± 0.1
30	30	30	4.1	4.3	3.2	4.4	3.3	3.8	2.4	3.6 ± 0.3
33	33	33	6.9	6.4	5.9	6.4	5.5	4.8	5.7	5.9 ± 0.2
24	15	18.8	2.5	–	–	–	2.6	–	–	2.6
27	15	20.0	2.9	3.9	3.1	4.2	2.3	2.8	2.4	3.1 ± 0.2
30	15	21.3	2.9	4.0	4.0	4.0	2.8	3.1	2.1	3.3 ± 0.2
33	15	22.5	2.8	4.1	4.0	4.8	3.0	3.0	2.5	3.5 ± 0.3
36	15	23.8	3.0	4.3	4.1	4.6	3.0	3.0	2.7	3.5 ± 0.3
21	33	28.0	4.5	–	4.8	4.6	3.9	4.0	3.8	4.3 ± 0.2
24	33	29.3	6.1	5.7	4.8	5.9	4.4	3.5	2.2	4.7 ± 0.5
27	33	30.5	6.1	5.5	4.9	5.5	5.3	3.4	3.6	4.9 ± 0.4
33	33	33	6.9	6.4	5.9	6.4	5.5	4.8	5.7	5.9 ± 0.2
27	15	20.0	2.9	3.9	3.1	4.2	2.3	2.8	2.4	3.1 ± 0.2
27	21	23.5	2.1	3.0	2.2	2.9	2.0	2.9	2.1	2.5 ± 0.2
27	24	25.3	3.0	3.0	3.0	3.0	3.0	3.5	2.2	3.0 ± 0.2
27	27	27	3.5	3.0	3.3	3.0	3.0	3.0	2.2	3.0 ± 0.2
27	30	28.8	2.1	2.7	2.2	3.3	2.0	2.3	2.0	2.4 ± 0.2
27	33	30.5	6.1	5.5	4.9	5.5	5.3	3.4	3.6	4.9 ± 0.4

If 30°–30 °C is compared with 24°–33 °C and 27°–33 °C, it appears that, with almost equal mean temperatures, floral initiation was later in the treatments with the highest night temperature.

Under conditions of different night temperatures (group 4) a minimum number of days to floral initiation was found at 27°–24 °C. Especially at 27°–33 °C and 27°–15 °C floral initiation was delayed, except in TMV-2. The location of the first flower bud fluctuated somewhat in most varieties and was

not clearly associated with the temperature. The highest node was found at 27°–33 °C, except in TMV-2.

At a 10 + 7-hour photoperiod three temperature groups were applied:
1. Different constant temperatures: 21°, 24°, 27°, 30° and 33 °C.
2. The same night temperature (15 °C); different day temperatures: 24°, 27°, 30° and 33 °C.
3. The same day temperature (27 °C); different night temperatures: 21°, 24°, 30° and 33 °C.

As it not was possible to test the whole range of temperature combinations applied at the 10-hour photoperiod, the 36°–15 °C treatment was omitted, whereas the night temperature of 33 °C was only combined with a day temperature of 27 °C. This was not considered a serious drawback.

The intensity of the additional light was 1500 erg.sec.$^{-1}$cm^{-2} at plant level. The mean temperature is calculated as follows:

$$\frac{17 \times \text{day temperature} + 7 \times \text{night temperature}}{24}$$

Generally eight to twelve plants of each of the varieties Early Russian, N 1119-3, Margo, Venezuela-51, N.P.-6, TMV-2 and 41 were used in each treatment. Because of the variation in the results of the latter four varieties, the number of observations (between brackets) and the standard errors of means are given in table 8 and 9.

TABLE 8. Number of days to floral initiation at different temperature combinations. Photoperiod 10 + 7 hours; temperature in °C.

Temperature			Variety						
Day	Night	Mean	Early Russian	N1119-3	Margo	Venezuela-51	N.P.-6	TMV-2	41
21	21	21	27	30	36	>53	36	>67	75 (4)
24	24	24	23	25	35	>67	34	>67	>67
27	27	27	25	31	32	43±6.0 (6)	35	76±2.4(11)	100±2.0 (4)
30	30	30	25	34	41	43±1.4(12)	65±9.2(6)	101±4.3 (9)	>122
33	33	33	35	35	43	42±1.2(13)	95±4.4(5)	101±5.5(12)	109 (1)
24	15	21.4	25	39	35	48±1.6 (4)	26	36±1.0(12)	31 (10)
27	15	23.5	29	40	36	49 (4)	24	33 (9)	33 (11)
30	15	25.6	27	37	33	40±1.0 (6)	24	37±1.0 (7)	34±2.3 (7)
33	15	27.8	23	35	36	48±2.5 (8)	26	–	–
27	15	23.5	29	40	36	49 (4)	24	33 (9)	33 (11)
27	21	25.3	23	27	33	49±2.5 (6)	27	61±3.8 (5)	70±4.2 (6)
27	24	26.1	26	26	29	48±1.5 (3)	28	47±3.0 (8)	89±5.8 (5)
27	27	27	25	31	32	43±6.0 (6)	35	76±2.4(11)	100±2.0 (4)
27	30	27.9	27	29	33	43±1.5 (7)	41	72±2.1 (8)	95 (1)
27	33	28.8	29	32	41	39±1.6 (7)	48	83±1.5 (5)	92±7.0 (2)

At constant temperatures (group 1) the optimum temperature for floral initiation was about 24° to 27 °C; however, the value for Venezuela-51, TMV-2 and 41 is not exactly known, as most plants of these varieties succumbed before

TABLE 9. Average node number of the first flower bud at different temperature combinations. Photoperiod 10 + 7 hours; temperature in °C.

Temperature			Variety						
Day	Night	Mean	Early Russian	N1119-3	Margo	Venezuela-51	N.P.-6	TMV-2	41
21	21	21	4.0	4.8	4.0	–	4.5	–	4.0
24	24	24	4.7	5.0	4.6	–	6.6	–	–
27	27	27	5.4	6.7	5.9	7.2 ± 0.6	7.0	11.4	11.9 ± 0.6
30	30	30	6.3	6.9	6.1	7.8 ± 0.5	11.4 ± 1.1	12.3 ± 0.2	–
33	33	33	9.2	8.7	7.2	8.4 ± 0.4	19.2 ± 0.8	14.5 ± 0.6	24.0
24	15	21.4	4.0	7.0	5.0	6.0	5.0	5.8	5.2
27	15	23.5	5.6	8.6	5.9	7.0	5.0	6.8	5.7 ± 0.3
30	15	25.6	5.6	8.7	5.5	8.2	5.4	7.5	6.7 ± 0.4
33	15	27.8	5.6	7.3	5.8	8.6 ± 0.5	5.3	–	–
27	15	23.5	5.6	8.6	5.9	7.0	5.0	6.8	5.7 ± 0.3
27	21	25.3	4.5	6.3	5.2	9.0 ± 0.8	6.2	9.6 ± 0.6	9.5 ± 0.5
27	24	26.1	4.6	6.5	4.9	8.7	6.5	8.8	9.9 ± 1.1
27	27	27	5.4	6.7	5.9	7.2 ± 0.6	7.0	11.4	11.9 ± 0.6
27	30	27.9	6.0	7.0	6.0	6.9	8.6	10.9	10.0
27	33	28.8	6.5	7.4	6.6	7.3	10.6	12.0	12.5

floral initiation at 21° and 24 °C. Only a few plants of variety 41 attained the reproductive phase before the experiment was terminated.

The node number of the first flower bud increased with an increase in temperature.

Under conditions of low night temperatures (group 2) only small differences appeared in the number of days to floral initiation and the node number of the first flower bud.

Comparing group 1 and group 2 shows that in Early Russian, N 1119-3 and Margo floral initiation was delayed by low night temperatures. At a day temperature of 33 °C, however, floral initiation was advanced by low night temperatures in Early Russian and Margo. In N.P.-6, TMV-2 and 41 floral initiation was markedly advanced by low night temperatures, especially at high day temperatures.

At different night temperatures (group 3) there was not much conformity in the behaviour of the varieties. Floral initiation in Early Russian was earliest at 27°–21 °C, in N 1119-3 and Margo at 27°–24 °C, whereas in the varieties N.P.-6, TMV-2 and 41 it was delayed in the range of 27°–15 °C to 27°–33 °C; in Venezuela-51 no significant differences were found. Generally the node number of the first flower bud became higher as the number of days to floral initiation increased.

IV-2-4. *Temperature under natural light conditions.* The effect of high night temperatures was investigated in an experiment started in the A-greenhouse on April 21, 1959. One compartment could be heated electrically and in this way minimum night temperatures were maintained above 25 °C, and varied between 25 °C and 35 °C. Without heating minimum night temperatures varied from 15°–20 °C. The photoperiod was 10 + 10 hours and the intensity of the additional light 2000 erg.sec.$^{-1}$cm^{-2}. This experiment was done to verify the results

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found in the Indian varieties N.P.-6, TMV-2 and 41 under controlled tempe-
rature conditions. The fact is that in these varieties the delaying effect of long
photoperiods on floral initiation was greatly compensated for by low night
temperatures. As the U.S.A. varieties Early Russian, N 1119-3, Margo and
Venezuela-51 were not interesting in this respect, a few more varieties from
tropical regions were used in this experiment, viz. the Indian varieties S 85 and
T 10, the Burmese varieties Hnan Yin and Judium, and the Nigerian variety
Botanist 055. The photoperiodic response of these varieties (T 10 excepted)
under greenhouse conditions had already been tested previously (see p. 30), and
it was shown that floral initiation was delayed at photoperiods longer than
$11\frac{1}{2}$ hours. The number of days to floral initiation and flowering was determined,
see table 10.

TABLE 10. Number of days to floral initiation and flowering at different night temperatures,
and average node number of the first flower bud; photoperiod $10 + 10$ hours.

Variety	Night temperature 25°–35 °C			Night temperature 15°–20 °C		
	Fl. Init.	Flowering	Av. node number	Fl. Init.	Flowering	Av. node number
Bot. 055	42	72	14.0	43	67	12.0
Hnan Yin	60	90	17.4	36	57	9.7
Judium	32	62	11.0	32	54	9.4
T 10	37	81	15.2	37	85	12.9
TMV-2	39	71	11.0	37	61	8.9
N.P.-6	28	57	10.0	30	57	9.4
41	37	63	10.8	39	70	10.7
S 85	72	116	21.2	59	110	15.6

From table 10 it is evident that in most varieties the number of days to floral
initiation was not increased by night temperatures above 25 °C. There were
two exceptions: in Hnan Yin an increase of 24 days and in S 85 an increase of
13 days was found. The delaying effect of high night temperatures at long photo-
periods which was found in N.P.-6, TMV-2 and 41 under artificial light con-
ditions (controlled environment rooms), was not shown under greenhouse
conditions in this experiment.

Flowering was somewhat retarded in the varieties Botanist 055, Judium,
TMV-2, S 85, highly retarded in Hnan Yin, and accelerated in T 10 and 41
by night temperatures in the range of 25°–35 °C. These differences are difficult
to explain, as all varieties originated from tropical regions.

The number of nodes produced before floral initiation was larger at night
temperatures above 25 °C, probably as a result of an improvement of the grow-
ing conditions. Apparently growth of these tropical varieties is favoured by
high night temperatures, although diminution of diurnal fluctuations in tem-
perature may exert the most important effect.

IV-2-5. *Light*. On April 25, 1958, a preliminary experiment on the effect
of the photoperiod on the reproductive development was started. The photo-
period consisted of daylight whether or not prolonged by weak light from
daylight fluorescent tubes. In the A-greenhouse the intensity of the additional
light was 2000 erg.sec.$^{-1}$cm^{-2} at plant level. In the C-greenhouse the plants were
darkened by black cloth laid on frames and the intensity of the additional light

was 250 erg.sec.$^{-1}$cm^{-2} at plant level. In the first experiment the following photoperiods were given: 7, 7 + 3, 7 + 9, 10, 10 + 3, 10 + 6, 13, 13 + 3 hours in the A-greenhouse and 8½ and 11½ hours in the C-greenhouse. The varieties involved were two from temperate zones, viz. Early Russian and Venezuela-51 (U.S.A.); six from tropical regions: Hnan Yin (Burma), Judium (Burma), TMV-2 (India), N.P.-6 (India), 41 (India) and Botanist 055 (Nigeria). Some treatments were limited in Botanist 055 and 41, owing to lack of space in the greenhouses. The results are shown in table 11.

TABLE 11. Number of days to floral initiation and flowering at different photoperiods. Between brackets C-greenhouse control.

Photoperiod in hours	Early Russian		Venezuela-51		Judium		Hnan Yin	
	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering
7	18	42	20 (18)	46 (45)	17 (17)	37 (37)	19 (19)	41 (41)
7 + 3	17	39	19	45	17	37	21	41
7 + 9	18	40	28	56	21	44	35	52
8½	17	38	18	41	18	36	19	39
10	15	35	18 (17)	40 (40)	16 (16)	36 (34)	19 (20)	38 (39)
10 + 3	16	34	19	43	18	38	22	43
10 + 6	18	37	28	54	25	46	28	49
11½	15	34	18	39	16	36	20	39
13	17	35	18	41	18	40	22	43
13 + 3	18	37	27 (27)	57 (56)	28 (28)	49 (49)	30 (35)	53 (55)

Photoperiod in hours	TMV-2		N.P.-6		41		Botanist 055	
	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering
7	18 (18)	42 (42)	18	38	–	–	–	–
7 + 3	18	40	17	37	–	–	–	–
7 + 9	27	50	18	39	27	50	33	56
8½	17	39	16	35	16	36	20	41
10	17 (17)	39 (39)	17	35	15	33	20	40
10 + 3	19	41	18	35	15	34	25	48
10 + 6	29	54	24	40	27	51	33	58
11½	18	39	15	33	16	37	18	41
13	20	42	17	36	–	–	–	–
13 + 3	31 (33)	54 (56)	24	43	29	52	35	61

All varieties attained the reproductive phase at the photoperiods thus chosen. The smallest number of days to floral initiation was found at photoperiods of 10 and 11½ hours. If the photoperiod was longer than 11½ hours floral initiation was delayed. The delay from 11½ to 16 hours varied between three and fifteen days depending on the variety. At photoperiods shorter than 8½ hours, floral initiation was retarded by only a few days.

A photoperiod of 7 + 3 instead of 10 hours, induced a delay of two days at most. No differences were found between 7 + 9, 10 + 6, and 13 + 3 hours in the varieties Early Russian, Venezuela-51, TMV-2, 41 and Botanist 055. In Judium and N.P.-6 the number of days to floral initiation was increasing in the order of the above photoperiods, whereas in Hnan Yin the smallest number of days was found at 10 + 6 hours.

The treatments had to be spread over two greenhouses. With regard to the number of days to floral initiation and flowering in some varieties tested, no essential difference was found between both greenhouses. This was demon-

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strated in Venezuela-51, TMV-2, Hnan Yin and Judium at photoperiods of 7, 10, and 13 + 3 hours (table 11).

The 13 + 3-hour treatments in both greenhouses differed not only in climatical conditions, but also in the intensity of the additional illumination. In the compartments of the A-greenhouse the intensity of the additional light was much higher than under the frames, covered by black cloth, in the C-greenhouse. It was not possible to increase the light intensity in the C-greenhouse by suspending more lamps on the frames, as this shaded the plants too much during the daytime. But even this difference gave no rise to essential discrepancies.

In the second experiment, however, when the treatments had to be spread again over two greenhouses, the difference in intensity of supplemental light was reduced by using only one lamp in the compartments. In this experiment, which was set up on June 19, 1958, attention was paid to photoperiods in the ranges of 16 to 24 hours, and 7 to 5 hours. The same equipment was used as in the first experiment, but the intensity of the additional light in the A-greenhouse was 500 erg.sec.$^{-1}$cm^{-2}.

In the C-greenhouse the photoperiods were: 5, 5 + 1, 5 + 2, 6 + 1, 7, 8½, 11½ hours; in the A-greenhouse: 10, 10 + 3, 10 + 6, 10 + 10, 10 + 14, 13, 13 + 7, 13 + 11 hours. Early Russian and Venezuela-51 were used again, whereas the photoperiodic response of some other varieties was tested, viz. Dulce (U.S.A.), S 85 (India) and Boke Htaung (Burma). Moreover the aim of this experiment was to observe vegetative growth (p. 11) and fruit production (p. 51). Of each variety ten plants were used; S 85 and Boke Htaung could not be included in the 7-, 8½-, 11½- and 13-hour treatments. The data on floral initiation and flowering are given in table 12, and some of the results are entered in graph 11.

The results are in accordance with the data from the first experiment. The number of days to floral initiation increased at photoperiods longer than 10 to 11½ hours. This increase was hardly significant in the range of 11½ to 13 hours, including the photoperiod of 10 + 3 hours. Early Russian was not delayed up to a photoperiod of 16 hours.

In the range of 16 to 24 hours the greatest delay in floral initiation was found at 24 hours. This amounted to 10, 11, 15, 23 and 65 days for Boke Htaung, Dulce, Early Russian, Venezuela-51 and S 85 respectively.

The differences between 10 and 13 hours of daylight at photoperiods of the same length but of different composition were slight. In Venezuela-51 and Boke Htaung the plants placed at 10 + 10 hours were somewhat earlier than those at 13 + 7 hours, but the difference disappeared at 24 hours. In Early Russian and Dulce the plants grown at 10 + 3 hours were somewhat earlier than those at 13 hours. The data on S 85 at photoperiods of 13 + 7 and 13 + 11 hours were unreliable because too many plants had to be used for dissection.

An increasing delay in floral initiation was found at photoperiods in the range of 10 to 5 hours, especially in Early Russian, Dulce and Venezuela-51, and to a less extent in Boke Htaung and S 85.

If the photoperiod was only 7 hours or less, its composition became important. At photoperiods of 7 hours (7, 6 + 1 and 5 + 2 hours) floral initiation was earliest if the photoperiod consisted of daylight only. The difference between 5 + 2 and 7 hours was 10 days in Early Russian and Dulce, and 7 days in Venezuela-51.

No differences existed between 5, 5 + 1 and 5 + 2 hours with respect to the date of floral initiation.
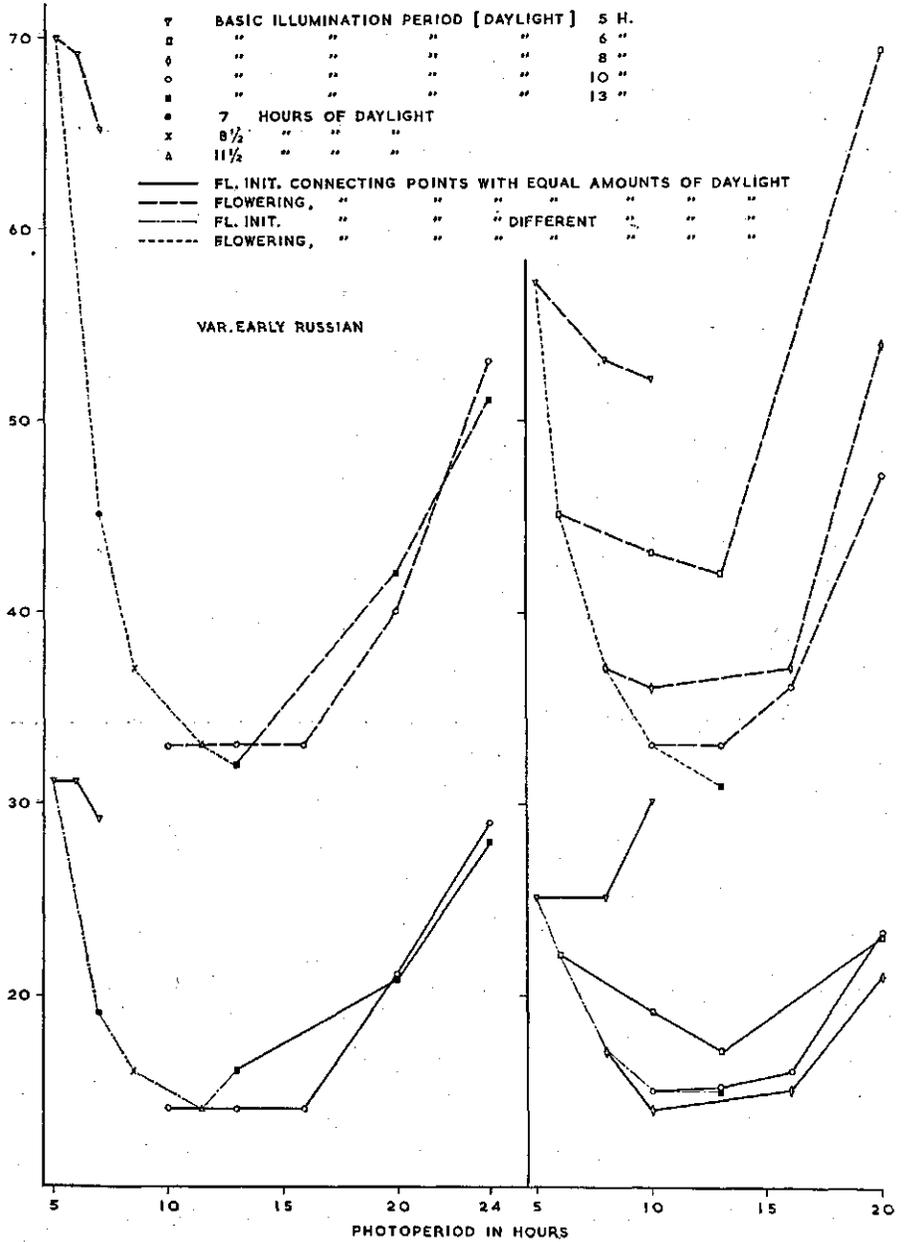
GRAPH 11. Number of days to floral initiation and flowering at different photoperiods for variety Early Russian; to the left 1958, to the right 1959.

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From these data the conclusion is justified that the delay in floral initiation in the range of 7 to 5 hours was mainly caused by a photosynthetic effect. The first flower bud of Early Russian, Dulce, Venezuela-51 and S 85 was found in the second or third node, and in Boke Htaung in the first or second node, at all photoperiods between 5 and 10 hours. The average position at different photoperiods is shown in table 13. It appeared that the delay in floral initiation was not attended by an increase in the number of leaves produced.

TABLE 12. Number of days to floral initiation and flowering at different photoperiods.

Photoperiod in hours	Early Russian		Dulce		Venezuela-51		S 85		Boke Htaung	
	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering
5	31	70	31	72	29	74	24	57	23	47
5 + 1	31	69	30	74	30	73	23	53	23	46
5 + 2	29	65	30	70	29	71	23	52	23	48
6 + 1	24	52	26	53	25	58	22	45	22	42
7	19	45	20	46	22	50	–	–	–	–
8½	16	37	18	40	20	44	–	–	–	–
10	14	33	18	36	16	40	16	35	14	33
10 + 3	14	33	16	37	19	43	16	36	15	34
10 + 6	14	33	19	39	21	48	25	52	17	37
10 + 10	21	40	25	49	29	63	40	67	19	45
10 + 14	29	53	27	56	39	78	81	>100	24	46
11½	14	33	17	36	17	38	–	–	–	–
13	16	32	19	38	19	43	–	–	–	–
13 + 7	21	42	26	50	34	70	–	–	23	48
13 + 11	28	51	26	59	39	73	–	–	24	52

TABLE 13. Average node number of the first flower bud and flower at different photoperiods.

Photoperiod in hours	Early Russian		Dulce		Venezuela-51		S 85		Boke Htaung	
	Flower-bud	Flower	Flower-bud	Flower	Flower-bud	Flower	Flower-bud	Flower	Flower-bud	Flower
5	2.5	3.4	3.0	3.8	2.0	2.8	2.0	2.7	1.5	2.5
5 + 1	2.8	3.7	3.0	4.4	3.0	3.8	2.1	3.0	1.5	2.0
5 + 2	2.5	3.4	3.0	3.3	2.8	4.0	2.1	3.0	1.5	2.1
6 + 1	2.7	3.5	3.0	3.2	2.2	2.7	2.2	3.0	1.0	1.3
7	2.5	3.5	2.4	2.8	2.0	2.3	–	–	–	–
8½	2.3	3.4	2.5	3.0	2.1	2.9	–	–	–	–
10	2.2	2.5	3.0	3.0	2.7	3.5	2.5	3.0	1.0	2.0
10 + 3	2.2	2.4	3.0	3.0	3.0	4.0	3.0	3.4	1.9	2.1
10 + 6	2.2	2.9	3.0	3.1	3.7	5.5	6.1	6.6	2.3	2.6
10 + 10	4.2	5.0	4.9	5.5	6.0	7.9	9.0	10.2	3.0	3.9
10 + 14	7.2	7.6	6.1	6.9	8.7	11.7	16.7	–	3.2	4.0
11½	2.0	2.5	2.6	2.9	2.0	3.2	–	–	–	–
13	2.3	2.4	3.0	3.4	3.0	4.5	–	–	–	–
13 + 7	4.8	5.5	5.4	5.7	8.3	9.5	–	–	4.0	4.9
13 + 11	7.3	7.5	6.2	7.4	8.4	9.8	–	–	5.3	6.0

If the photoperiod was longer than 10 hours the average node number of the first flower bud rose as the number of days to floral initiation increased. In other words a delay in floral initiation was accompanied by an increase in the number of leaves produced during the vegetative stage.

A supplemental experiment in the C-greenhouse was set up to investigate the nature of the delay in floral initiation at extremely short photoperiods. In this

experiment twenty plants of the varieties Early Russian, Dulce and Boke Htaung were grown at a photoperiod of 13 + 7 hours. After 23 days six expanded and six unexpanded leaves had formed. By this time the long-day treatment was discontinued and a short-day treatment, consisting of 5 or 10 hours of light daily, was given. The plants were still in the vegetative phase when the short-day treatment was started. Both the plants which received 5 hours of daylight as well as those receiving 10 hours attained the reproductive phase after six days. Apparently after reaching a certain level of vegetative growth, the plant shows no further delay in floral initiation at a photoperiod of 5 hours.

A third experiment was started on April 23, 1959. Special attention was paid to the differences between photoperiods of the same duration and composed of different periods of daylight. The whole experiment was carried out in the C-greenhouse with the varieties Early Russian, Dulce, Venezuela-51 and S 85. Vegetative growth (p. 15) in Venezuela-51, Early Russian and Dulce, and capsule production (p. 52) in the two latter varieties were also observed. The number of plants per treatment was twenty-one in Early Russian and Dulce, fourteen in Venezuela-51 and seven in S 85. The following photoperiods were given: 5, 5 + 3, 5 + 5, 6, 6 + 4, 6 + 7, 6 + 14, 8, 8 + 2, 8 + 8, 8 + 12, 10, 10 + 3, 10 + 6, 10 + 10 and 13 hours; the intensity of the additional light in the compartments was 2000 erg.sec.$^{-1}$cm^{-2}. The results are shown in table 14, and some of them are illustrated in graph 11.

TABLE 14. Number of days to floral initiation and flowering at different photoperiods.

Photoperiod in hours	Early Russian		Dulce		Venezuela-51		S 85	
	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering
5	25	57	34	60	34	62	25	52
5 + 3	25	53	33	61	31	61	25	50
5 + 5	30	52	34	61	33	61	25	51
6	22	45	25	49	26	52	22	45
6 + 4	19	43	21	47	24	52	20	42
6 + 7	17	42	21	48	24	57	25	50
6 + 14	23	69	42	69	57	91	61	100
8	17	37	18	40	21	45	18	38
8 + 2	14	36	18	41	18	45	17	36
8 + 8	15	37	26	50	30	59	35	58
8 + 12	21	54	32	59	54	83	49	105
10	15	33	16	37	18	41	17	35
10 + 3	15	33	15	36	16	41	20	45
10 + 6	16	36	19	43	22	53	36	62
10 + 10	23	47	25	50	31	73	46	93
13	15	31	15	35	17	43	23	47

The shortest vegetative phase in S 85 occurred at 10 hours, in Dulce and Venezuela-51 at 10–13 hours, and in Early Russian at 10–16 hours. The composition of the photoperiod in this optimal region was of minor importance, provided that at least 8 hours of daylight were given.

At super optimal photoperiods floral initiation was delayed. The number of days to floral initiation increased as the part of the photoperiod consisting of artificial light became longer. In Early Russian and S 85, however, the differences between 8 +8 and 10 +6 hours on the one hand, and 8 + 12 and 10 +10 hours on the other, were slight. The differences between basic illumination

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periods of 6 and 10, and 8 and 10 hours were not constant, but increased at lengthening photoperiods. This did not hold true for Early Russian and S 85, though in the latter variety the difference between 6 and 10 hours of daylight was greatest at the longest photoperiod. In Venezuela-51 the difference between 8 and 10 hours of daylight rose from 0 days at 10 hours to 23 days at 20 hours. The behaviour of Dulce was less extravagant.

At sub-optimal photoperiods, i.e. shorter than 10 hours, the delay in floral initiation increased as the part consisting of daylight decreased, see table 15 (data taken from table 14).

TABLE 15. Effect of the composition of the photoperiod. Delay in floral initiation in days compared with controls which received 10 hours of daylight.

Variety	Photoperiod						
	10 hours			13 hours	16 hours	20 hours	
	5 + 5	6 + 4	8 + 2	6 + 7	8 + 8	6 + 14	8 + 12
Early Russian	15	4	−1	2	−1	0	−2
Dulce	18	5	2	6	7	17	7
Venezuela-51	15	6	0	8	8	26	23
S 85	7	3	0	5	−1	15	3

Only minor differences were found between photoperiods of 5, 5 + 3 and 5 + 5 hours. Floral initiation in plants placed at 6 hours was somewhat delayed as compared with those having received 6 + 4 hours; a similar tendency occurred at 8 and 8 + 2 hours.

From these results it appears that the actual photoperiodic effect is of minor significance in this range of sub-optimal photoperiods. Comparison of 5 + 5 with 10 hours and of 6 + 4 with 10 hours, however, reveals significant differences at photoperiods of the same duration. Evidently the delay in floral initiation at sub-optimal photoperiods was primarily caused by poor growth.

As in the previous experiment there was little variation in the position of the first flower bud at all photoperiods between 10 and 5 hours, see table 16.

TABLE 16. Average node number of the first flower bud and flower at different photoperiods.

Photoperiod in hours	Early Russian		Dulce		Venezuela-51		S 85	
	Flowerbud	Flower	Flowerbud	Flower	Flowerbud	Flower	Flowerbud	Flower
5	2.6	3.7	3.0	4.7	3.0	4.5	2.9	3.1
5 + 3	2.9	3.3	3.3	5.0	3.1	5.2	2.9	3.2
5 + 5	3.0	3.9	3.8	5.1	3.2	5.1	2.9	3.3
6	2.1	3.1	2.7	3.2	–	–	2.6	2.8
6 + 4	2.0	3.0	2.9	3.4	3.0	–	2.7	3.0
6 + 7	2.0	2.9	2.2	3.1	3.4	5.6	3.7	3.9
6 + 14	5.8	11.2	6.4	8.2	10.4	12.6	10.8	16.4
8	2.0	2.7	2.2	3.0	2.8	3.9	2.1	2.7
8 + 2	2.0	2.7	2.0	3.0	2.2	4.4	2.8	3.3
8 + 8	2.0	2.9	5.0	5.1	5.7	7.4	7.3	8.3
8 + 12	3.9	7.2	6.1	6.9	9.8	12.0	12.7	20.0
10	1.9	2.3	2.2	2.4	2.2	3.2	2.7	2.9
10 + 3	2.0	3.0	2.3	2.8	2.8	4.1	5.9	6.0
10 + 6	3.0	3.7	4.0	4.0	4.9	6.7	8.9	9.7
10 + 10	5.8	6.8	5.9	6.4	8.8	10.7	13.9	22.0
13	2.0	2.6	2.2	2.4	2.7	4.4	7.2	7.2

A slight increase in the average node number of the first flower bud sometimes occurred at photoperiods consisting of 6 hours of natural daylight or less. In the range of 10 to 20 hours, however, a much larger increase in the average node number of the first flower bud was found.

The great number of days to floral initiation at a photoperiod of 6 + 14 hours (Dulce, Venezuela-51 and S 85) was not accordingly reflected in the production of leaves (nodes) before floral initiation.

In an experiment in the A-greenhouse, started on April 21, 1959, the photoperiodic behaviour of the varieties Botanist 055, Hnan Yin, Judium, Stamboom 54, T 10, TMV-2, N.P.-6, 41 and Burmese mountain variety was tested. Most varieties had already been used in a previous experiment (p. 30). Some results had to be verified, whereas vegetative growth was also observed (p. 16). The following photoperiods were applied: 10, 10 + 3, 10 + 6 and 10 + 10 hours. The intensity of the additional light was 2000 erg.sec.$^{-1}$cm^{-2} at plant level. Eight to ten plants of each variety were used in the treatments.

The results are shown in table 17. The optimal photoperiod for floral initiation was 10 hours. The number of days to floral initiation rose slowly with an increase in the photoperiod from 10 to 10 + 3 hours, and more rapidly from 10 + 3 to 10 + 10 hours.

Botanist 055, Hnan Yin, Judium, T 10, TMV-2, N.P.-6 and 41 were less sensitive to the length of the photoperiod than Burmese mountain variety and Stamboom 54.

In all varieties the average node number of the first flower bud increased as the photoperiod became longer (see table 18).

TABLE 17. Number of days to floral initiation and flowering at different photoperiods.

Variety	10 hours		10 + 3 hours		10 + 6 hours		10 + 10 hours	
	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering	Fl. Init.	Flowering
Bot. 055	20	40	25	48	35	58	43	67
Hnan Yin	17	37	20	40	30	52	36	57
Judium	15	32	15	34	22	49	32	54
Stamboom 54	20	44	24	48	43	64	78	106
T 10	15	33	15	32	20	46	37	85
TMV-2	16	36	18	42	31	53	37	61
N.P.-6	15	32	15	32	19	38	30	57
41	15	33	15	34	32	53	39	70
B. mount. var.	16	39	30	55	49	97	110	135

TABLE 18. Average node number of the first flower bud and flower at different photoperiods.

Variety	10 hours		10 + 3 hours		10 + 6 hours		10 + 10 hours	
	Flowerbud	Flower	Flowerbud	Flower	Flowerbud	Flower	Flowerbud	Flower
Bot. 055	4.2	4.2	7.3	7.3	10.2	10.2	12.0	12.6
Hnan Yin	3.5	3.5	4.9	5.1	9.0	9.0	9.7	10.2
Judium	2.5	2.5	3.0	3.2	8.0	8.2	9.4	9.5
Stamboom 54	5.2	5.4	6.4	6.4	10.7	11.1	19.7	20.6
T 10	2.4	2.9	2.8	3.0	5.7	6.5	12.9	19.2
TMV-2	3.0	3.4	4.1	4.8	7.8	7.8	8.9	10.1
N.P.-6	2.3	2.5	2.6	2.6	3.7	5.0	9.4	11.7
41	1.5	2.4	2.2	2.9	7.3	7.4	10.7	11.8
B. mount. var.	3.3	4.6	9.5	9.5	14.0	15.6	29.5	29.5

The effect of short days preceding a long-day treatment has already been discussed (p. 21). In another experiment (A-greenhouse; June 12, 1959) short days were applied to interrupt the long-day treatment in the following way. Thirty plants of variety 41 were grown at a photoperiod of 10 + 10 hours. One control only received short days (photoperiod 10 hours) and another only long days (photoperiod 10 + 10 hours). After 15 days, i.e. when the vegetative phase under constant short-day conditions was past, the thirty plants were divided into five groups. A short-day interruption consisting of 1, 2, 3, 6 or 9 days was given, after which the long-day treatment was resumed.

In a similar experiment carried out in 1958, the effect of 3, 6, 9, 12 and 15 short days was investigated. The results of both experiments correspond very well and are illustrated in the same graph (12).
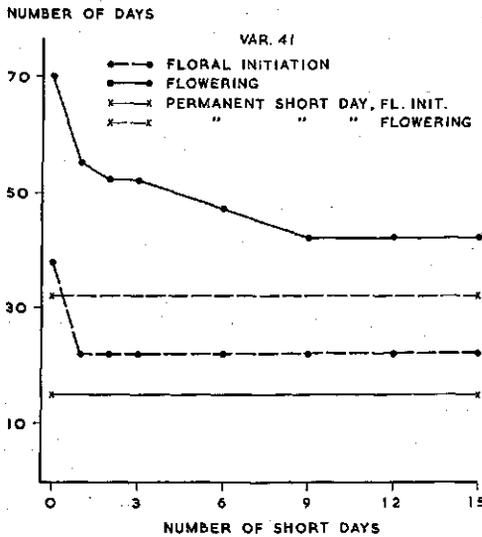
GRAPH 12. Number of days to floral initiation and flowering at different numbers of short days, followed by long-day conditions.

Floral initiation was advanced by 17 days when one short day was given to interrupt the long-day treatment. More short days did not result in a further shortening of the vegetative period. Compared with the long-day control, flowering was advanced by 15 to 28 days, depending on the number of short days. Extension of the treatment after 9 short days had no effect.

A similar experiment with Burmese mountain variety showed that floral initiation was advanced by 87 days if six short days were applied as an interruption of the long-day treatment. A short-day treatment for three days was not effective in most cases and no difference was found between the long-day control and the treatments with one or two short days. Flowering was inhibited by the long photoperiod of 10 + 10 hours, independent of an interruption by short days.

In variety 41 the number of short days giving a maximal advance in floral initiation was reduced from ten, if applied immediately after sowing (p. 22), to one, if applied fifteen days after sowing. In Burmese mountain variety these numbers were respectively fifteen (just after sowing) and six (sixteen days after sowing).

IV-2-6. *Discussion.* Although the juvenile phase does not actually belong to the reproductive phase, the method by which it is investigated justifies a discussion in this section.

Considering that emergence takes two or three days, the actual juvenile phase in variety 41 is only 2–3 days, and in Burmese mountain variety 7–8 days. In this respect no difference was made between a juvenile phase for the (invisible) induction and for the (visible) floral initiation, as these processes cannot be

distinguished, as in most plants (10, 118). In literature no reference is made to a juvenile phase in sesame.

The very short juvenile phase is in accordance with the observation that the cotyledons are capable of perceiving the floral stimulus under favourable photoperiodic conditions. This was also found to be the case in several other crops (120).

No published data are available on floral initiation as determined by microscopic examination. Only reference is made to the bud stage (1, 56, 90, 92). Points of resemblance exist in Epilobium (22).

It has been shown that floral initiation was earliest at photoperiods of 10 to 13 hours, consisting of at least 8 hours of daylight.

No definite connection was found between photoperiodic behaviour and origin of the varieties tested. On the one hand varieties from tropical zones may highly differ in photoperiodic sensitivity (e.g. Boke Htaung and Burmese mountain variety, both being local Burmese varieties), whereas on the other hand varieties from different regions sometimes show a great similarity (e.g. Boke Htaung and the U.S.A. variety Early Russian). Of course at higher latitudes, where the growth of sesame is restricted to the summer, sensitive varieties, like Stamboom 54 or Burmese mountain variety, will not occur, since the long daylength prevents them from producing sufficient flowers before the end of the growing season.

In literature it is pointed out that sesame is a short-day plant, although the photoperiodic response of different varieties may vary greatly. RHIND and BA THEIN (81) and RHIND (80) already distinguished between photoperiodically insensitive Hnan Yin types and sensitive Hnangyi types, both of them occurring in Burma. Flowering of the latter types in Burma was poor, if sown in summer. In a date-of-sowing experiment SEN and PAIN (90) compared the natural daylength – varying from 10½ to 13½ hours – with photoperiods of 10 to 14 hours. In the latter case the daylength was prolonged by artificial light. They found that the bud stage was always earliest at a 10-hour photoperiod. The difference between 10 and 14 hours as regards the number of days to the bud stage, was greatest in summer (82 days) and smallest in winter (6 days). According to SEN GUPTA and SEN (92) and GHOSH (41) the vegetative phase was shortened by darkening for some hours daily. KURNIK (56) imitated the daylength conditions of 0°, 20°, 30°, 35° and 40° latitude in Hungary (47° latitude), by darkening for certain periods daily. He found that the period from emergence to budding was prolonged at higher latitudes.

The data mentioned in literature have only restricted value as always different periods of daylight are compared. In this way the photosynthetic and the photoperiodic effect cannot be distinguished. In research on photoperiodism only photoperiods consisting of the same amount of photosynthetic light, are fully comparable (83, 115).

No data are available on the effect of different amounts of daylight at photoperiods of the same duration. The differences found in the results between 6 and 10, and 8 and 10 hours of daylight as basic illumination tended to increase as the photoperiod became longer (table 15). No clear-cut explanation can be given for this; moreover the effect did not occur in all varieties.

At photoperiods shorter than 10 hours the number of days to floral initiation in sesame was dependent on the period of daylight, supplemental artificial light being of minor importance (p. 35). Evidently the photosynthetic level in this range is so low that the photoperiodic response does not become manifest,

Floral initiation even occurred at a 5-hour photoperiod, but the minimum photoperiod required and the light intensity are not known.

Soybean for instance required at least two hours of daylight and six hours of artificial light (intensity 10–20 ft.c.), or eight hours of artificial light (intensity 100 ft.c.) for floral initiation (16, 76).

Fully defoliated plants with the cotyledons left, were not capable of initiating floral primordia at a photoperiod of 10 + 10 hours (p. 23), but such plants produced at least sixteen pairs of leaves. It is possible that inhibition of floral initiation was caused by limitation of photosynthesis. At 20-hour photoperiods floral initiation was retarded in the order 10 + 10, 8 + 12, and 6 + 14 hours. Probably complete defoliation is the final link in this process of increasing delay in floral initiation.

Although floral initiation was possible under long-day conditions, it was greatly accelerated in the varieties tested (41 and Burmese mountain) by a short-day break (p. 37). In variety 41 the effect on flowering was still more pronounced, but in Burmese mountain flowering was suppressed under long-day conditions, when following the short-day break.

If a short-day treatment preceded long-day conditions, ten short days in variety 41 and fifteen in the Burmese mountain variety, given just after sowing, caused a maximal advance in floral initiation (p. 22). In variety 41 the number of days to flowering could be reduced further by giving more than ten short days (p. 22). ALEKSEEEV (1) found that the number of days to the flower bud stage was smallest if the natural daylength (Rostov, 47° latitude) was reduced to 9 hours for at least 15 days, after emergence of the seedlings. More short days caused no further advance in the "bud stage" but did accelerate flowering by a few days. This seems to agree with the data found for variety 41, but the "bud stage" is not fully comparable with floral initiation, as, according to ALEKSEEV, the "bud stage" is only 2 to 9 days before flowering.

In the first experiments the intensity of the additional light was different (250, 500 or 2000 erg.sec.$^{-1}$cm^{-2}). The effect of this difference was not distinct and completely dominated by seasonal changes in temperature and light intensity. The minimum intensity of photoperiodically effective light is not known, and, according to the data found for other crops (10, 20, 84), this may also depend on the wave length. Therefore incandescent lamps that radiate more red light might have been more economical than daylight fluorescent tubes (84, 104).

Not much is known about the effect of temperature on floral initiation. SEN and PAIN (90) report that the difference between photoperiods of 10 and 14 hours was greatest in summer and smallest in winter. This is in accordance with the fact that low night temperatures offset the retarding effect of long photoperiods (p. 28). Similar results were obtained with strawberry (6) and other short-day crops (86).

Floral initiation in some varieties was greatly retarded by high night temperatures at long photoperiods under conditions of artificial light only, but not under greenhouse conditions. Probably the minimum night temperature in the greenhouse should have been higher than 25 °C.

An increase in the number of days to floral initiation was not always attended with a rise in the average node number of the first flower bud. PATON (77) emphasizes that the photoperiodic response of pea is not exactly expressed in the node number of the first flower bud, as the rate of node production is affected by the temperature ($Q_{10} = 2$). His conclusion may also apply to sesame.

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IV-3-1. *General*. From floral primordia extrafloral nectaries or flower buds
arise. Nectaries should be regarded rudimentary flower buds; a transition stage
between nectary and flower bud is shown in figure 3. This conception is also
found in literature (23, 49, 61, 78, 79, 94, 96), but transition stages are not re-
ported. Flower buds may either remain dormant or develop into flowers.
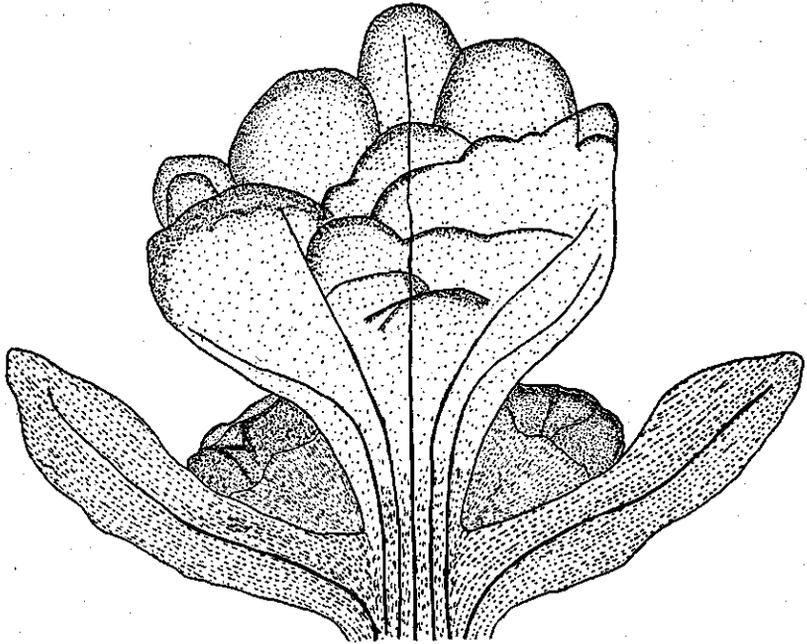
FIG. 3. Transition stage between nectary and flower bud. Lateral floral primordia in the axils
of bracts. Magnification 40 ×.

According to SINGH (94) and other authors (79, 99) the flowers of sesame are
borne in racemes either single or in twos or threes in the axils of the leaves;
when borne singly, the two rudimentary buds in the axils remain undeveloped.
This is not exact; the inflorescences should be called cymes, since they are com-
posed of one central flower on a short pedicel and two lateral extrafloral nec-
taries, whether or not replaced by flowers, in the axils of two bracts.

The experiments on flowering described in this section were mainly done
with Early Russian, which has one flower per axil, and Dulce with one to three
flowers per axil. Flowers open in acropetal succession, the central flowers about
ten days before the lateral flowers.

IV-3-2. *Light*. The experiments described in section IV-2-5 also served to
investigate the effect of photoperiods on flowering. The photoperiodical treat-
ments applied in these experiments were continued until flowering or until
ripening of the capsules.

In a preliminary experiment (p. 29) it was found that the varieties Early
Russian, Venezuela-51, Hnan Yin, Judium, TMV-2, N.P.-6, 41 and Botanist 055

flowered at all photoperiods in the range of 7–16 hours (see table 11). The smallest number of days from sowing to flowering occurred at a photoperiod of 10–11½ hours. Beyond this optimal range flowering was delayed, but the increase in lateness was only six to seventeen days at 16 hours, and three to eight days at 7 hours. By varying the composition of 16- and 10-hour photoperiods an attempt was made to separate the effects of daylight and supplemental light. A photoperiod of 7 + 3 hours caused a delay of some days compared with 10 hours, but the differences between 7 + 9, 10 + 6 and 13 + 3 hours were somewhat conflicting.

In a second experiment (June 19, 1958) the number of days from sowing to flowering was determined in Early Russian, Dulce, Venezuela-51, S 85 and Boke Htaung in the range of 5–24 hours, see p. 31, table 12 and graph 11. An illumination period of 10–11½ hours was optimal for early flowering. There was not much difference between 11½, 10 + 3 and 13 hours as regards the date of flowering. An increasing delay was found in the range of 13–24 hours, but Early Russian was only retarded at photoperiods of 16 hours or longer.

At photoperiods of 13, 20 and 24 hours, either 10 or 13 hours of daylight were given as basic illumination. The flowering times were mainly the same in the 10 + 3- and 13-hour treatments. Flowering in Dulce and Boke Htaung was delayed at 13 + 7 and 13 + 11 hours as compared with 10 + 10 and 10 + 14 hours respectively. This is also true of Early Russian and Venezuela-51 so far as the 20-hour treatments are concerned, but the reverse was found with respect to the 24-hour treatments.

The number of days to flowering increased, notably in Early Russian, Dulce and Venezuela-51, as the photoperiod was shortened from 10 to 5 hours. Substitution of daylight for artificial light in the 7-hour treatment induced a considerable delay in flowering, as is particularly shown in the 5 + 2-hour treatment.

At a 5-hour daylight period flowering was not essentially advanced by one or two hours of supplemental light. Thus at photoperiods in the range of 7 to 5 hours the date of flowering depended primarily on the amount of daylight. For instance the differences were 5, 2 and 3 days between 5 + 2 and 5 hours, but 20, 24 and 21 between 5 + 2 and 7 hours for Early Russian, Dulce and Venezuela-51 respectively.

At photoperiods ranging from 13 to 24 hours an increase in the number of days to flowering was coupled with an increase in the average node number of the first flower (table 13). This rule does not apply to the other photoperiodic treatments, as at photoperiods in the range of 5 to 13 hours the positions of the first flower were more or less the same, whereas the numbers of days to flowering were rather different.

The times of floral initiation were equal at 5- and 10-hour photoperiods, if these treatments were preceded by long-day conditions inducing vigorous growth (see p. 34). In that case there was only a difference of four days between the numbers of days to flowering. When, however, the 5-hour treatment was given immediately after sowing, a considerable delay in flowering occurred. This shows that in this case the reproductive development was retarded by a lack of photosynthetic products which inhibits normal growth. In the next experiment it will be pointed out that the actual photoperiodic effect at photoperiods shorter than 10 hours is of minor significance.

41.

In a third experiment (April 23, 1959) the flowering response of Early Russian, Dulce, Venezuela-51 and S 85 was tested at photoperiods ranging from 5 to 20 hours; moreover the effect of different amounts of daylight at photoperiods of the same length was examined more comprehensively, see p. 34, table 14 and graph 11. The results of the preceding experiment were confirmed. Flowering in Early Russian, Dulce and Venezuela-51 was earliest at a photoperiod of 10–13 hours, the differences between 10, 10 + 3 and 13 hours not being significant. S 85 flowered earliest at 10 and 8 + 2 hours. Beyond this optimal region flowering was delayed, according as a greater part of the illumination period consisted of artificial light, especially in the treatments 8 + 12 and 6 + 14 hours. For S 85 the flowering times were equal in the 8 + 2- and 10-hour treatments, but earlier at 8 + 8 and 6 + 14 hours as compared with 10 + 6 and 8 + 12 hours respectively.

The differences in the times of flowering due to the application of various basic illuminations, 6, 8 or 10 hours of daylight, were not constant but increased as photoperiods became longer, although exceptions existed in the case of Early Russian and S 85 at 6 + 7 and 8 + 8 hours, see table 19 (data taken from table 14).

TABLE 19. Effect of the composition of the photoperiod. Delay in flowering in days as compared with controls receiving 10 hours of daylight.

Variety	Photoperiod						
	10 hours			13 hours	16 hours	20 hours	
	5 + 5	6 + 4	8 + 2	6 + 7	8 + 8	6 + 14	8 + 12
Early Russian	19	10	3	9	1	22	7
Dulce	24	10	4	12	7	19	9
Venezuela-51	20	11	4	16	6	18	10
S 85	16	7	1	3	−4	7	12

The greatest delay in flowering was found at 6 + 14 hours, although a substantial increase in the number of days to flowering also occurred at 5, 5 + 3 and 5 + 5 hours. In the sub-optimal region (photoperiod shorter than 10 hours) the effect of supplemental light was slight in comparison with the effect of daylight. In the series 5, 5 + 3 and 5 + 5 hours flowering was advanced by 5 days at most (Early Russian). Since the results at 6 + 4 and 6 hours on the one hand, and 8 + 2 and 8 hours on the other, were also mainly equal, the actual photoperiodic effect is of minor importance.

At photoperiods ranging from 13 to 20 hours a delay in flowering was accompanied by an increase in the average node number of the first flower. This rule does not hold true for the various 13-hour and 20-hour treatments of S 85 (table 16).

Whereas the flowering dates were rather different at photoperiods in the range of 5 to 13 hours, the average positions of the first flower remained more or less the same. In Early Russian, Dulce and Venezuela-51, however, the average node number of the first flower increased somewhat in the 5-, 5 + 3- and 5 +5-hour treatments. Similarly, in S 85 the average position of the first flower increased at photoperiods longer than 10 hours.

Finally the number of days to flowering was determined in nine varieties (Botanist 055, Hnan Yin, Judium, Stamboom 54, T 10, TMV-2, N.P.-6, 41

and Burmese mountain variety) at photoperiods of 10, 10 + 3, 10 + 6 and 10 + 10 hours (see p. 36). The results are shown in table 17.

Flowering was earliest at photoperiods ranging from 10 to 13 hours, depending on the variety. The difference between 10 and 10 + 3 hours, as regards the date of flowering, was small in Hnan Yin, Judium, Stamboom 54, T 10, N.P.-6 and 41, whereas a more substantial delay occurred in TMV-2 (6 days), Botanist 055 (8 days) and Burmese mountain variety (16 days). In all varieties the number of days to flowering was maximal in the 10 + 10-hour treatment. The rate of increase in Burmese mountain variety and Stamboom 54 was much greater than in the other varieties.

Table 18 moreover shows that the average node number of the first flower and flower bud were rising at lengthening photoperiods.

The time lapse between floral initiation and flowering proved to be dependent on the photoperiod. This is demonstrated in table 20; the number of days to floral initiation (table 14) has been subtracted from the number of days to flowering.

TABLE 20. Length of the period in days between floral initiation and flowering at different photoperiods; data taken from table 14.

Photoperiod in hours	Early Russian	Dulce	Venezuela-51	S 85
5	32	26	28	27
5 + 3	28	29	30	25
5 + 5	22	27	28	26
6	23	24	26	23
6 + 4	24	26	28	22
6 + 7	25	27	33	25
6 + 14	46	27	34	39
8	20	22	24	20
8 + 2	22	23	27	19
8 + 8	22	24	29	23
8 + 12	33	27	29	56
10	18	21	23	18
10 + 3	18	21	25	25
10 + 6	20	24	31	26
10 + 10	24	25	42	47
13	16	20	26	24

In view of the results obtained, it was supposed that the period between floral initiation and flowering becomes longer, if the photoperiod is not optimal for these two stages in the reproductive development. This was proved for a sensitive variety (Stamboom 54), by applying different photoperiodical treatments (10, 10 + 6 and 10 + 10 hours) just after floral initiation, which took place at a 10-hour photoperiod. As compared with the 10-hour photoperiod, flowering was delayed by six days at 10 + 6 hours, and by eighteen days at 10 + 10 hours.

The flowering date for variety 41 was highly advanced by short days preceding, or interrupting, a long-day treatment (p. 39). To some extent the period between floral initiation and flowering depended on the number of short days given. But in all varieties tested flowering also took place under permanent long-day conditions; only in Burmese mountain variety it was sometimes completely suppressed in the 10 + 10-hour treatment.

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In the 5-hour treatments flowers were very small and often remained closed. Continuous illumination (24-hour photoperiods) did not prevent flowers from opening. Moreover flowers opened in prolonged darkness, as was shown by placing plants in darkness at least two days before the expected date of flowering.

The photoperiodic treatments applied in the experiment of June 19, 1958, (p. 31) were continued until flowering had ceased and fruits had ripened. At that time the total number of flowers produced was determined in ten plants of each of the varieties Early Russian and Dulce in the following treatments: 5, 5 + 1, 5 + 2, 6 + 1, 7, 8½, 11½ hours (C-greenhouse), and 10, 10 + 3, 10 + 6, 10 + 10, 10 + 14, 13, 13 + 7 and 13 + 11 hours (A-greenhouse). In Early Russian, a branching variety, flowers on the main stem and branches were counted separately; if the number of flowers on branches was less than three on an average, it was not considered in counting the total number of flowers per plant. The results are shown in table 21.

TABLE 21. Number of flowers and capsules per plant and percentage of fruit setting at different photoperiods. Numbers of flowers on main stem and branches are given between brackets.

Photoperiod in hours	Early Russian			Dulce		
	Number of flowers	Number of capsules	% Fruit setting	Number of flowers	Number of capsules	% Fruit setting
6 + 1	11.4	4.7	41.9	23.3	6.1	27.4
7	14.3	10.2	72.7	24.8	11.2	47.7
8½	13.0	11.4	87.8	13.8	9.0	73.2
10	22.7	21.0	92.0	48.6	32.2	65.6
10 + 3	27.6(22.2 + 5.4)	22.3(19.8 + 2.5)	82.6	60.2	34.5	58.2
10 + 6	33.5(25.3 + 8.2)	23.0(19.7 + 3.3)	77.1	66.4	29.7	45.0
10 + 10	53.9(42.4 + 11.5)	33.8(28.9 + 4.9)	57.5	77.2	23.2	27.8
10 + 14	86.6(58.3 + 28.3)	38.1(31.7 + 6.4)	41.2	34.7	5.3	22.1
11½	17.7	15.5	89.9	39.9	26.0	66.4
13	22.4	20.1	91.2	61.5	41.1	66.9
13 + 7	88.9(50.4 + 38.5)	43.0(34.5 + 8.5)	50.0	68.9	17.2	23.8
13 + 11	84.9(49.8 + 35.1)	35.3(25.0 + 10.3)	41.4	18.5	5.0	29.0

At photoperiods consisting of 5 hours of daylight (5, 5 + 1 and 5 + 2 hours) flowering was very poor in both varieties, only a few very small flowers being produced on each plant. The data are not recorded in table 21. When 6 hours of daylight (photoperiod 6 + 1 hours) were given, the number of flowers was at least triplicated in each variety. Further lengthening of the period of daylight up to 13 hours increased the number of flowers in Dulce, although declines occurred at 8½ and 11½ hours. This is also applicable to the flower production in Early Russian, though no difference was found between 10 and 13 hours.

The effect of supplemental artificial light was investigated at a 10-hour and a 13-hour basic illumination. In Dulce the highest number of flowers was produced at 20-hour photoperiods, i.e. 10 + 10 and 13 + 7 hours, but a sharp decrease occurred at 24 hours (10 + 14 and 13 + 11 hours). Early Russian produced more flowers on main stem and branches at photoperiods ranging from 10 + 3 to 10 + 14 hours, but no difference was found between 10 and 10 + 3 hours in the number of flowers on the main stem only. Similarly, at photoperiods of 13 + 7 and 13 + 11 hours the number of flowers was larger than at 13 hours, but in this case it was highest at 13 + 7 hours.

As regards photoperiods of the same duration but of different composition the differences between $10+3$ hours and 13 hours were or minor importance for both varieties. Early Russian, however, produced a few flowers on branches only at $10+3$ hours. In Dulce flower production at $13+7$ and $13+11$ hours was lower than at $10+10$ and $10+14$ hours, respectively. Flowering in Early Russian was more abundant at $13+7$ than at $10+10$ hours. There was not much difference between $13+11$ and $10+14$ hours in the total flower production, but at $13+11$ hours more flowers were produced on the main stem and less on the branches.

At most photoperiods Dulce produced more flowers than Early Russian, but the reverse was found at $10+14$, $13+7$ and $13+11$ hours. The large number of flowers on branches in Early Russian at $13+7$ hours may account for the different situation at this photoperiod. Probably the sharp decrease at 24-hour photoperiods in Dulce was caused by the rather unfavourable location of the Dulce plants in the vicinity of more vigorously growing plants of Early Russian. It is difficult to interpret the declines at $8\frac{1}{2}$ and $11\frac{1}{2}$ hours, although differences in greenhouse conditions may also play a part.

In view of the experiences gained it was found to be necessary to perform an experiment in only one greenhouse with more plants per treatment, to obtain more reliable mean values. To this end an experiment was set up in the C-greenhouse on April 23, 1959 (see p. 34). More attention was paid to photoperiods of equal duration but of different composition, but it was not possible to include 24-hour photoperiods. Flower production in Early Russian and Dulce was determined at the following photoperiods: 5, $5+3$, $5+5$, 6, $6+4$, $6+7$, $6+14$, 8, $8+2$, $8+8$, $8+12$, 10, $10+3$, $10+6$, $10+10$ and 13 hours. The different photoperiodic treatments were continued until the fruits had ripened. Since growth conditions vary with length and composition of the photoperiod, the spacing was more or less adapted to the degree of vegetative growth expected in the different treatments. Therefore the number of plants of each variety was rather large (thirty) at photoperiods of 5, $5+3$, $5+5$ and 6 hours, rather small (about eighteen) at $6+14$, $8+12$ and $10+10$ hours, and intermediate (about twenty) at the other photoperiods. In all treatments the flowers of each plant of each variety were counted daily, but in the 5-, $5+3$- and $5+5$-hour treatments this was terminated two weeks after the onset of flowering. The total number of flowers produced in each plant was then only four at $5+5$ hours, and three or two at $5+3$ and 5 hours respectively, whereas only at $5+5$ hours a few capsules were found in some plants. In the remaining treatments the total flower production in each plant was determined by adding up the daily numbers of flowers; this total corresponded to the sum of flowers shed (their place of insertion was recognizable) and capsules. Mean total and daily production and length of the flowering period are shown in table 22. In Dulce the total number of flowers has been subdivided into central and lateral flowers according to the position in the inflorescence; for each of these types the percentages are given.

In Dulce, at photoperiods consisting of daylight only, the number of flowers increased in the range of 6 to 10 hours, whereas further lengthening up to 13 hours had no effect. In Early Russian the number of flowers on the main stem rose with an increase in the photoperiod up to 13 hours, but the total numbers at 10 and 13 hours were not significantly different, owing to the production of flowers on branches at 10 hours. The effect of supplemental light, tested at 6, 8 and 10 hours of daylight as basic illumination, was marked. In

TABLE 22. Total number of flowers per plant, daily average, and length of flowering period in days, at different photoperiods. Between brackets number of flowers on main stem and branches.

Photoperiod in hours	Early Russian		
	Total number of flowers	Daily number of flowers	Length of flowering period
6	11.7 ± 0.42*	0.24	49
6 + 4	11.8 ± 0.35	0.31	38
6 + 7	13.6 ± 0.46	0.37	37
6 + 14	52.4 ± 2.10	0.59	89
8	17.3 ± 0.62	0.49	35
8 + 2	18.1 ± 0.50	0.50	36
8 + 8	19.1 ± 0.67	0.71	27
8 + 12	50.4 ± 2.80	0.79	64
10	26.4 ± 1.90 (20.8 ± 0.88; 5.6)	0.71 (0.56 + 0.15)	37
10 + 3	22.2 ± 1.11	0.60	37
10 + 6	30.7 ± 1.80 (25.4 ± 0.81; 5.3)	1.14 (0.94 + 0.20)	27
10 + 10	75.7 ± 6.50 (50.2 ± 1.90; 25.5)	1.22 (0.78 + 0.44)	64
13	24.9 ± 0.77	0.64	39

| Photoperiod in hours	Dulce				
	Total number of flowers	% Central flowers	% Lateral flowers	Daily number of flowers	Length of flowering period
6	25.1 ± 1.60	53	47	0.93	27
6 + 4	38.3 ± 1.90	54	46	1.47	26
6 + 7	50.3 ± 3.00	55	45	1.62	31
6 + 14	54.9 ± 4.10	91	9	0.72	76
8	33.1 ± 2.30	56	44	1.38	24
8 + 2	38.9 ± 2.80	55	45	1.56	25
8 + 8	63.5 ± 4.00	56	44	1.06	60
8 + 12	94.9 ± 7.70	58	42	1.58	60
10	42.3 ± 2.60	50	50	1.84	23
10 + 3	43.7 ± 3.30	55	45	1.62	27
10 + 6	67.0 ± 4.80	55	45	1.12	60
10 + 10	98.2 ± 7.80	54	46	1.64	60
13	42.4 ± 3.50	57	43	1.24	35

* Standard error of mean

Dulce the number of flowers increased with lengthening photoperiods in all series, viz. 6 to 6 + 14 hours, 8 to 8 + 12 hours, and 10 to 10 + 10 hours. The differences in the results between 6 + 7 and 6 + 14 hours, 8 and 8 + 2 hours, 10 and 10 + 3 hours, were not significant (P = 0.05). Early Russian, too, produced more flowers on the main stem as the photoperiod, consisting of daylight and artificial light, became longer. However, the differences between 6 and 6 + 4 hours, 8 and 8 + 2 hours, 8 + 2 and 8 + 8 hours, 10 and 10 + 3 hours, were not significant, but a sharp rise was found at the longest photoperiods. The total flower production at 10 + 3 hours was not significantly lower than at 10 hours in spite of the absence of flowers on branches. Likewise, the totals of 10 and 10 + 6 hours did not deviate significantly. A high number of flowers on branches only occurred at 10 + 10 hours.

In Dulce the numbers of flowers were largely equal at photoperiods of the same length but consisting either of 8 or 10 hours of daylight as a basic illu-

mination. Likewise no significant differences were found between 6 + 4, 8 + 2 and 10 hours, and between 6 + 7, 10 + 3 and 13 hours. However, flowering at 10 + 10 and 8 + 12 hours was more abundant than at 6 + 14 hours. In Early Russian flower production at 8 + 2, 8 + 8 and 8 + 12 hours was lower than at 10, 10 + 6 and 10 + 10 hours respectively. Similar differences were found between 6 + 4, 8 + 2 and 10 hours and between 6 + 7, 10 + 3 and 13 hours. At 20-hour photoperiods the numbers of flowers on the main stem were alike, but the total number was largest at 10 + 10 hours, owing to the flowers on branches.

In Dulce the ratio central/lateral flowers was about 55/45 at all photoperiods,

NUMBER OF FLOWERS

LENGTH OF THE FLOWERING PERIOD IN DAYS IS RECORDED NEXT TO EACH CURVE
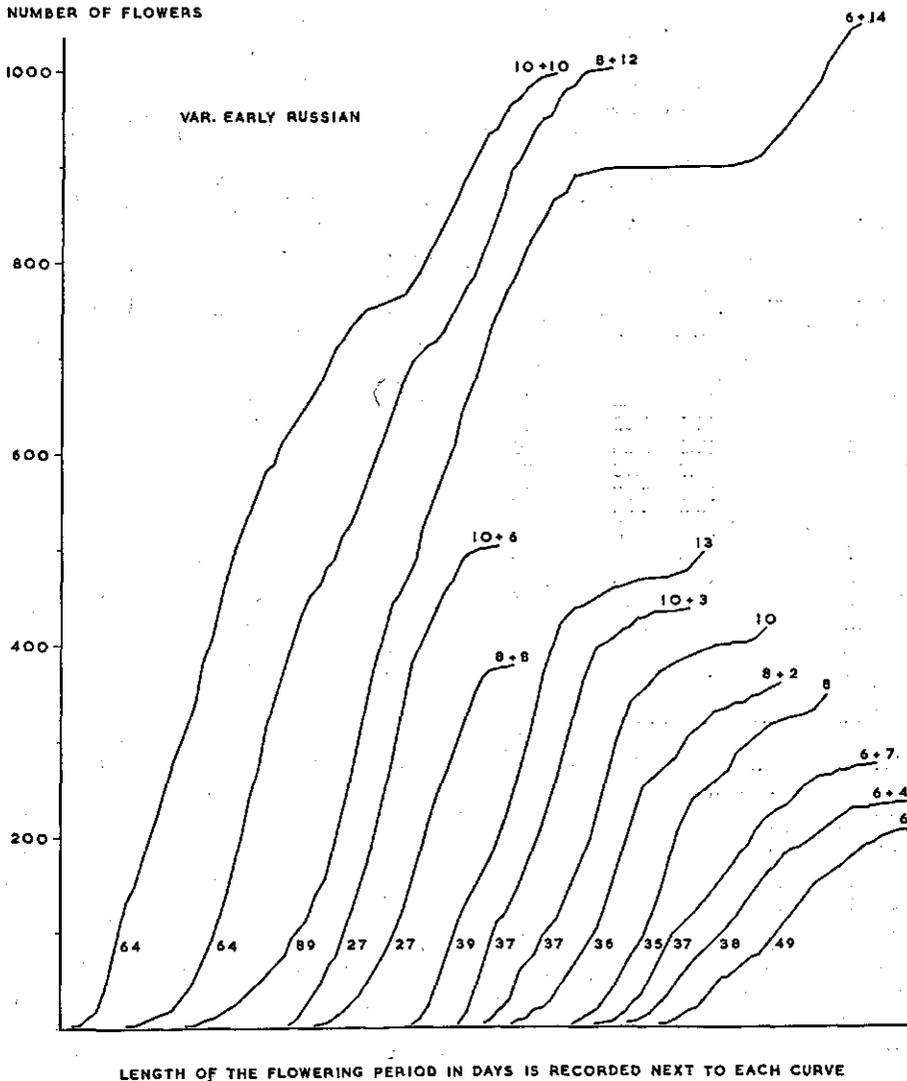
GRAPH 13. Total number of flowers on the main stem (cumulative) per 20 plants of variety Early Russian at different photoperiods (indicated next to each peak).

only at 6 + 14 hours it was much lower. Apparently at 6 + 14 hours the production of lateral flowers almost completely failed. Probably as a result of the short period of daylight only the production of central flowers was continued in the whole range of 6 + 7 to 6 + 14 hours. In the range of 10 + 3 to 10 + 10 hours, however, both the total number and the number of central and lateral flowers increased (ratio central flowers/lateral flowers constant!).

The flower production of Dulce was by far the highest. Only at 6 + 14 hours the difference between the varieties was small, due to the absence of lateral flowers in Dulce. The main points of the previous experiment, i.e. the rise in the

NUMBER OF FLOWERS

LENGTH OF THE FLOWERING PERIOD IN DAYS IS RECORDED NEXT TO EACH CURVE
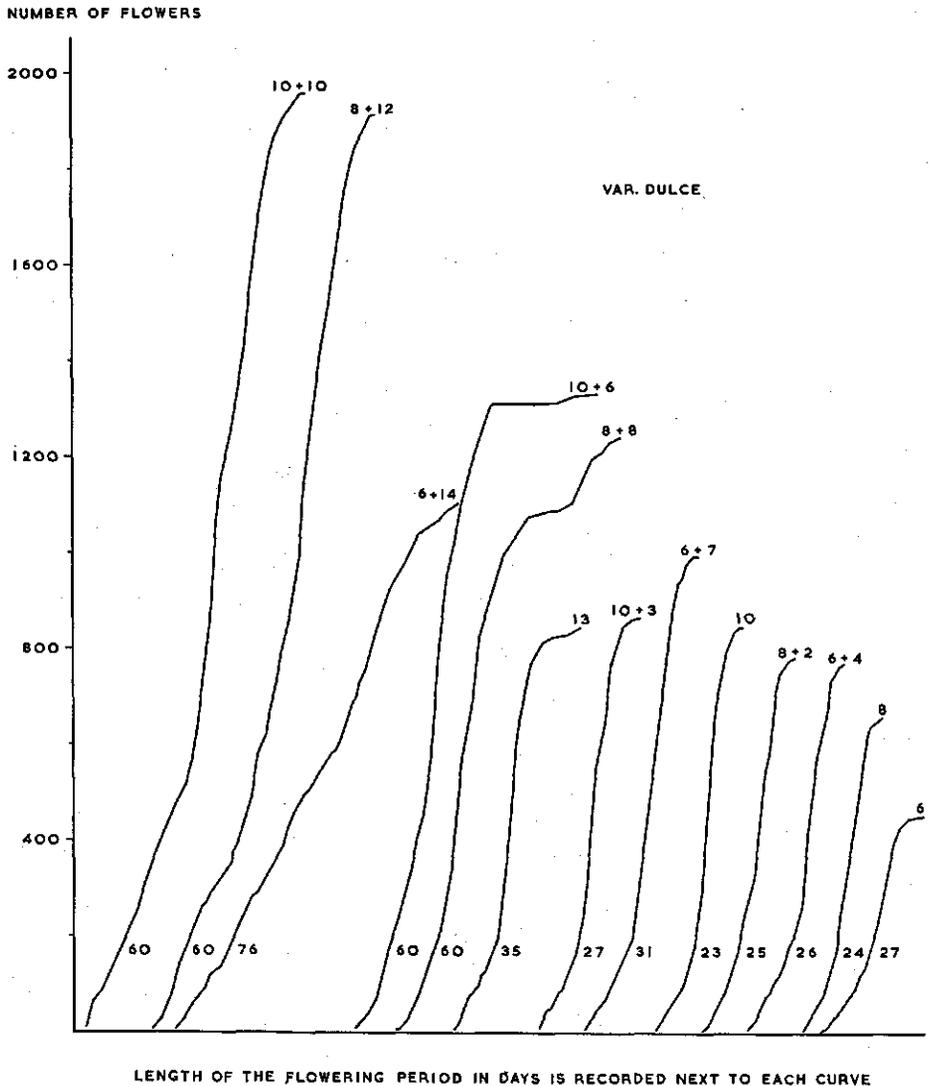
GRAPH 14. Total number of flowers (cumulative) per 20 plants of variety Dulce at different photoperiods (indicated next to each peak).

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number of flowers as the photoperiod became·longer and the higher flower production of Dulce, were confirmed, but declines did not occur.

The cumulative totals, converted to twenty plants in each variety and in each treatment, are illustrated in graph 13, 14. The length of the whole flowering period is recorded next to each curve, according to the method applied in peanut by BOLHUIS (12). Only flowers of the main stem are represented by the curves, since the production of flowers on branches (Early Russian) was not important at all photoperiods, except $10 + 10$ hours.

The Dulce curves are characterized by a rapid rise which ceases abruptly after some time, depending on the photoperiod; the $10 + 6$- and $8 + 8$-hour curves are more flattening towards the end. The peaks mark the total flower production per twenty plants, i.e. the twentyfold average flower production per plant at different photoperiods (see table 22). On the whole the curves for Early Russian, drawn on the same scale as those for Dulce, have a smaller gradient and are more flattening towards the end.

In Dulce the length of the flowering period at photoperiods ranging from 6 to 13 hours was much shorter than at photoperiods of 16 hours and more. The differences within these ranges were of minor importance, mainly because it was not possible to determine the length of the flowering period exactly. In Early Russian the flowering period was longest at 20-hour photoperiods, notably at $6 + 14$ hours. Within the group of photoperiods shorter than 20 hours, a minimum occurred at 16 hours, and a maximum at 6 hours.

Within the two ranges of photoperiods distinguished in Dulce, viz. 6–13 and 16–20 hours, the daily number of flowers, calculated for the whole flowering season, was more or less varying with the total flower production (see table 22). With almost equal total numbers of flowers at e.g. 10, $10 + 3$ and 13 hours, the daily number was highest at the shortest flowering period. Since in the range of 13–16 hours the length of the flowering period increased more rapidly than the total flower production, the daily number of flowers declined. At 20-hour photoperiods, except $6 + 14$ hours, the daily number of flowers attained the 13-hour level again, due to the increase in the total flower production. In Early Russian the daily number of flowers on the main stem generally increased as the photoperiod became longer, except at $10 + 10$ hours. However, the total daily flower production, flowers on branches included, was higher at $10 + 10$ than at $10 + 6$ hours. At photoperiods of the same length the effect of daylight was dominating, for instance the daily number of flowers was smaller at $8 + 2$ than at 10 hours.

IV-3-3. *Discussion.* Photoperiods ranging from 10 to 13 hours, and consisting of at least 8 hours of daylight, were not only optimal for early floral initiation, but also for early flowering. It was also shown (p. 43) that the intervening period was not constant, but increased as the photoperiod deviated further from the optimum. The divergence between curves representing the number of days to floral initiation and those indicating the number of days to flowering, is smallest at a 10- to 13-hour photoperiod (see graph 11). This is in accordance with SEN and PAIN (90) who found that the lapse of time between bud stage and date of flowering increased as the photoperiod was lengthened from 10 to 14 hours. KURNIK (56), however, imitating the daylength conditions of 0°, 20°, 30°, 35°, 40° and 62° latitude in Hungary (47° latitude), reports, that the period between budding and onset of flowering remained almost constant in all his·photoperiodic treatments. He might have found differences, however, if he had used

more sensitive varieties (e.g. Venezuela-51 or S 85) or a wider range of photo-periods.

Only at photoperiods of over 10 or 13 hours the number of days to floral initiation was more or less reflected in the average node number of the first flower bud. A similar relation was found between the number of days to flowering and the average node number of the first flower (p. 41). Not much difference in the position of the first flower (bud) occurred at photoperiods of less than 10 or 13 hours.

The first flower bud did not always develop into a flower. In most cases, however, the difference between the average node number of the first flower bud and the average node number of the first flower was of minor significance, and did not depend on the photoperiod. Only in some treatments (6 + 14 and 8 + 12 hours in Early Russian and S 85; 10 + 10 hours in T 10 and S 85) a relatively large number of first flower buds remained dormant, which caused a further delay in flowering.

Times of floral initiation and flowering were similarly influenced by using artificial light instead of daylight at various photoperiods, but in most cases the shift in the time of flowering was strongest (cf. table 15 with table 19).

It was also shown (p. 42) that the delay in the time of flowering at photoperiods of less than 10 hours was mainly caused by restricted photosynthesis, inducing a decline in growth. This was evidenced by applying 5- and 10-hour illumination periods after the plants had reached a certain level or vegetative growth; in this case the difference in flowering times was only four days. The absolute minimum photoperiod and light intensity required for flowering are not known. According to ILYINA (50) no normal flowers developed in sesame if, under normal daylength conditions (Russia), the intensity of daylight was reduced to 6800 lux (27.000 erg.sec.$^{-1}$cm^{-2}) by shading.

Some Indian authors (49, 72, 78) state a specific time of the day (3 a.m. to 6 a.m.) at which sesame flowers open. Under greenhouse conditions at Wageningen, however, no relation could be established between either light or darkness and opening time of flowers (p. 44).

A substantial increase in the length of the flowering period was found at 20 hours for Early Russian, and at 16 or 20 hours for Dulce. Such an effect does not show from the results of KURNIK (56).

In literature data on the numbers of flowers produced each day are not available. The pattern of the cumulative curves for sesame (graph 19, 20) shows much resemblance to that for peanut (12).

The data on the numbers of flowers and capsules will be discussed in section 4-2.

IV-4. FRUIT SET

IV-4-1. *Light.* Flowering continues until maturity, so the period of fruit setting falls within the flowering season (see also p. 3).

In Early Russian the time lapse between opening of flowers and full development of the capsules was determined. At 10- and 10 + 10-hour photoperiods the capsules attained their maximum size about eight days after flowering; the period necessary for ripening of the seeds was not ascertained.

In the experiments discussed in the previous section fructification as well as flowering was investigated. The production of fruits will be discussed in this section.

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The results of the first experiment (1958) are shown in table 21. Neither Dulce nor Early Russian bore capsules when only 5 hours of daylight were given. The production of capsules in Dulce was favoured by extending the period of daylight to 13 hours, but declines occurred at 8½ and 11½ hours. The same applies to Early Russian, but the maximum flower production was already attained at 10 hours, whereas there was only a decline at 11½ hours.

When artificial light was given in addition to a 10-hour daylight period, capsule production increased in the range of 10 to 10 + 3 hours, but then declined. Similarly, the number of capsules was smaller at 13 + 7 and 13 + 11 hours than at 13 hours. The capsule production in the 24-hour treatments was adversely affected, since the Dulce plants were more or less shaded by vigorous Early Russian plants. No important difference in the results was found between 10, 10 + 3 and 10 + 6 hours in Early Russian, but the number of capsules on the main stem and branches increased as the photoperiod was lengthened to 10 + 14 hours. In the same way more capsules were produced when, in addition to a 13-hour daylight period, 7 or 11 hours of artificial light were given; most capsules were produced at 13 + 7 hours.

Comparison of photoperiods of the same length but of different composition shows that the results of Dulce were equal at 10 + 14 and 13 + 11 hours. The capsule production at 10 + 3 hours was lower, and at 10 + 10 hours higher than at 13 and 13 + 7 hours respectively. In Early Russian the 10 + 3- and 13-hour treatments gave almost identical results, apart from the production of a few capsules on branches. As regards the two 20-hour photoperiods, 13 + 7 hours proved to be more favourable than 10 + 10 hours. The difference between the total capsule production at 13 + 11 and 10 + 14 hours was small; the number of capsules on the main stem was larger at 10 + 14 hours but the reverse was found for the number of capsules on branches.

Percentages of fruit set (= total number of capsules: total number of flowers × 100 %) were calculated per plant in each treatment; the averages are shown in table 21. In Dulce the percentage of fruit setting increased when the period of daylight was lengthened from 6 to 8½ hours, and became somewhat lower at 10 hours. Further extension of the daylight period had no effect. The same is true of Early Russian, but in this variety the percentage of fruit setting remained almost constant in the range of 8½ to 13 hours.

The effect of supplemental light was marked. At each basic illumination, 10 or 13 hours of daylight, the percentage of fruit set in each variety declined as photoperiods became longer, apart from an unimportant improvement at 13 + 11 hours in Dulce.

In Dulce, at photoperiods of the same length but of different composition, the percentages of fruit setting were somewhat higher at 13 and 13 + 11 hours than at 10 + 3 and 10 + 14 hours respectively, but the reverse was found at 13 + 7 and 10 + 10 hours. In Early Russian the percentages at 13 + 11 and 10 + 14 hours were equal. At a 20-hour photoperiod best results were obtained with the 10 + 10 combination; at a 13-hour photoperiod, however, 13 hours of daylight was most favourable.

Dulce generally produced more capsules than Early Russian, except at 20-hour and 24-hour photoperiods, but fruit setting was much better in Early Russian.

The results of the second experiment (1959) are shown in table 23. When the photoperiod consisted of 5 hours of daylight, whether or not extended by arti-

TABLE 23. Number of capsules and total seed weight per plant, and percentage of fruit setting at different photoperiods. Between brackets number of capsules on main stem and branches.

Photoperiod in hours	Early Russian		
	Number of capsules	% Fruit setting	Total seed weight
6	5.4 ± 0.47*	45.7 ± 3.5	0.42 ± 0.05
6 + 4	8.3 ± 0.41	67.0 ± 3.0	0.52 ± 0.05
6 + 7	9.5 ± 0.37	70.2 ± 2.5	0.71 ± 0.05
6 + 14	30.5 ± 2.00	57.6 ± 2.4	3.40 ± 0.38
8	14.5 ± 0.44	84.7 ± 2.3	1.33 ± 0.06
8 + 2	15.3 ± 0.51	84.2 ± 1.6	1.33 ± 0.07
8 + 8	14.8 ± 0.86	76.6 ± 3.3	1.63 ± 0.12
8 + 12	31.5 ± 2.20	62.7 ± 2.8	4.19 ± 0.37
10	21.3 ± 1.80 (17.8 ± 0.74; 3.5)	82.8 ± 3.0	2.33 ± 0.09
10 + 3	20.2 ± 1.08	90.7 ± 1.9	2.35 ± 0.15
10 + 6	24.6 ± 1.80 (21.2 ± 1.10; 3.4)	79.2 ± 2.6	2.78 ± 0.19
10 + 10	42.2 ± 3.70 (32.3 ± 1.70; 9.9)	56.1 ± 3.1	5.74 ± 0.43
13	19.5 ± 0.68	78.9 ± 2.4	2.47 ± 0.16

Photoperiod in hours	Dulce				
	Number of capsules	% Central capsules	% Lateral capsules	% Fruit setting	Total seed weight
6	8.9 ± 0.7	89	11	35.6 ± 2.1	0.62 ± 0.07
6 + 4	18.1 ± 0.8	86	14	47.8 ± 1.4	1.64 ± 0.08
6 + 7	26.0 ± 2.7	67	33	50.8 ± 4.2	2.25 ± 0.23
6 + 14	26.2 ± 2.1	98	2	47.5 ± 1.9	3.06 ± 0.34
8	18.4 ± 1.6	79	21	57.1 ± 3.1	2.09 ± 0.08
8 + 2	21.1 ± 1.8	71	29	55.0 ± 3.0	2.24 ± 0.07
8 + 8	38.8 ± 3.0	65	35	60.4 ± 2.0	5.97 ± 0.55
8 + 12	32.4 ± 3.8	76	24	34.1 ± 1.9	4.24 ± 0.59
10	25.4 ± 1.8	58	42	60.3 ± 2.3	3.35 ± 0.15
10 + 3	27.1 ± 2.9	62	38	61.9 ± 3.6	3.57 ± 0.18
10 + 6	37.6 ± 4.1	61	39	55.4 ± 3.0	6.00 ± 0.76
10 + 10	38.5 ± 4.2	75	25	38.3 ± 2.0	5.34 ± 0.67
13	27.3 ± 2.6	60	40	65.0 ± 3.1	3.75 ± 0.19

* Standard error of mean

ficial light, fruit set failed almost completely in each variety. Only at 5 + 5 hours some plants bore a few capsules, but these were not taken into consideration.

Both Dulce and Early Russian produced more capsules as the daylight period became longer, but the difference between 10 and 13 hours was not significant.

Supplemental light, given after daylight periods of 6, 8 or 10 hours, caused an increase in the number of capsules produced. Dulce attained its maximum production at 16-hour photoperiods, but the differences between 16- and 20-hour photoperiods were not significant. This is also true of the differences between 6 + 7 and 6 + 14 hours, 8 and 8 + 2 hours, 10 and 10 + 3 hours. Early Russian bore most capsules at 20-hour photoperiods. Their number remained almost constant in the ranges of 8 to 8 + 8 hours, and 10 to 10 + 6 hours; the difference between 10 and 10 + 6 hours, so far as capsules on the main stem are concerned, was significant however.

In Dulce the results remained mainly the same when the basic illumination at 10-, 16- and 20-hour photoperiods was either 8 or 10 hours of daylight. Substituting 13 hours of daylight for $6+7$ or $10+3$ hours had no marked effect. The numbers of capsules were smaller at $6+4$ and $6+14$ than at 10 and $10+10$ hours respectively, but the differences between 6 and 8 hours' basic illumination at 10- and 20-hour photoperiods were not significant. In Early Russian the number of capsules generally decreased when artificial light was used instead of daylight. The totals at $10+3$ and 13 hours, and the numbers of capsules on the main stem at $6+14$, $8+12$ and $10+10$ hours were about equal however. A considerable number of capsules on branches was only found in the $10+10$-hour treatment.

Relatively, much more central than lateral flowers developed into capsules in Dulce. Where the ratio central/lateral flowers was 55/45, the corresponding ratio for the capsules was at least 60/40. The ratio was smallest at photoperiods ranging from 10 to 16 hours with a basic illumination of 10 or 13 hours of daylight, but increased if the daylight period was shorter. The proportion also increased if the photoperiod was shorter than 10, or longer than 16 hours. Percentages of fruit setting (calculated on the total number of flowers) were lowest at 6-, $8+12$- and $10+10$-hour photoperiods. Absence of lateral flowers explains the rather high value at $6+14$ hours. The remaining percentages were more or less the same, apart from a minimum and a maximum occurring at daylight periods of 6 and 13 hours respectively.

Photoperiods ranging from 8 to 13 hours, with a least 8 hours of daylight, were optimal for a high percentage of fruit set in Early Russian. A maximum was found at $10+3$, and a minimum at $6+4$ and $6+7$ hours, but the other values were not significantly different. The percentage of fruit setting declined when the photoperiod was shorter than 8, or longer than 13 hours. The percentages were mainly equal at the 16-hour photoperiods, whether the basic illumination was 8 or 10 hours of daylight. Likewise no significant differences were found between $6+14$, $8+12$ and $10+10$ hours.

As in the previous experiment Dulce produced more capsules than Early Russian, except at 20-hour photoperiods, whereas the percentage of fruit set was lower. Moreover it was confirmed that the number of capsules of Early Russian increased as the photoperiod became longer, whereas the percentage of fruit setting was highest in the range of 8 to 13 hours. In contrast with the results of the previous experiment, artificial light given in addition to a 10-hour daylight period induced an increase in the number of capsules of Dulce, whereas there was only a significant decrease in the percentage of fruit setting at $10+10$ hours. The latter results are of greater value, however, since in the 1958 experiment the number of plants per treatment was rather small, and spacing was not adapted to the varying degree of vegetative growth.

In all treatments the number of capsules and the seed weight per plant were closely correlated; the coefficients calculated were 0.97 and 0.99 for Dulce and Early Russian respectively. The effects of the photoperiod on capsule production and on seed weight run very much parallel. This is clearly shown in table 23. In Dulce, however, the seed weight sometimes decreased significantly, whereas the number of capsules was not significantly affected by using artificial light instead of daylight; such discrepancies were found at $8+2$ and $6+4$ hours, 10 and $8+2$ hours, $10+3$ and $6+7$ hours.

IV-4-2. *Discussion.* In the 1959 experiment on flower and capsule production the space available for each plant in the various photoperiodic treatments was adapted as much as possible to the amount of vegetative growth expected. This is necessary since the number of flowers and capsules and the seed production per plant depend on plant density; according to KAMEL (51) and SINGH (94) the relation is inversely proportional. Since in the 1958 experiment spacing was not varied with a view to the amount of vegetative growth expected, the results are less reliable, and consequently not discussed in this section.

Generally the number of flowers and capsules, and the seed weight per plant increased as the photoperiod became longer. In Dulce, however, no further increase in number of capsules and seed production occurred at 20-hour photo-periods, whereas both in Dulce and Early Russian the percentage of fruit setting declined rapidly. Apparently an improvement in vegetative growth (Chapter III) is accompanied by a rise in the number of flowers and capsules, resulting in an increase in yield. Abundant flowering, however, has an adverse effect on the development of capsules, especially of lateral capsules.

According to ALEKSEEV (1) the number of capsules and the seed weight per plant decreased as an increasing number of short days (9 hours of daylight) were given just after sowing. KURNIK (56) in his photoperiodic treatments imitating the daylength conditions of various latitudes, found that the seed weight per plant increased with higher latitudes. A similar effect was shown when supplemental light was given in the various treatments. This was not only true of sesame, but also of other oil crops, like soybean and perilla. On the whole this agrees with the results found for Early Russian and Dulce, but the authors do not mention the numbers of flowers and the percentages of fruit setting.

In contrast with the ratio central/lateral flowers in Dulce, the ratio central/lateral capsules was by no means constant. A decrease in photosynthesis by shortening the period of daylight was in the first place detrimental to the production of lateral capsules. This agrees with the observation made by SINGH (94), that high plant densities may inhibit fruit setting of lateral flowers; in this case a decrease in photosynthesis is caused by reduced light intensity.

CHAPTER V

RELATION BETWEEN VEGETATIVE AND REPRODUCTIVE
DEVELOPMENT

V-1. FLOWERING AND FRUIT SET AS OBSERVED AT VARIOUS DEGREES
OF DEFOLIATION

In an experiment in the C-greenhouse, started on July 1, 1959, the following degrees of defoliation were applied in variety Dulce:
1. Leaves removed as they appeared, after the development of the cotyledons.
2. As in 1, but one leaf on the 1st node left.
3. As in 1, but both leaves on the 1st node left.
4. As in 1, but both leaves on the 1st and 2nd node left.
5. Defoliation started at the onset of flowering; all leaves above the node of the first flower removed and newly grown leaves cut back.

The number of plants was varied from 20 to 24 in group 3, 4 and 5, to 35 in group 1 and 2 according to the amount of vegetative growth expected. Photoperiods of 10 hours and 10 + 10 hours were given; the intensity of the additional

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light was 2000 erg.sec.$^{-1}$cm^{-2}. In group 5 the formation of the first flower indicated the beginning and the place of defoliation, whereas in the other groups defoliation was started after the production of a certain number of leaves. Therefore the number of leaves left on the plants of group 5 differed with the photoperiod, being six at 10 hours and thirteen at 10 + 10 hours (the average node number of the first flower was 3.0 and 6.5 respectively).

It has already been pointed out (Chapter IV-2-2) that floral initiation was not affected by the various degrees of defoliation in both photoperiodic treatments. There was one exception, at a 10 + 10-hour photoperiod the plants of group 1 did not initiate floral primordia.

Independent of the degree of defoliation the plants of all groups (except group 1) flowered simultaneously with the non-defoliated control, i.e. 32 days, or 47 days after sowing in the 10-, and 10 + 10-hour treatment respectively. After 80–90 days some plants of group 1 (10-hour photoperiod) bore flowers, which, however, remained closed. In the other groups flowers were normal.

The number of flowers and capsules, and percentage of fruit setting are shown in table 24; for completeness stem lengths and numbers of leaves are also given.

TABLE 24. Influence of different degrees of defoliation on number of flowers and capsules per plant, percentage of fruit setting, stem length and leaf production.

	Photoperiod 10 hours				
	Control	6 leaves left at the onset of flowering	4 leaves left	2 leaves left	1 leaf left
Number of flowers	42.6 ± 1.7*	44.5 ± 3.2	73.6 ± 2.2	29.2 ± 1.1	21.1 ± 0.5
Ratio central: lateral flowers	46:54	49:51	38:62	73:27	87:13
Number of capsules	31.0 ± 1.6	11.9 ± 0.6	7.6 ± 0.4	2.8 ± 0.3	1.9 ± 0.2
Ratio central: lateral capsules	50:50	79:21	64:36	100:0	100:0
% Fruit set	72.4 ± 2.0	28.9 ± 2.2	10.6 ± 0.5	9.2 ± 1.0	10.6 ± 1.0
Stemlength (mm)	606	510	510	288	223
Total number of leaves formed	27.2	32.0	42.6	47.6	39.6

	Photoperiod 10 + 10 hours				
	Control	13 leaves left at the onset of flowering	4 leaves left	2 leaves left	1 leaf left
Number of flowers	91.8 ± 3.3	82.7 ± 3.5	74.2 ± 3.6	23.7 ± 1.2	13.7 ± 0.1
Ratio central: lateral flowers	51:49	52:48	41:59	100:0	100:0
Number of capsules	32.5 ± 3.0	21.2 ± 1.7	4.2 ± 0.5	0	0
Ratio central: lateral capsules	78:22	79:21	67:33	–	–
% Fruit set	34.5 ± 1.7	25.5 ± 1.8	5.4 ± 0.8	0	0
Stemlength (mm)	1202	1052	533	258	204
Total number of leaves formed	61.8	59.8	55.6	55.8	51.4

* Standard error of mean

The results of group 1 have been omitted since most plants died from starvation without having borne any flowers.

Defoliation at the onset of flowering (group 5) in each of the photoperiodic treatments had no significant effect on the production of flowers, but had an adverse effect on fruit set. Especially at a 10-hour photoperiod the number of lateral capsules decreased; this was not the case at $10 + 10$ hours. The decrease in the total number of capsules was comparatively greater in the 10-hour treatment. As a matter of fact the plants receiving $10 + 10$ hours of light possessed twenty-five leaves in various stages of development at the onset of flowering, but the plants placed at 10 hours had only formed eighteen leaves at the onset of flowering. Since at $10 + 10$ hours and at 10 hours thirteen and six leaves were left respectively, the remaining leaf mass available for the production of capsules was proportionally smaller in the latter case. This corresponds with the greater decrease in the number of capsules in the 10-hour treatment. The removal of leaves was detrimental to stem growth, but the total production of leaves was but little influenced.

In the two photoperiodic treatments of group 2, 3 and 4 equal numbers of leaves were left, i.e. one, two or four leaves respectively. At a 10-hour photoperiod the plants of group 4 produced more flowers, notably lateral flowers, than the control; further defoliation (group 3, 2) caused a decrease, whereas the ratio central/lateral flowers increased. Apparently removal of leaves stimulates the production of flowers, provided the total leaf area left is not limiting for the supply of photosynthetic products. In the $10 + 10$-hour treatment, however, the number of flowers diminished as the number of leaves left became smaller, whereas the formation of lateral flowers ceased entirely in group 3 and 2. Considering that the controls produced varying numbers of leaves, the defoliation as applied in group 4, 3 and 2 is relatively stronger in the $10 + 10$-hour than in the 10-hour treatment. This may be an explanation of the fact that at a $10 + 10$-hour photoperiod the plants of group 4 did not bear more flowers than the control. At both photoperiods the number of capsules decreased with higher degrees of defoliation. Likewise stem growth was adversely affected by the removal of leaves, especially in the $10 + 10$-hour treatment. This was not accompanied by a proportional decrease in the number of leaves, whereas in the 10-hour treatment leaf production was even stimulated.

Summarizing it can be said that all degrees of defoliation applied were detrimental to fruit set. Obviously the amount of photosynthetic products required for flower formation is rather small, since only the highest degrees of defoliation could induce a reduction in the number of flowers. It should also be considered, however, that removal of leaves, within certain limits, stimulated the formation of flowers. Similar effects were found by DE ZEEUW (118) in *Lycopersicum esculentum* and *Phaseolus vulgaris*.

V-2. VEGETATIVE GROWTH AND FLOWERING AS INFLUENCED BY REMOVAL OF FLOWERS AND CAPSULES

Simultaneously with the defoliation experiment the effect of flower and capsule removal was investigated. In each treatment twenty to twenty-four plants of the varieties Early Russian and Dulce were used. Flowers were counted daily about 9 a.m. and either cut off at the base of the pedicel, or allowed to bring forth capsules. In the latter case the capsules were removed after attaining a

length of about 1 cm, i.e. four to five days after flowering. Photoperiods of 10 and 10 + 10 hours were given. The length of main stem and branches, the number of leaves and flowers as determined for the different treatments, are shown in table 25. The results obtained from the 10-hour treatments will be discussed first.

TABLE 25a. Influence of removal of flowers and developing capsules on flower production and number of branches per plant, stem length and leaf production. Photoperiod 10 hours.

	Early Russian		
	Control	Developing fruits removed	Flowers removed
Stem length in mm.;	740	848	910
number of leaves on main stem	33.2	44.6	44.6
Number of branches	1.3	8.5	11.4
Total length of branches in mm.;	278	1545	1960
number of leaves on branches	18.3	157	226
Number of flowers on main stem	23.2 ± 0.78*	41.1 ± 0.8	41.3 ± 1.41
Number of flowers on branches	7.9 ± 1.71	122.7 ± 10.8	212.6 ± 16.4

	Dulce		
	Control	Developing fruits removed	Flowers removed
Stem length in mm.;	606	810	954
number of leaves on main stem	27.2	49.8	61.8
Number of branches	–	1.2	2.7
Total length of branches in mm.;	–	124	322
number of leaves on branches	–	14.3	33.5
Number of flowers on main stem	42.6 ± 1.82	114.8 ± 5.7	155.2 ± 7.8
Number of flowers on branches	–	15.9 ± 3.0	50.7 ± 11.4
Ratio central: lateral flowers	46:54	38:62	37:63

* Standard error of mean

At a 10-hour photoperiod removal of flowers or developing capsules favoured stem growth, leaf production and branching. Branching was even found in Dulce, which does not ramify under normal conditions. Treated Early Russian plants formed a considerable number of branches with relatively large numbers of leaves and, as a result, short internodes; rosettes of leaflets were often built on the tops of lateral axes of the second and third order. The branches attained a total length which was five to seven times greater than the corresponding value in the control, but their average length was somewhat shorter. Dulce plants ramified to a less extent, and did not get a bushy appearance. As a rule full prevention of fruit set (removal of flowers) had the greatest effect.

Cutting of flowers and removal of developing capsules greatly stimulated flower production and gave rise to the occurrence of aberrant types of flowers. The nectaries of treated Early Russian plants were swollen, and sometimes brought forth flowers with a narrow and lengthened corolla tube. Moreover flowers having separated petals instead of the usual tubular corolla were not uncommon. Such split flowers are structurally sterile because the absence of the tube

permits the style to curve upwards, thus separating the stigma from the anthers (63, 94). About forty-five to fifty days after the onset of flowering large, sometimes double, erect flowers with greatly reduced lips were formed on the tops of the main stem of treated Early Russian plants. Consequently stem growth ceased, whereas flowers on the main stem were no more produced. This phenomenon is not uncommon in strongly branching varieties (94). Sometimes flowers with neither stamens nor corolla were found on the branches of Dulce plants; such incomplete flowers were, however, not counted.

The removal of flowers had the largest influence on the intensity of flowering. In Early Russian, however, the effect on the production of flowers on the main stem was in both cases the same. As a matter of fact in this variety full or partial prevention of capsule setting affected in the first place the degree of branching and consequently the production of flowers on lateral axes, and to a much less extent the growth and the flowering capacity of the main stem.

Relatively, the number of lateral flowers in Dulce increased more than the number of central flowers (see table 25a); in this respect no difference was found between the treatments. The flowers on branches have not been subdivided further.

The daily numbers of flowers of twenty plants have been plotted for each variety in graph 15 and 16. The stimulating effect on the production of flowers, caused by either full or partial prevention of capsule setting, became manifest seventeen or twenty days after the onset of flowering in Early Russian and Dulce respectively. By that time flowering of the controls almost ceased (although the Early Russian control showed another flowering peak afterwards), whereas the treated plants continued to bear flowers for several weeks. Neither variety showed a difference between the treatments as regards the lengths of the flowering period, but on most days the flowering intensity was highest in the treatment in which fructification was entirely inhibited. As compared with the controls, the fluctuation in the daily numbers of flowers of the treated plants became greater, especially in Dulce. While in both treatments of Early Russian the daily numbers of flowers attained much higher values than in the control, the flowering peak of the Dulce control was only surpassed in the treatment in which development of capsules was fully prevented.

When discussing the results obtained from the various 10 + 10-hour treatments, it should be taken into consideration that the experiment had to be terminated in November (i.e. after three months), owing to the low daylight intensities prevailing at that time of the year (see graph 2). The controls could be harvested in due time; in the treatments, however, the stimulating effect on stem growth, leaf production, branching and flowering, might have been more marked, if the experiment could have been continued for some more weeks. Probably the untimely termination of the experiment also accounts for the fact that the flower production in the 10 + 10-hour treatments (except the treatment of Dulce in which capsules were removed) was lower than in the corresponding 10-hour treatments, whereas the reverse was true of the respective controls.

On the whole the results obtained at photoperiods of 10 and 10 + 10 hours are similar. Also at a 10 + 10-hour photoperiod full or partial prevention of capsule setting favoured stem growth, leaf production and flowering (see table 25b). However, branching was not distinctly stimulated; treated Dulce plants did not ramify, whereas in only one treatment (removal of developing capsules) Early Russian produced branches which had a greater total length than those

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TABLE 25b. Influence of removal of flowers and developing capsules on flower production and number of branches per plant, stem length and leaf production. Photoperiod 10 + 10 hours.

	Early Russian		
	Control	Developing fruits removed	Flowers removed
Stem length in mm.;	1499	1942	2112
number of leaves on main stem	60.6	116.2	127.4
Number of branches	1.4	2.4	2.1
Total length of branches in mm.;	764	1092	717
number of leaves on branches	34.1	76.5	50.7
Number of flowers on main stem	45.5 ± 1.15	99.9 ± 3.4	112.2 ± 1.9
Number of flowers on branches	25.3 ± 4.4	59.2 ± 13.0	42.4 ± 10.0

	Dulce		
	Control	Developing fruits removed	Flowers removed
Stem length in mm.;	1202	1373	1458
number of leaves on main stem	61.8	82.8	90.0
Number of branches	—	—	—
Total length of branches in mm,;	—	—	—
number of leaves on branches	—	—	—
Number of flowers on main stem	91.8 ± 4.2	158.1 ± 10.1	179.8 ± 10.5
Number of flowers on branches	—	—	—
Ratio central: lateral flowers	51:49	43:57	42:58

of the control. Moreover rosettes of leaflets and aberrant types of flowers did not occur. Neither variety showed a significant difference between the treatments in the total number of flowers produced at the time the experiment had to be terminated. It is not known whether, irrespective of the duration of the experiment, an essential difference between the 10 + 10-hour treatments should have become manifest. As a matter of fact it is possible that, owing to the higher level of vegetative development at the 10 + 10-hour as compared with the 10-hour photoperiod (cf. the controls), the difference in the effect on the flower production between full and partial prevention of capsule setting should have decreased.

From graph 15 and 16 it is evident that the stimulating effect on the production of flowers became marked about thirty-one or forty-three days after the onset of flowering in Early Russian and Dulce respectively. The flowering period of the treated plants of both varieties was much prolonged, but occasionally the daily numbers of flowers slightly surpassed the flowering peak of the controls. As compared with the controls, the degree of fluctuation in the daily numbers of flowers was somewhat higher. No difference was found between the treatments in length of the flowering period, daily numbers of flowers, and fluctuation in the daily flower productions.

Summarizing and discussing the results, it can be said that vegetative development and flower production were greatly stimulated by the suppression of fruit setting, and the flowering period was much prolonged. Even when capsules were allowed to set for only five days, vegetative development and flowering

NUMBER OF FLOWERS

VAR. EARLY RUSSIAN

PHOTOPERIOD 10 + 10 HOURS

PHOTOPERIOD 10 HOURS

- - - - - - - UNTREATED
———— FLOWERS REMOVED
———— CAPSULES REMOVED

DAYS OF FLOWERING
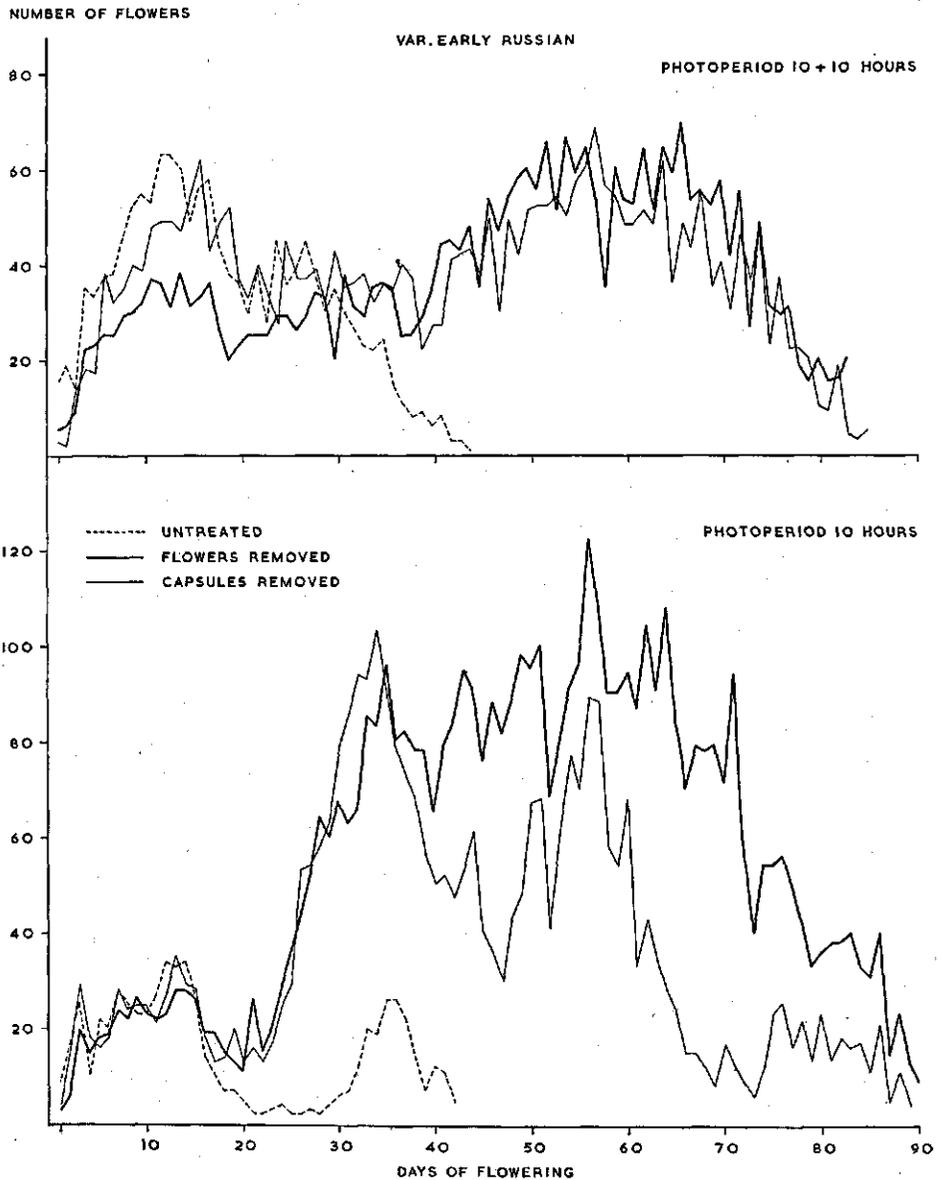
GRAPH. 15. Total number of flowers per day per 20 plants of variety Early Russian in different treatments.
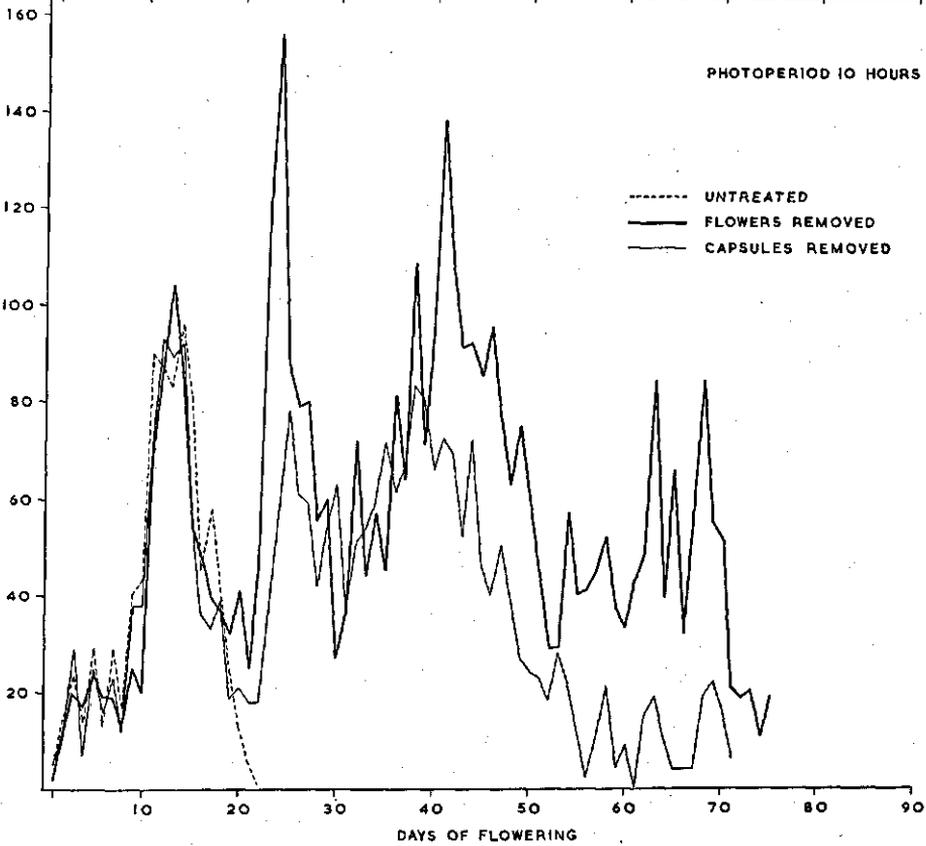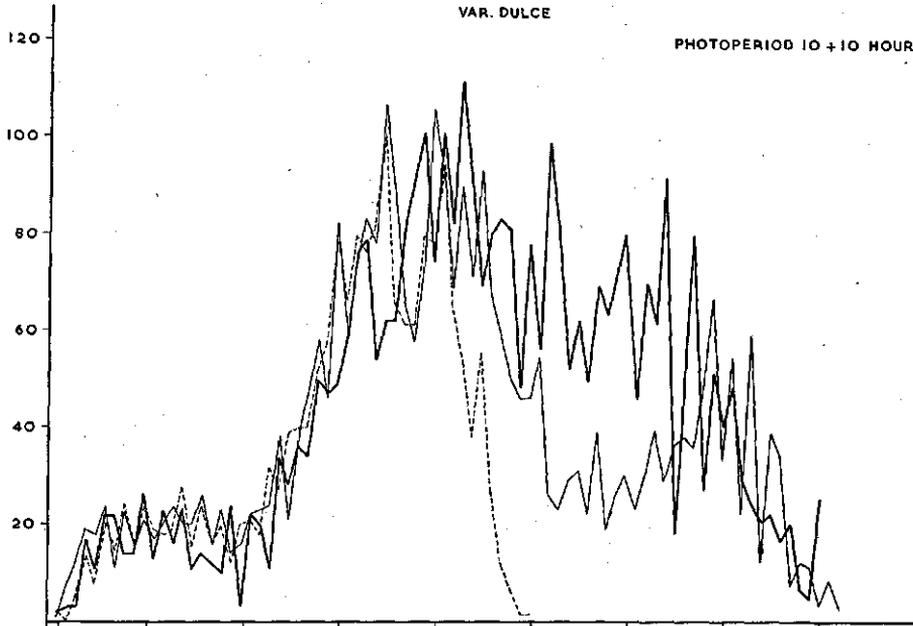
GRAPH 16. Total number of flowers per day per 20 plants of variety Dulce in different treat-
    ments.

intensity were adversely affected. Probably this is caused by a nutritional competition between developing capsules on the one hand, and vegetative growth and production of flowers on the other. At a $10 + 10$-hour photoperiod the difference between full and partial prevention of fructification was less obvious, which may be caused by the more vigorous vegetative development under these photoperiodic conditions. This is also in accordance with the observation that, as compared with a 10-hour photoperiod, more time elapsed before the effect of the treatments and the difference between them (if occurring at all at a $10 + 10$-hour photoperiod) appeared. No explanation can be given for the fluctuation in the daily numbers of flowers. Temporary shortage of photosynthetic products may restrict the production of flowers after a high flowering peak, but this seems not very likely since no great quantities of assimilates are required for flowering. Unfortunately data on this subject are not available in literature. From their experiments on peanut FORTANIER (39) and BOLHUIS (13, 14) obtained similar results. In this crop removal of flowers also greatly lengthened the flowering period, and flower production, stem growth, leaf production and branching were highly stimulated. BOLHUIS observed a great fluctuation in the daily numbers of flowers of the treated plants, but found no convincing explanation for this phenomenon.

CHAPTER VI

GENERAL DISCUSSION

In Chapter III it was shown that stem length, dry weight of stem base, number of leaves and leaf area increased as the photoperiods became longer. This was found both for photoperiods consisting of daylight only, and for those consisting of a certain basic illumination supplemented with fluorescent light. Since the intensity of this light was very low (one per cent. of the daylight intensity at most), its influence on the production of dry matter cannot be ascribed to an increase in photosynthesis, but is more likely due to an increase in the leaf area. Actually, net assimilation rate and leaf area are decisive for the effect of light on the production of dry matter (25). The optimal light intensities for photosynthesis and leaf development are quite different, as is shown from some data in literature. According to SCHWABE (89) shortening of the daylight period and reduction of the light intensity induced an increase in the leaf size in *Xanthium pennsylvanicum, Kalanchoe blossfeldiana* and other crops (cf. VAN DER VEEN and MEYER (100). Supplementary light of low intensities (fluorescent or incandescent light) may affect the leaf area in a similar way, as was found in chrysanthemum (102) and peanut (39).

In sesame not only leaf growth, but also stem elongation and leaf production were favoured by supplementary light, which was not photosynthetically effective. Similar results were obtained with potato by WASSINK and STOLWIJK (105), and more examples are available in literature (15, 84). SCHWABE (87) suggests that additional weak light may raise the auxin level and consequently promote stem elongation.

Replacement of daylight by artificial light was not always detrimental to stem growth, leaf production and accumulation of dry matter (Chapter III-2, 3). At some photoperiods shortening of the daylight period even had a favourable influence. This again shows that both daylight and supplementary

light affect the vegetative development of sesame. This holds also true for the leaf development, but at all photoperiods substituting daylight for artificial light had an adverse effect.

It was shown (Chapter IV-5) that long periods of supplemental light (as applied in 6+14-, 8+12- and 10+10-hour photoperiods) delayed flowering considerably. Consequently the period preceding fruit setting was also lengthened, which resulted in a more vigorous development (cf. table 4, Chapter III). There is evidence that the photoperiodic effect in these cases at least partly accounts for the influence of supplementary light on the vegetative development. In fact, fructification has an adverse effect on stem growth and leaf production; suppression of fruit set stimulated the vegetative development (Chapter V-2). This is in accordance with the fact that early flowering (short photoperiods) was accompanied by a short growing period (graph 4, 5) in which the maximum growth rate was soon attained. However, no clear-cut connection was found between maximum growth rate and onset of flowering. ALEKSEEV (1) and SEN and PAIN (90), who also worked with sesame, did not obtain positive results either. Another phenomenon demonstrates the antagonism between vegetative and reproductive development. The leaves that are formed after the onset of flowering, decrease in size and become more lanceolate in shape. Consequently the number of large oval leaves decreases with a decrease in the number of days to flowering. SEN and PAIN (90) also pointed out that formation of lanceolate leaves is connected with the beginning of flowering. DE ZEEUW (116) reports similar observations in other crops.

The effects of the photoperiod on vegetative development and on seed production are very much the same. Vegetative development and seed production are closely interconnected, as appears from the coefficients calculated for the correlation between seed production and stem length, seed production and dry weight of the stem base, seed production and number of leaves, seed production and leaf area. These values (calculated from table 3, 5 and 23) were respectively 0.89, 0.96, 0.86 and 0.88 for Early Russian and 0.55, 0.69, 0.65 and 0.86 for Dulce. Apparently in Dulce the seed yield is not fully reflected in the vegetative development. However, a more distinct connection was found between the number of flowers and the vegetative development. In this case the respective correlation coefficients, in the above order, were: 0.78, 0.94, 0.88 and 0.74 (calculated from table 3, 5 and 22). Apparently in Dulce an improvement in growth causes an increase in the number of flowers which is not accompanied by a proportional increase in the number of capsules. As was pointed out on p. 54, abundant flowering probably limits the amount of photosynthetic products available for fruit setting. In Early Russian the competition between flowers and developing capsules seems to be less important, which is in accordance with the relatively small numbers of flowers (no lateral flowers) and the high percentages of fruit set in comparison with Dulce (cf. table 22 and 23).

SUMMARY

The influence of light and temperature on vegetative and reproductive development of sesame varieties was studied.

The optimum germination temperature was found to range from 32° to 35°C. Floral initiation under short-day as well as long-day conditions was not

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advanced by vernalizing seeds at 3° to 5°C; vernalization for more than five days adversely affected germination (Chapter III-1).

In controlled environment rooms stem growth and production of leaves increased as the average temperature was raised from 24° to 33°C; alternating day and night temperatures were not beneficial. Under greenhouse conditions diminution of the diurnal temperature fluctuation, by keeping the night temperature above 25°C, favoured the vegetative development. Lengthening the daylight period as well as extending daylight with fluorescent light (intensity 2000 erg.sec.$^{-1}$cm^{-2}) caused an increase in stem length, dry weight of the stem base, number of leaves and leaf size. The longer the photoperiod (in the range of 6 to 20 hours), irrespective of its composition, the more vigorous the vegetative development (Chapter III-2,3).

Seedlings were not sensitive to the length of the photoperiod for three to eight days after emergence, depending on the variety (Chapter IV-1). The transition from the vegetative to the reproductive stage has been described (Chapter IV-2-1). Under favourable photoperiodic conditions even the small area of the cotyledons was sufficient for floral induction (Chapter IV-2-2).

A constant temperature of 24° to 27°C was optimal for early floral initiation, whereas both high (33°C) and low (15°C) night temperatures caused a delay. The retarding effect of high (low) night temperatures was more or less counteracted by low (high) day temperatures. Moreover, low night temperatures offset the retarding effect of long photoperiods (Chapter IV-2-3).

The photoperiodic response was investigated at photoperiods ranging from 5 to 24 hours, and consisting of a basic illumination of daylight supplemented with different periods of weak fluorescent light (intensity at least 250 erg. sec.$^{-1}$cm^{-2}). The number of days to floral initiation and flowering was minimal at photoperiods ranging from 10 to 13 hours, consisting of at least 8 hours of daylight. The delay at photoperiods of 10 to 5 hours was mainly caused by restricted photosynthesis, resulting in a decline in growth. Although being accelerated by a short-day break, in most varieties floral initiation and flowering occurred eventually under long-day conditions, even at 20- to 24-hour photoperiods. At photoperiods of the same length no difference was found between basic illumination periods of 10 and 13 hours, but in most varieties shortening of the daylight period to 8 hours or less caused a delay in floral initiation and flowering, especially at long photoperiods. Within the group of varieties originating from low latitudes, various degrees of photoperiodic sensitivity occurred, but all varieties from higher latitudes were rather insensitive (Chapter IV-2-5, IV-3-2).

The number of flowers and capsules and the seed production per plant increased as the photoperiod, irrespective of its composition, was lengthened from 6 to 20 hours (intensity of the supplemental light 2000 erg.sec.$^{-1}$cm^{-2}). Abundant flowering was accompanied by a decrease in the percentage of fruit setting (Chapter IV-3-2, IV-4-1).

Continuous removal of leaves above the node of the first flower did not influence the production of flowers, but was detrimental to fruit setting. Continuous defoliation started at an earlier stage (after the formation of four leaves), hardly affected, and in some cases even stimulated the production of flowers, but fruit set was greatly reduced (Chapter V-1).

Partial, and in particular complete inhibition of fructification greatly stimulated the vegetative development and the production of flowers, and the flowering period was prolonged (Chapter V-2).

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It is suggested that supplemental light influences the production of dry matter, owing to its effect on the leaf area and the time of flowering. Vegetative development and seed production proved to be closely interconnected, but the connection was more or less confused by a competition between the formation of flowers and the developing capsules (Chapter VI).

SAMENVATTING

De invloed van het licht en de temperatuur op de vegetatieve en generatieve ontwikkeling van sesam variëteiten werd bestudeerd.

Een temperatuur van 32°–35°C bleek optimaal te zijn voor de kieming. De bloeiinitiatie werd noch bij lange, noch bij korte fotoperioden versneld door zaadvernalisatie by 3°–5°C; de kiemkracht liep sterk terug wanneer langer dan vijf dagen gevernaliseerd werd (Hoofdstuk III-1).

Een onderzoek naar de invloed van de temperatuur op de stengelgroei en de aanleg van bladeren in klimaatkamers wees uit, dat beiden bevorderd werden door een stijging van de gemiddelde temperatuur van 24° tot 33°C; wisselende dag- en nachttemperaturen waren niet gunstig. In kassen had een vermindering van de dagelijkse temperatuur fluctuatie door een verhoging van de nachttemperatuur tot minstens 25°C, een gunstige invloed op de vegetatieve ontwikkeling. Stengellengte, drooggewicht van de stengelbasis, aantal bladeren en bladoppervlak namen toe naarmate de periode van daglicht, of de aanvullende belichting met TL lampen (intensiteit 2000 erg.sec.$^{-1}$cm^{-2}) langer genomen werd. Ongeacht de samenstelling, gaf een verlenging van de fotoperiode van 6 tot 20 uur een krachtiger vegetatieve ontwikkeling (Hoofdstuk III-2,3).

De juveniele fase was, afhankelijk van de variëteit, drie tot acht dagen na de opkomst der zaailingen afgelopen (Hoofdstuk IV-1). De overgang van het vegetatieve naar het generatieve stadium is beschreven (Hoofdstuk IV-2-1). Bij gunstige fotoperioden was zelfs het kleine oppervlak van de cotylen voldoende voor bloeiinductie (Hoofdstuk IV-2-2).

Bloeiinitiatie was optimaal bij een constante temperatuur van 24°–27°C, terwijl zowel hoge (33°C) als lage (15°C) nachttemperaturen een vertraging veroorzaakten. De vertragende werking van hoge (lage) nachttemperaturen werd meer of minder gecompenseerd door lage (hoge) dagtemperaturen. Bovendien werd de vertragende invloed van lange fotoperioden opgeheven door lage nachttemperaturen (Hoofdstuk IV-2-3).

De fotoperiodiciteit werd onderzocht bij fotoperioden van 5 tot 24 uur, bestaande uit een basisbelichting van daglicht aangevuld door zwak TL-licht met een intensiteit van minstens 250 erg.sec.$^{-1}$cm^{-2}. Het aantal dagen tot de bloeiinitiatie en de bloei bereikte een minimum bij fotoperioden variërend van 10 tot 13 uur, waarin minstens 8 uur daglicht werd gegeven. De vertraging in het traject van 10 tot 5 uur werd vrijwel uitsluitend veroorzaakt door een slechtere groei, tengevolge van een gebrek aan assimilaten. In de meeste variëteiten trad uiteindelijk wel bloeiinitiatie en bloei op bij lange fotoperioden, zelfs bij 20 en 24 uur, maar een aantal korte dagen versnelde beide processen in hoge mate.

Bij fotoperioden van gelijke duur werd het tijdstip van bloeiinitiatie en bloei niet beïnvloed door een verkorting van de basisbelichting van 13 tot 10 uur, maar een verdere verkorting tot 8 uur veroorzaakte een vertraging, vooral bij lange fotoperioden. De variëteiten afkomstig van lage geografische breedten

verschilden onderling nogal in fotoperiodische gevoeligheid, maar de variëteiten van hogere breedtegraden waren alle tamelijk ongevoelig. (Hfdst. IV-2-5, IV-3-2.)

Het aantal bloemen en vruchten en de zaadproductie per plant namen toe wanneer de fotoperiode, ongeacht de samenstelling, verlengd werd van 6 tot 20 uur (intensiteit van de bijbelichting 2000 erg.sec.$^{-1}$cm^{-2}). Bij overvloedige bloei was het aantal vruchten procentueel lager (Hoofdstuk IV-3-2, IV-4-1).

Voortdurend verwijderen van blad boven de knoop van de eerste bloem beïnvloedde de productie van bloemen niet, maar verminderde het aantal vruchten. Voortgezette ontbladering na de vorming van het tweede bladpaar had weinig invloed op, of stimuleerde zelfs de aanleg van bloemen, maar de vorming van vruchten werd sterk onderdrukt (Hoofdstuk V-1).

Algehele of gedeeltelijke verhindering van de vruchtzetting begunstigde de vegetatieve ontwikkeling en de aanleg van bloemen, terwijl de bloeiperiode verlengd werd (Hoofdstuk V-2).

Verondersteld wordt, dat de aanvullende belichting door zijn invloed op het bladoppervlak en fotoperiodieke werking de productie van droge stof beïnvloedt. De vegetatieve ontwikkeling en de zaadproductie stonden in nauw verband met elkaar, maar de correlatie werd in meerdere of mindere mate verstoord door een concurrentie tussen bloemen en vruchten onderling (Hoofdstuk VI).

ACKNOWLEDGEMENTS

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