635.936.692:581.143.035/.036+581.145.1.035/.036

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 67-13 (1967)

EFFECTS OF LIGHT AND TEMPERATURE ON GROWTH AND FLOWERING OF CARNATION (*DIANTHUS CARYOPHYLLUS* L.)

De invloed van licht en temperatuur op groei en bloei van de anjer

A. M. ABOU DAHAB

Publication 298, Laboratory of Horticulture, Agricultural University, Wageningen, The Netherlands

(Received 27-VI-1967)

H. VEENMAN & ZONEN N.V. – WAGENINGEN – 1967

Mededelingen Landbouwhogeschool
Wageningen 67–13 (1967)
(Communications Agricultural University)
is also published as a thesis

CONTENTS

1. GENERAL 1
1.1. The growing of carnations 1
1.2. Literature 3
1.2.1. Light 3
1.2.2. Temperature 4
1.2.3. Gibberellic acid 5
1.2.4. Timing of carnation crop 5
1.3. Scope of investigations 7

2. MATERIAL AND METHODS 8
2.1. Plant material 8
2.2. Growth conditions 8
2.3. Abbreviations 9
2.4. Observations 9
2.5. Stages of flower bud initiation 10

3. LIGHT 11
3.1. Introduction 11
3.2. General effects of light 11
3.3. Effects of daylength 12
3.3.1. General effects on initiation and flowering 12
3.3.2. Effects of changes in daylength before and at the time of initiation 15
3.3.3. Effects of night interruption 16
3.4. Effects of light intensity 17
3.4.1. General effects on initiation and flowering 17
3.4.2. Effects of changes in light intensity 19
3.4.2.1. Before and at the time of initiation 19
3.4.2.2. After flower bud emergence 22
3.5. Discussion 23

4. TEMPERATURE 24
4.1. Introduction 24
4.2. Effects on initiation and flowering 24
4.2.1. Effects of photoperiod and temperature 24
4.2.2. Effects of low temperature followed by high temperature 27
4.2.3. Effects of day and night temperature 28
4.3. Effects of low temperature (5 °C) 32
4.3.1. Effects of duration of 5 °C and interaction with photoperiod 32
4.3.2. The optimum period of 5 °C 35
4.3.3. The optimum size for 5 °C 37
4.3.4. Effects of daylength and light quality during 5 °C 38
4.3.5. Effects of temperature after 5 °C 39
4.3.6. Effects of interruption of 5 °C with high temperature 39
4.4. Discussion 41

5. GIBBERELLIC ACID 44
5.1. Effects of gibberellic acid (GA_3) 44
5.2. Discussion 48

6. TIMING OF CARNATION CROP 49
6.1. Introduction 49
6.2. Timing of carnation crop by planting date and low temperature treatment . 49
6.3. Discussion 56

7. CONCLUSIONS 60

ACKNOWLEDGEMENTS 62

SAMENVATTING 63

REFERENCES 66

1. GENERAL

1.1. THE GROWING OF CARNATIONS

Like many fragrant plants, the carnation has been grown for a very long time. THEOPHRASTOS already mentions it as Diosanthos (flower of the Gods). The wild species, *Dianthus caryophyllus* L., occurs in the Mediterranean area. The great variability in flower colour of the cultivated forms no doubt arose by mutation, but the strong and vigorous stems of the modern type are contributed by some authors to the influence of *D. suffruticosus* Willd. and the perpetual flowering habit to *D. caesius* Smith. There does not seem to be any critical research on this. It is certain, however, that the modern carnation was bred in France, and particularly in the USA where it was introduced in 1856.

Nowadays the carnation is an important flower crop and garden plant in most affluent countries of the temperate zone. The modern cultivars flower the year round with a great range of colours which comprises white, pink, salmon, red, violet and yellow.

In Spain, Southern France and Italy carnations are grown in the open. In the more northern parts of Europe and in the USA they are grown in greenhouses. This discussion will be limited to the latter method of cultivation, which will be shortly described.

The carnation is propagated by cuttings. The three principal sources for these in commercial greenhouses are lateral shoots: 1. from flowering stems either taken before the flowers were cut, or from the flower stems on the grading bench, 2. which have developed following cutting the flowers in late spring, and 3. from mother plants grown especially for the production of cuttings. The latter method is increasing in popularity.

Material for cuttings should be left on mother plants until they are of a uniformly large size: at least 5 to 6 pairs of expanded leaves and weighing at least 10 grams. After removing the cuttings from the mother plants they are usually treated by an auxin to promote rooting (e.g. by naphthalene acetic acid at a strength of 0.25% in talc).

Cuttings can be planted in different media for the rapid formation of healthy roots. Commonly, coarse sand, mixtures of sand and peat, or perlite are used.

Water is an essential factor in controlling root formation and diseases during the propagation period. The amount of water used should be just enough to prevent wilting. Excess water merely increases the leaching of sugars and nutrients from the leaves and may elongate cuttings too much (HOLLEY and BAKER, 1963). The best method for watering cuttings is the use of a mist propagation system. Full sunlight during the propagative period produces cuttings which grow most rapidly following propagation. This does not mean, however, that carnation cuttings will fail to root under low light intensity.

Carnation cuttings are rooted under a wide range of temperatures. The accepted temperatures for winter propagation is 10°C air temperature to keep top growth within bounds and a 3° to 5°C higher rooting medium temperature to

stimulate root formation. Under such conditions cuttings usually root in 14–21 days.

There are two methods for planting carnations: 'Direct benching' is the method where the cuttings are planted directly in the bench where they are to flower. A second method of producing young transplants involves the use of a nursery bed or peat pots. The plants can be held here for 6 or 8 weeks and are afterwards moved and planted into the production benches. As the planting distance does not affect final yield much (at least not within the limits 15 to 25 cm) the grower is rather free in his choice, which will depend on other growing measures, e.g. pinching, supporting etc.

After the cuttings are firmly established in the soil they are stopped back by a single pinch, later followed by a second. This second time, not all the young shoots have to be pinched; sometimes one pinches only half or three quarters of them.

Disbudding is bound to be necessary and the plants should be gone over each week to remove all the buds large enough to handle, except the terminal bud. The unwanted buds should not be removed when very small as this is apt to damage the stem, nor should the lateral buds be left until nearly fully developed, for this takes food from the central bud and reduces the size of the ultimate flower (CHITTENDEN, 1951).

The principles of support are to hold the body of the plant off from the soil for a free circulation of air underneath, and to support the flower stems in a way so as not to impair the plant in its freedom of growth, and leave free access to cut the blooms with any desired length of stem (BAILEY, 1904).

Water should be given freely when needed and care be taken to make the watering thorough, reaching the bottom of the bench.

The carnation is rather a heavy feeder, and quantity and quality of blooms depend largely on the nourishment supplied. The necessity for feeding depends on the richness of the soil, and to avoid a disastrous over-feeding, food has to be applied judiciously. Nitrogen, potassium, phosphorus, calcium and trace elements have been shown essential for carnation growth.

The flowers should be cut when they have developed to about three-quarters of their final size. They are taken off with long stem cut just above a joint with a sharp knife. Cutting should be done in the early morning and the flowers should be put at once into water in a dark room for a few hours, after removing some of the lower leaves. If cut at the right stage the flowers will improve in these conditions. The water should be only slightly cooler than the temperature of the house from which the flowers are taken and the flowers should be given plenty of room, stand erect and have three-quarters of their stems submerged in the water which should be changed after 24-hour.

If flowers have to be sent any distance they should be packed in a strong box and fixed so that they cannot move about.

Carnation may at various times be attached by various diseases, caused by virus, bacteria and fungi. Some of these can be disastrous. In carnation houses it is therefore necessary to carry out periodical soil sterilization by heat or

chemicals. Also cuttings must be taken only from healthy plants. Meristem culture is used nowadays to obtain virusfree material. Carnations may also be attached by several pests such as spider mites, aphids or thrips.

Although carnations are being grown successfully for 2, 3 and even 4 years, the most profitable system is 2-year. After this period it is too difficult to control the diseases.

1.2. Review of literature

1.2.1. *Light*

Originally the carnation was a long day plant, flowering only in summer. The development of its perpetual flowering habit by the French breeders, and later by American breeders rid this plant of most its response to daylength. The modern carnation has been considered as insensitive to photoperiod as it will flower under all daylengths. However, Laurie and Poesch (1932), Arthur and Harvill (1938), and White (1960) obtained an increase in flower production with additional illumination. Pokorny and Kamp (1960) carried out an extensive experiment on the effect of photoperiods of 8 and 16 hours on the variety 'Sidney Littlefield'. They concluded that plants grew better and flowered earlier under a 16-hour photoperiod. Plants in an 8-hour photoperiod had longer stems, a lower yield, slightly larger flowers and more side shoots than those in a 16-hour photoperiod.

Relatively few workers have attempted to distinguish between the effects of the photoperiod flower initiation and the effects on subsequent flower development. Post (1952) and Rünger (1957) stated that flower bud initiation was not affected by daylength, but that subsequent flower development was more rapid in long days than in short days. Blake (1955) classified carnation as a facultative long day plant with respect of flower initiation. His experiments showed that flower initiation was delayed by short day. Blake and Harris (1960) and Harris and Harris (1962) reported similar responses to daylength. They also stated that photoperiod had no appreciable effect on growth in terms of dry weight or on rates of leaf initiation, but that internode length was greater in long days than in short days.

Blake (1956) found that up to the time of flower bud initiation daylength was the most important environmental factor. Once the buds were formed, temperature became more important than daylength.

Harris and Griffin (1961) and Harris and Harris (1962) found that a period of illumination given in the middle of the night was more effective in promoting flower initiation than an equivalent period given to extend the day. In these experiments, internode length was more affected by the night interruption.

Effects of light intensity on flower initiation have received little attention. The effect of light intensity on growth and flower production of carnation in glasshouses has been noted by Holley (1942). Nelson and Kiplinger (1957) found that flower initiation was most rapid in the summer months and attributed this to higher light intensities at that time of year. Harris and Harris

(1962) reported that low light intensities delayed flower initiation and that this delay was associated with reduced rates of growth in terms of dry weight, reduced rates of leaf initiation and an increased number of leaves formed below the flower. They also found that under the low light intensity of mid-winter leaf initiation continued but flower initiation was inhibited.

1.2.2. *Temperature*

HOLLEY and BAKER (1963) reported that carnation is very sensitive to temperature. This factor strongly influences such practically important characteristics rate of growth, size and shape of flowers, stems and leaves, water content of the plant tissues and keeping quality of the cut flowers. HALLIDAY and WATSON (1953), BLAKE and SPENCER (1958), HARRIS and HARRIS (1962) found that low night temperature caused flower initiation to occur after fewer leaves had been formed and that, conversely, high night temperature delayed flower initiation and increased the number of leaves formed below the flower. POST (1942), RÜNGER (1957) and BLAKE and SPENCER (1958) also noted that relatively high temperature may be retard flower initiation, but found it promoted the development of the flower subsequent to initiation. BLAKE and SPENCER (1958) reported that in the variety 'White Sim' flower buds appeared earlier when night temperatures were low (40° or 50°F) than when they were high (60°F).

HANAN (1959) found, that the highest average quality of the flowers was obtained when the plants grown at a day temperature of 65°F and a night temperature of 52°F. FREEMAN and LANGHANS (1965) reported that temperature did not greatly affect the total production of flowers, but that it affected the percentage of flowers with a split calyx, although the precise relationship was not clear. In addition, temperature controlled the grade of flowers.

HOLLEY and BAKER (1963), LAURIE et al. (1958) and POST (1949) considered 50°F (10°C) the best growing temperature for the carnation. According to HOLLEY and BAKER (1963), SCHMIDT grew the variety 'Red Sim' under accurately controlled night temperatures of 48°–50°, 50°–52° and 54°F with a relatively constant day temperature (fluctuating between 60° and 68°). He concluded that in Colorado 50° or 54°F was the ideal night temperature. Several workers report that increasing the growing temperature of carnations above the generally recommended values led to a decrease in internode length, stem length and stem dry weight, an increase in node number, and a decrease in leaf width. Growth became weak, plants budded sooner, flower bud initiation and development were hastened, and so was flowering, flower colour was improved, flower size and weight decreased, petal weight and number decreased, the quality of flowers was lower, but the keeping life of cut flowers increased.

In addition to direct effects of temperature on flowering in carnation, there may also be indirect effects. A pre-treatment at a low temperature appears to promote subsequent flowering. BLAKE (1956) in a preliminary report stated that a period of 3 weeks or more at 36°–41°F given when the plants had 9 to 11 pairs of leaves caused flower initiation to occur at a lower node number, provided that the cold treatment was followed by long days and low temperature conditions

(50°F night temperature). Short-day conditions and high temperature given after the cold treatment were claimed to reverse or reduce the effect. HARRIS and HARRIS (1962) also found that a low temperature treatment (40°F=4.5°C for one month) promoted subsequent flower initiation and reduced the number of leaves formed below the flower.

1.2.3. *Gibberellic acid*

In 1956 LANG found that biennial *Hyoscyamus niger*, which requires a period of low temperature followed by long days to flower, could be induced to flower without low temperature by the application of gibberellic acid (GA_3). Since then, GA has been shown to induce flowering not only in non-vernalised cold requiring plants, but also in many long day plants grown under short day conditions. GA does not promote flower initiation in short day plants. *Bryophyllum crenatum* and *B. daigremontianum*, which require long days followed by short days to flower, are induced by GA to flower in continuous long days (BÜNSOW and HARDER, 1956). In *Chrysanthemum morifolium* 'September Yellow', GA substituted for low temperature but not for short days (DOORENBOS, 1957).

This negative reaction of short day plants appears to be general, but the rule that GA substitutes for low temperature and long days has still many exceptions (e.g. WELLENSIEK, 1958).

EBBEN (1959) was the first and so far the only author who applied GA_3 to carnations. His aim was to obtain more or longer cuttings from mother plants, and to induce faster plant growth in order to reduce the possibility of wilt pathogens penetrating the young shoots. He found no response of several months old stock plants when lanolin paste with 1% GA was applied to the base of the stem where small axillary shoots had begun to appear. One month old plants however, to which 20 cc of water was applied with 0.2 mg of GA showed an acceleration of shoot growth which after 17 days had led to a 40–43% increment over the controls.

1.2.4. *Timing of carnation crop*

BING (1960) in Long Island, USA, reported that January planting gave a heavy crop of flowers from June onwards, i.e. after 5 months. The April planting flowered profusely in July (3 months). The July planting flowered well in October (3 months) and November but poorly from December to March. The August planting flowered fairly well during the winter months. The September planting did not flower profusely until April, i.e. after 7 months. A better winter production was obtained by early planting followed by continuous pinching from July to early September. An August pinch gave an even better winter production. HOLLEY and HILL (1961) in Colorado, USA, reported that planting carnations in May or June followed by a single pinch produced a higher grade of flowers during the following winter and early spring than planting on July 15. DAVIDSON (1953) equated the available light during each month with the light in June = 100, and calculated that in Rutgers, New Jersey, for

instance, January and December have on the average only sufficient light to give 30% of the growth in the month of June. KORNS and HOLLEY (1962) in Colorado, USA, reported that while for the periods beginning in November and December light energy decreased to about 45% of the energy in the month of June, carnation growth decreased to 15% of the fastest rate in June.

One may assume a relation between the reaction of the plant to light intensity and the prevailing temperature. HANAN (1959) advised carnation growers to let day temperature closely follow the available light intensity. Also MANRING and HOLLEY (1960) reported that the day temperature should vary with the amount of solar energy received by the plants. They concluded that when solar energy is high (May to August) in Colorado, USA, the day temperature should be 18° to 21°C; and it should be decreased gradually by decreasing the solar energy. In January, when the solar energy is small, day temperature should be 14°C. They reported also that night temperature should be 10° to 12°C the whole year.

HOLLEY and WAGNER (1952) stated that with carnation plants pinched once most growers in Colorado, USA, should be able to produce two complete crops in a year. HOLLEY, (1959) stated that when light is limiting the second (return) crop often extends over a period of at least 10 to 12 weeks; in general, the higher the amount of solar energy at the time a crop is cut, the shorter the duration the harvesting period. HOLLEY and BAKER (1963) reported that two complete crops of flowers can be cut from 'single-pinched' plants in a period of 38 to 47 weeks following the planting of rooted cuttings. Planting on May 15 produces 2 crops in the shortest possible time; planting in late June and July leads to the longest time to finish two crops. BING and MAIER (1953) found that in Long Island, USA, the period between first and second crop varies between 3 and 9 months. The return crop from a September cut takes 5–9 months to develop; while the return crop from a February cut only takes 3–5 months. Shoots left when the flowers have been cut in mid-January usually flower in June. The return crop from the September cut is harvested over a long period of time while the return from the February cut gives a high percentage of flowers in a relatively short period in June and early July.

From the data reported in the literature it appears that the evaluation of the effect of a certain planting date depends on which aspects of the crop is considered. If the criterium is the time between planting date and harvesting one would favour planting between April and July as this leads to flowers after 3 months. If on the other hand one is primarily interested in a good crop during the winter months, one should plant in August. Finally, if the time between the first and second crop is an important criterium one should consider planting in August; the plants will flower in February and the return crop will take 3–5 months, at least under Long Island conditions.

1.3. Scope of the investigations

The object of the investigations was to study the effects of photoperiod, light intensity, and temperature on growth and development of the carnation plant, making a clear distinction between the effects of these factors on each stage of plant development from planting to anthesis, with an emphasis on the actual flower initiation. Particular attention was paid to the effects of a period of low temperature on subsequent flowering behaviour. Also the effect of gibberellic acid on growth and flowering was studied. The data on the effect of light and temperature were used to get some insight into the relation between planting date and flowering in the greenhouse.

2. MATERIAL AND METHODS

2.1. PLANT MATERIAL

The cultivar 'William Sim' was used in most of the experiments described here. This variety was produced in 1938 or 1939 by WILLIAM SIM of North Berwick, Maine (HOLLEY and BAKER, 1963). It is the most successful carnation variety produced so far. Grown wherever carnations are found, it is the leading cultivar in most places. It has given a large number of mutations. One of these, 'Keefer's Cheri Sim', was used in some experiments when 'William Sim' was not available. It may be assumed, however, that the sport although it differs in flower colour, is identical with the mother cultivar in its physiological reactions.

All experiments started from rooted terminal shoot cuttings, 10–15 cm long with 5 to 7 pairs of expanded leaves. They were obtained from Messrs. P. KOOY GZN and ZN, Aalsmeer.

One or two weeks after planting the cuttings were stopped back by pruning away the stem tip. At this time of stopping usually several of the plants had macroscopically visible flower buds. It may be assumed that in these cases flower initiation had occurred before the cuttings were taken from the stock plants. There was no evidence of any difference in the growth or flowering behaviour of the shoots from generative and vegetative plants, provided of course the generative plants were stopped back to a vegetative bud and not to one of the flower buds which develop in the axils of the five or six leaf pairs immediately below the terminal flower (HARRIS and HARRIS, 1962). Of the shoots which grew out as a result of stopping, only the uppermost one or two were retained. The others were removed at an early stage.

The rooted cuttings were planted in 10–14 cm plastic pots containing steam sterilized soil.

2.2. GROWTH CONDITIONS

Many experiments were carried out in the phytotron, earlier described by DOORENBOS (1964). Plants could be grown either in strong fluorescent light (Philips TL 40W/55, maximal intensity 40.000 erg cm^{-2} sec^{-1} (measured with a flat photometer at table level in the center of the room), or under natural daylight, both at temperatures of 9°, 12°, 15°, 18°, 21° or 24°C. The plants could also be placed at approximately 22°C under 12 different light conditions: daylength 8, 12 or 16 hours, relative light intensities: 25%, 50%, 75% or 100%, corresponding with about 11.000, 22.000, 32.000 or 40.000 erg cm^{-2} sec^{-1} in each daylength.

Some experiments were carried out in greenhouses, which were heated during winter but could not be cooled during the summer. The temperature was fairly constant at 20°C in winter, but in the summer months it was often higher during the day time.

Some photoperiodic and shading experiments were carried out on trolleys in the

open. The plants received 8 hours of natural light outdoors from 8.30 A.M. to 4.30 P.M. and were then moved into sheds. Long day conditions could be created by extending the natural days with 40 Watt incandescent bulbs. These lamps were usually 50–60 cm above the planted benches and 75 cm from each other.

Low temperatures were applied by placing plants in refrigerated rooms with a constant temperature of 5°C under either short day conditions (8 hours fluorescent light, one Philips TL 40 W/29 of 1.2 m length per 0.5 m^2), long day conditions (16 hours fluorescent light, the same source), or continuous incandescent light (24 hours incandescent light, one Philips Philinea tube 120 W and 1 m length per 0.45 m^2).

2.3. Abbreviations

The abbreviations which will be used throughout are as follow:

AL : artificial light
FL : fluorescent light
GA_3: gibberellic acid
Inc : incandescent light
LD : long day
NL : natural light
S : shaded
SD : short day
Uns : unshaded

2.4. Observations

In all experiments, the following data have been recorded:

1. Number of days from planting to microscopically visible flower bud initiation.
2. Number of days from planting to flower bud emergence from the leaves.
3. Number of days from planting to visible flower colour.
4. Number of days from planting to anthesis (flower maturity).
5. Number of leaf pairs below the flower.
6. Number of internodes.
7. Internode length.
8. Stem length.
9. Stem diameter.
10. Length and width of leaves.
11. Flower diameter.
12. Number of petals.
13. Fresh weight of flower, leaves and stem.
14. Dry weight of flower, leaves and stem.

To present all these data in the present publication would have required too much space. The tables therefore give only a representative selection from the total amount of data.

2.5. Stages of flower bud initiation

The vegetative apex of carnation plant is morphologically a simple structure initiating leaf primordia in alternating pairs. The two opposite initials appear to arise simultaneously and to continue growth at an almost identical rate. At maturity the two leaves of a pair have approximately the same areas and dry weight (Holley, 1942). The primary characteristic of this vegetative stage is the blunt or round apical meristem (Fig. 1 A).

Prior to the formation of the sepal primordia the apex appears to elongate and this elongation is thus the first visible sign of the switch from vegetative to generative development. Two pairs of bracts are initiated before the actual sepal primordia; in the initial stages, these are indistinguishable from leaf primordia (Thompson, 1944; Puri, 1951). The sepals arise in a whorl near the tip so that the apex appears broader and flatter. It also increases in size (Fig. 1 B). The sepals grow rapidly and arch over the other primordia; at this second stage of calyx initiation it appears as a kind of tube (Fig. 1 C). In the final stage of initiation the calyx (Fig. 1 D) clearly shows five sepals.

By removing part of the calyx (Fig. 2 E), the petal primordia can be observed. The apex ceases active growth with the formation of two or more carpel primordia, which grow up and over the apex, thus forming the ovary cavity. The central core of tissue forms the placentas bearing the ovules in an axile arrangement (Blake, 1962); while the primordia unite and extend to form the styles. During the beginning of style initiation, it is impossible to distinguish yet between petals and stamens because their primordia look very similar.

When the stamens can be distinguished (Fig. 3) it also becomes apparent exactly how many styles there will be in the flower. In this stage all individual flower parts have been formed. Fig. 4 shows the styles in a flower bud just before the emergence of the flower bud from the leaves.

3. LIGHT

3.1. Introduction

It was mentioned in chapter 1 that the modern carnation has often been considered to be insensitive to the photoperiod. Some workers, however, obtained an increase in flower production with additional illumination. It has also been reported that flower bud initiation is delayed by short days and low light intensities.

The development of the carnation plant from planting of the cutting to anthesis may be divided into four stages, namely: (1) the vegetative stage (from planting until flower initiation); (2) the stage of flower initiation, i.e. the differentiation of the individual flower parts; (3) the development of the visible flower bud to the appearance of the flower colour; and (4) anthesis.

In this investigation of the effects of light (duration and intensity) on growth and flowering, particular attention was paid to its effect on the separate stages of the plant growth, especially on the actual time of flower bud initiation.

3.2. General effects of light

Experiment 1. – In this preliminary experiment the effects of different periods of artificial light on growth and flower bud initiation were studied. On March 1, 1965, rooted cuttings of the variety 'William Sim' were planted. After one week they were stopped back and moved to the phytotron where they exposed to 8, 12 or 16 hours AL at a temperature of 22 °C. Sixteen plants were used for each treatment.

Results (Tables 1 and 2): The plants which received 8 hours of light initiated flowers after 30 pairs of leaves; those in 12 hours of light after 24 leaf pairs and those in 16 hours after 20 leaf pairs. This shows a strong effect of light on the physiological moment of flower initiation. As could be expected, the effect of light on the moment at which flower initiation became visible was also considerable. Not only were flower primordia laid down at a much later date in 8 hours of light than in 16 hours, but also the time between microscopic flower initiation and flower bud emergence from the leaves was much longer (86 vs. 23 days) and the same holds true for the period between flower bud emergence from leaves and anthesis (47 vs. 25 days).

Table 1. Experiment 1 – Flower initiation and development (in days from planting) in plants grown in 8, 12 or 16 hours of artificial light (AL). Averages of 8 plants.

	AL		
	8 hours	12 hours	16 hours
Microscopically visible initiation	154.0	105.0	91.0
Flower bud emergence from the leaves	239.7	178.8	113.7
Colour	278.7	205.7	140.0
Anthesis	287.3	216.1	149.0

As could be expected because of the larger number of internodes, stems were longer in 8 hours than in 12 or 16 hours of light, although mean internode length was greater at higher light quantities. At high quantities, stems were thicker, leaves shorter but broader, and flowers were larger and had more petals.

TABLE 2. Experiment 1 – Effects of 8, 12 or 16 hours of artificial light (AL) measured at the time of flowering. Averages of 8 plants.

	AL		
	8 hours	12 hours	16 hours
Number of leaf pairs below flower	30.3	24.0	19.8
Length of leaf (cm)	10.2	10.3	8.7
Width of leaf (mm)	7.3	7.9	9.1
Stem length (cm)	100.7	91.4	88.0
Mean internode length (mm)	34.2	41.2	47.0
Stem diameter (mm)	2.8	3.1	3.3
Flower diameter (mm)	57.3	63.5	63.1
Number of petals	55.0	56.6	69.7
Total dry weight of plant (g)	6.4	6.2	4.8

Because of the shorter stems and smaller number of leaves, however, the total weight of the plant at flowering time was lower at higher light quantities.

In conclusion, it is clear that light has an enormous influence on both growth and development of the carnation. From this preliminary experiment it is not clear whether this is due primarily to light intensity or to the photoperiod. This was studied in subsequent experiments; the effect of photoperiod in experiments 2 to 5 and the effect of light intensity in experiments 6 to 9.

3.3. EFFECTS OF DAYLENGTH

3.3.1. *General effects on initiation and flowering*

Experiment 2. – Effect of daylength on flower initiation and development. On May 22, 1965, rooted cuttings of variety 'William Sim' were planted, and on June 10, they were stopped back and the treatments were begun. The plants received 8 hours natural day light (NL) from 8.30 A.M. to 4.30 P.M., which was extended by weak light from 40 Watt incandescent lamps to photoperiods of 8, 12, 16 or 20 hours. There was a fifth group which received natural daylength. There were 16 plants in each treatment.

Results (Tables 3 and 4): From the data of this experiment (Table 3) it is immediately clear that the differences in flower initiation found in experiment 1 are mainly due to the photoperiod. A long duration of the supplementary irradiation led to a smaller number of leaves below the flower, i.e. to quicker flower initiation. The development of the primordia into an open flower also proceeded faster as the photoperiod was longer. This acceleration could be noticed in all stages of flower development. The flower had a greater diameter and more petals when the photoperiod was longer.

TABLE 3. Experiment 2 – Effects of photoperiod (8 hours natural light + 0, 4, 8 or 12 hours incandescent light). Averages of 16 plants.

	Photoperiod				
	8+0	8+4	8+8	8+12	NL
Number of leaf pairs	19.3	18.7	16.0	14.6	15.2
Days from planting to anthesis	175	158	130	115	151

The difference in stem length noticed in experiment 1 also proved to be due to the photoperiod: the longest stems were found in the longest photoperiod, a consequence not of internode number, which was smaller, but of much greater internode length. The diameter of the stem did not show the same trend as in experiment 1 as it decreased with increasing daylength.

This may be ascribed to the strong elongation of the internodes in long day. In experiment 1, a long day meant more light and more photosynthesis, so that the internode could expand both in length and in width. In the present experiment, however, light quantity did not increase with light duration so that the lengthening of the internodes caused by a long photoperiod had to proceed at the cost of stem width.

In contrast to experiment 1, there was no difference in leaf length, nor in leaf width. The total leaf area was, of course, larger in the plants at the shortest photoperiod, because of the greater number of leaves.

The relation between photoperiod and dry weight of the different organs can be explained by the foregoing: as the photoperiod increases, flower dry weight increases, stem dry weight decreases and leaf dry weight decreases very strongly. Obviously, total dry weight is lower as the photoperiod is longer.

TABLE 4. Experiment 2 – Effects of photoperiod (8 hours natural light + 0, 4, 8 or 12 hours incandescent light) on the dry weight (g). Averages of 10 plants.

	Photoperiod				
	8+0	8+4	8+8	8+12	NL
Flower (g)	1.66	1.65	1.80	1.75	1.30
Leaves (g)	4.46	3.61	3.01	2.18	3.08
Stem (g)	3.84	3.99	3.71	3.16	4.10
Total weight (g)	9.96	9.25	8.52	7.09	8.48

The group of plants in natural day are not strictly comparable. As the daylength in early summer is long, the values could be expected to lie between those of the groups that received 8+8 and 8+12 hours of light. In general, this is the case. It is striking, however, that the flowers of this group were small (although the number of petals was as could be expected) and that stems and leaves were rather short.

Experiment 3. – On October 20, 1965, rooted cuttings of the variety 'William Sim' were potted and on November 3, the plants were stopped back and the treatments were begun. The daylengths employed were: (1) 'short day' = natural day in winter (7 to 8 hours). (2) 'long day' = natural day extended by 40 Watt incandescent lamps to a 20-hour photoperiod. The temperature was about 15 °C, but after 5 months from planting it was increased to about 20 °C. Fifteen plants were used for each treatment.

Results (Tables 5 and 6): The data show that even when the plants are exposed to the weak light intensity of winter at this latitude, flowering is promoted by extending the day by weak incandescent light. The difference between the plants in an 8 hour and those in a 20 hours photoperiod was even more pronounced than in the previous experiments. The difference in internode number was about 7, so that although the internodes in 20 hours were 'stretched to capacity' (they were only half as thick as those in 8 hours), total stem length was still greater in 8 hours. The internodes in both 8 and 20 hours were larger than those in the corresponding group of experiment 2, which points to an etiolating effect of the weak winter light. The flowers were smaller in 20 hours than in 8 hours. The differences in dry weight of all organs were very pronounced and proportionally much larger than those in stem length and leaf number. One may perhaps conclude that at low light intensity the stimulation of elongation by the extension of the photoperiod upsets the balance between photosynthesis and growth and causes the plants to become etiolated. Meanwhile, the promotive effect of long photoperiod on flower initiation is maintained.

TABLE 5. Experiment 3 – Effects of an extension of natural day during winter to 20 hours with incandescent light on flower initiation and development. Averages of 8 plants.

	Photoperiod	
	NL	20 hours (NL+inc.)
Microscopically visible initiation	108 days	59 days
Flower bud emergence from the leaves	157	78
Colour	192	147
Anthesis	208	158

TABLE 6. Experiment 3 – Effect of an extension of natural day during winter to 20 hours with incandescent light. Averages of 8 plants.

	Photoperiod	
	NL	20 hours (NL+Inc.)
Stem length (cm)	92.1	72.9
Stem diameter (mm)	5.0	2.6
Number of internodes	18.9	11.7
Mean internode length (mm)	46.0	57.7
Flower diameter (mm)	77.5	60.8
Dry weight of flower (g)	1.85	0.75
Dry weight of leaves (g)	3.06	0.46
Dry weight of stem (g)	4.90	0.78

3.3.2. *Effect of changes in daylength before and at the time of initiation*

Experiment 4. – This experiment was carried out in the artificial light rooms of the phytotron. On October 20, 1965, rooted cuttings of the variety 'William Sim' were planted and on November 2, they were stopped back and the treatments were begun. One group of plants was grown in 16 hours of artificial light (AL) at 75% of maximum intensity and moved to 12 hours AL of 100% intensity and vice versa. Another group was changed between 16 hours AL 50% and 8 hours 100% and vice versa. This means that for both groups the amount of light was the same but the photoperiods differed. The plants were changed from one photoperiod to another 8 weeks after stopping, i.e. well before flower initiation, and after 13 weeks, i.e. at the time of initiation. The temperature was 22°C. These were 12 plants in each treatment. On May 20, 1966, the treatments were terminated. At that time, three of the 12 treatments had not yet flowered.

Results (Tables 7 and 8): It is again confirmed that long photoperiod promotes flower initiation. The plants in 16 hours (75%) initiated flowers after 18.9 internodes and those in 12 hours (100%) after 21.7 internodes. The data also show that the daylength in which plants were grown for the first 8 weeks had little effect on flower initiation. The plants in 16 hours 75%/12 hours 100% initiated flowers after 21.3 internodes, which is about the same as the 21.7 internodes formed by those in 12 hours 100% continuously, while the number of 19.5 internodes formed in 12 hours 100%/16 hours 75% is close to the 18.9 internodes formed by plants in 16 hours 75% continuously. This is confirmed by the flowering behaviour, as determined by the number of days from flower initiation to anthesis. When plants were shifted after 13 weeks internode number was intermediate between the internode number of plants that stayed in 16 hours 75% or 12 hours 100% throughout. Again, the period from initiation to anthesis shows the same trend.

TABLE 7. Experiment 4 – Effects of changing the plants from 16 hours at 75% intensity to 12 hours at 100% intensity after 8 or 13 weeks. Averages of 7 plants.

	16 hours 75%	12 hours 100%	8 weeks		13 weeks	
			16 hrs 75% 12 hrs 100%	12 hrs 100% 16 hrs 75%	16 hrs 75% 12 hrs 100%	12 hrs 100% 16 hrs 75%
Number of internodes	18.9	21.7	21.3	19.5	20.0	20.2
Stem length (cm)	90.0	78.3	83.0	87.0	76.8	82.8
Mean internode length (mm)	45.3	33.6	37.9	41.8	35.8	38.6
Number of petals	55.4	49.0	53.0	59.0	54.3	52.7
Total dry weight of plants (g)	4.7	5.1	5.1	4.8	5.1	4.7

The data show that the differences caused by the photoperiod concern mainly the number of days between the beginning of the treatments and microscopically

visible initiation, and between this moment and flower bud emergence from the leaves. The subsequent phases require about the same number of days in all photoperiods:

stages	photoperiod	
	16 hours AL 75%	12 hours AL 100%
From planting to initiation	92 days	106 days
From initiation to flower bud emergence from the leaves	34	49
From bud emergence to colour	34	30
From colour to anthesis	11	12

These results were the same in the groups which were moved from long to short photoperiod or vice versa.

Comparison of the plants in 16 hours AL 75% and 16 hours AL 50% shows that the lower light intensity retarded visible initiation as well as the development from initiation to bud emergence. The later stages of flower development are not retarded, and even slightly promoted, by the lower intensity. At the same amount of light the long photoperiod increased the stem length (Table 8). Other data are in accordance with those in experiment 2: in long photoperiods, the internode lengths are longer and the flowers have more petals. The data of the plants switched between two photoperiods show that internode length was strongly affected by the photoperiod given during the second of the two periods. The total dry weight of the plants was greater in short photoperiod, as could be expected because of the greater number of leaves. However, switching the plants between two photoperiods had no effect on the dry weight of the plants.

TABLE 8. Experiment 4 – Effects of changes in the photoperiod after 8 or 13 weeks on flower initiation and development. Averages of 7 plants.

	16 hrs 75%	16 hrs 75% / 12 hrs 100% 8 weeks	16 hrs 75% / 12 hrs 100% 13 weeks	12 hrs 100%	12 hrs 100% / 16 hrs 75% 8 weeks	12 hrs 100% / 16 hrs 75% 13 weeks	16 hrs 50%	8 hrs 100% / 16 hrs 50% 8 weeks	8 hrs 100% / 16 hrs 50% 13 weeks
Microscopically visible initiation	92.0	98.0	92.0	106.0	95.0	106.0	101.0	107.0	116.0
Flower bud emergence from the leaves	126.0	145.8	132.1	155.0	131.9	150.0	152.0	156.4	165.8
Colour	160.4	181.8	171.0	185.3	165.9	179.8	182.0	182.8	190.8
Anthesis	171.4	191.8	182.0	197.0	175.7	190.2	192.0	193.0	199.3

3.3.3. *Effects of night interruption*

Experiment 5. – This experiment was carried out to establish if the carnation responds to a light interruption of a long night, like other plants sensitive

to the photoperiod. On November 26, 1964, rooted cuttings of the variety 'William Sim' were planted, and on December 11, they were stopped back and subjected to three treatments in the artificial light rooms of the phytotron, namely: 10 hours AL per day, 16 hours AL per day, and 8 hours AL per day with a night interruption of 2 hours AL after 6 hours of darkness. The temperature was 22 °C. Twelve plants were used for each treatment.

Results: The data show that the effect of night interruption has been slight. The difference in flower initiation was only 1 internode; in time it was 9 days (117 days after planting for 8+2 hours and 126 days for 10 hours). The mean internode length was only very slightly longer with interrupted nights (42.9 vs. 40.2 mm). The difference in total time required from planting to anthesis was 24.5 days; the flowers were slightly larger (59.5 vs. 56.5 mm) and had more petals (64 vs. 56).

The plants in 16 hours AL initiated flowers after 17 leaf pairs, and mean internode length was 55.1 mm. Stems were thicker, leaves broader and flowers larger than in the other groups, but here the greater quantity of light obviously also plays a role.

In conclusion, in this treatment the night interruption did not have a full long day effect. It is possible that the spectral composition of the light (fluorescent tubes) was such that an optimal effect could not be obtained by 2 hours of irradiation; this experiment should be repeated with incandescent lamps.

3.4. Effects of light intensity

3.4.1. *General effects on initiation and flowering*

Experiment 6. – This experiment was carried out in the artificial light rooms of the phytotron. On March 2, 1965, rooted cuttings of the variety 'William Sim' were planted, and after one week they were stopped back and exposed to three photoperiods viz. 8, 12 and 16 hours AL. There were four levels of light intensity in each photoperiod: 25%, 50%, 75% and 100%. The temperature was kept at 22 °C. Twelve plants were used for each treatment. On December 12, 1965, the treatments were terminated. At that time, four of the 16 treatments had not yet flowered.

Results (Table 9): Again, a long photoperiod promoted flower initiation. There was also a very strong effect of the light intensity, however. Low light intensities delayed flower bud initiation to such an extent that, e.g., a plant in 100% AL for 16 hours formed about 18 internodes below the flower, but one in 25% AL formed 35. Similar effects of light intensity occurred in the 12 hour photoperiod. The effect on flower bud development was also great: in a 16 hour photoperiod 58 days elapsed between flower initiation and anthesis in full light intensity; in 25% 190 days were required for the same phase. The differences were greatest during the development of the flower primordia to bud emergence from the leaves. From there on to visible colour the differences caused by the various light intensities were not so great, and the differences in the period between the first show of colour and anthesis were only slight.

Other characters affected by light intensity were stem length (greater in lower intensities), stem diameter, leaf length and width, flower diameter and number of petals (all greater in high intensities). All these characteristics appeared to be affected more by light quantity than by light duration. The mean internode length, however, was primarily affected by the photoperiod. The light intensity also had a very slight effect on internode length (longer in high light intensities). The results concerning dry weight confirm that a short photoperiod increases the total dry weight of the plants. The light intensity, however, had only a slight effect on the total dry weight, but strongly affected the dry weight of the flowers (greater in high light intensities).

TABLE 9. Experiment 6 – Effects of different photoperiods and light intensities. Averages of 8 plants.

	8 hrs	12 hours			16 hours			
	100%	50%	75%	100%	25%	50%	75%	100%
Stem length (cm)	100.7	110.8	100.7	91.4	158.0	108.6	102.6	88.0
Stem diameter (mm)	2.8	2.8	2.8	3.1	2.4	2.9	3.0	3.3
Number of internodes	28.3	31.0	27.7	21.9	35.0	22.8	20.3	17.9
Length of leaf (cm)	10.2	8.5	9.6	10.3	7.9	8.4	8.5	8.7
Width of leaf (mm)	7.3	6.4	6.6	7.9	6.3	7.8	8.4	9.1
Mean internode length (mm)	34.2	34.2	34.6	41.2	43.8	45.5	47.9	47.0
Flower diameter (mm)	57.3	56.0	63.0	63.5	52.0	52.8	63.8	62.7
Number of petals	55.0	54.0	55.6	56.6	50.0	65.0	65.3	69.7
Total dry weight of plant (g)	6.4	5.2	5.2	6.1	3.9	4.4	4.6	4.8

Experiment 7. – In this experiment the effect of daylength and light intensity on flower initiation and development was studied in a series of light regimes different from those in experiment 6. The plants all received 8 hours natural light, which was extended by weak irradiation by 40 Watt incandescent lamps to 8+0, 8+4, 8+8 or 8+12 hours. In each daylength half of the plants were covered by cheese cloth during the 8 hours natural light, which reduced the light intensity by about 40–50%. In addition there were two groups which received natural daylength; one of these was shaded throughout. For the other groups the natural light lasted from 8.30 A.M. to 4.30 P.M. On May 22, 1965, rooted cuttings of the variety 'William Sim' were planted and on June 10, they were stopped back and the treatments were begun. There were 16 plants in each treatment.

Results (Table 10): The data confirm those of previous experiments in many respects: extension of the daylength promoted flower initiation, flower development, and increased internode length, flower size, and petal number (slightly), while low light intensity retarded flower initiation (only slightly, however) and flower development, increased stem length and mean internode length, and decreased flower size and stem diameter. In contrast to the results of the

previous experiment, there was hardly any effect of light intensity on petal number and leaf width, while leaf length was actually increased by shading, except at the longest photoperiod.

TABLE 10. Experiment 7 – Effects of different photoperiods and light intensities. (S = shaded, Uns. = unshaded). Average of 10 plants.

	Photoperiod									
	8 + 0		8 + 4		8 + 8		8 + 12		NL	
	S.	Uns.	S.	Uns.	S.	Uns.	S.	Uns.	S.	Uns.
Microscopically visible initiation (days)	85.0	82.0	75.0	71.0	66.0	62.0	56.0	53.0	61.0	61.0
Days from planting to anthesis	216.0	175.0	181.0	158.0	160.0	130.0	125.0	115.0	168.0	151.0
Number of internodes	19.3	17.3	16.7	16.7	15.7	14.5	13.0	12.4	13.4	13.0
Stem length (cm)	82.4	58.2	96.6	70.1	104.0	69.4	86.3	73.5	87.0	69.1
Stem diameter (mm)	4.0	5.8	4.4	5.9	4.1	4.7	3.4	4.3	4.2	4.8
Mean internode length (mm)	40.1	30.6	54.6	38.9	63.1	44.2	62.3	54.8	61.7	44.5
Flower diameter (mm)	59.9	60.6	65.7	61.7	61.7	70.1	70.1	77.3	66.7	48.6
Number of petals	51.0	51.0	56.0	55.0	51.0	54.0	59.0	60.0	58.0	57.0
Length of leaf (cm)	9.8	8.2	9.5	8.6	8.7	8.5	7.1	8.4	8.1	7.1
Width of leaf (mm)	10.4	10.8	10.1	10.0	10.0	11.1	9.7	10.6	10.1	9.9

3.4.2. *Effects of changes in light intensity*

3.4.2.1. Before and at the time of initiation

Experiment 8. – Experiments 6 and 7 showed that light intensity affects both flower initiation and development. The present experiment was designed to investigate if there is a critical period for the effect of light intensity on these processes. It was done in the artificial light rooms of the phytotron with 16 hours artificial light (AL) at three levels of light intensity: 50%, 75% and 100%. On October 20, 1965, rooted cuttings of the variety 'William Sim' were planted and on November 2, they were stopped back and the treatments were begun. After 8 and 13 weeks from the date of the stopping – i.e. in the vegetative stage and at the time of flower initiation, respectively – the plants were moved from high to low light intensity and vice versa. Three groups remained in 50%, 75% or 100% AL (16 hours) until the end of the experiment, and served as controls. The temperature was 22°C. Twelve plants were used for each treatment.

Results (Tables 11, 12 and 13): Again, high light intensity promotes flower initiation. The plants in 100% initiated flowers after 16.8 internodes, those in 75% after 18.9 and those in 50% after 20.9 internodes. As these differences are

small, the effect of changes in the light intensity are not very clear. In all cases, however, the number of internodes is intermediate, and generally the effect of light intensity is stronger during the first period than during the second. This holds true when the switch was made after 8 weeks as well as when it was made after 13 weeks.

TABLE 11. Experiment 8 – Effects of changing the light intensity 8 or 13 weeks from stopping on the number of internodes. Daylength 16 hours AL. Averages of 7 plants.

Light intensity		changed after	
		8 weeks	13 weeks
100%	16.8		
100%/ 75%		18.0	17.8
75%/100%		18.2	18.6
75%	18.9		
75%/ 50%		18.1	18.6
50%/ 75%		19.0	19.6
50%	20.9		
100%/ 50%		19.0	18.3
50%/100%		17.2	19.3

This observation is in accordance with the data about the number of days required for the various phases of development of the flower. These show that the differences caused by the light intensities concern mainly the number of days between the beginning of the treatments and visible flower initiation and between this moment and flower bud emergence from the leaves. The subsequent phases require about the same number of days in all light intensities.

stages	light intensity		
	100%	75%	50%
From planting to initiation	86 days	92 days	101 days
From initiation to flower bud emergence from the leaves	22	34	51
From bud emergence to colour	33	34	30
From colour to anthesis	11	11	10

There even is an indication that the lowest light intensity actually accelerates the last phases of flower development. This is confirmed by the groups which were moved from high light intensity to 50% light and which all proceeded somewhat faster from visible bud to anthesis than the other groups. Perhaps if the switch had been made later, the group moved from 100% to 50% would have flowered together with or even before the group that remained in 100%; now it still lagged 4 or 6 days behind.

TABLE 12. Experiment 8 – Effects of changing the light intensity after 8 or 13 weeks. Daylength 16 hours AL. Averages of 7 plants.

	100%	8 weeks		75%	8 weeks		50%	8 weeks	
		100/75	75/100		75/50	50/75		50/100	100/50
Microscopically visible initiation (days)	86.0	94.0	97.0	92.0	98.0	100.0	101.0	95.0	92.0
Flower bud emergence from the leaves (days)	107.8	112.5	119.7	126.0	120.7	124.0	152.0	119.3	113.0
Colour	140.8	145.5	156.5	160.4	150.3	161.3	182.0	155.0	147.5
Anthesis	151.5	156.5	166.2	171.4	158.7	171.2	191.8	166.2	155.7
		13 weeks			13 weeks			13 weeks	
Flower bud emergence from the leaves (days)	107.8	112.7	124.5	126.0	121.7	131.3	152.0	126.7	117.5
Colour	140.8	143.8	162.5	160.4	154.2	167.7	182.0	164.0	148.3
Anthesis	151.5	154.5	172.8	171.4	163.2	177.0	191.8	175.0	157.5

The other data are in accordance with those of experiment 6. In the higher light intensity, the internodes are shorter and thicker and the flowers are larger and have more petals. The data of the plants switched between two light intensities are intermediate, similar to the data about flower initiation, with the important difference, however, that the dimensions of internodes and flowers are determined to a large extend by the light intensity given during the second of the two periods.

TABLE 13. Experiment 8 – Effects of changing the light intensity after 8 or 13 weeks, measured at the time of flowering. Daylength 16 hours AL. Averages of 7 plants.

	100%	8 weeks		75%	8 weeks		50%	8 weeks	
		100/75	75/100		75/50	50/75		50/100	100/50
Mean internode length (mm)	44.5	41.5	41.3	45.3	44.1	41.4	47.1	42.7	43.5
Stem diameter (mm)	3.1	2.9	3.2	2.7	2.7	2.5	2.4	3.2	2.6
Flower diameter (mm)	73.5	69.1	64.5	63.4	56.5	62.4	51.6	64.8	50.9
Number of petals	62.2	55.7	57.7	55.4	52.7	55.9	54.4	57.9	55.8
Total dry weight of plant (g)	5.5	4.7	5.9	4.7	3.9	4.8	3.7	5.9	4.3
		13 weeks			13 weeks			13 weeks	
Mean internode length (mm)	44.5	43.4	42.1	45.3	46.3	45.0	47.1	42.6	43.5
Stem diameter (mm)	3.1	3.0	3.1	2.7	2.7	2.8	2.4	3.0	2.7
Flower diameter (mm)	73.5	65.7	64.9	63.4	54.0	60.1	51.6	66.9	53.7
Number of petals	62.2	56.8	55.3	55.4	53.6	55.5	54.4	57.6	55.4
Total dry weight of plant (g)	5.5	4.7	6.2	4.7	4.6	4.9	3.7	5.9	4.5

The same holds true for the dry weight of the plant. This is, for obvious

reasons, proportional to the light intensity. When the plants are switched, the dry weight values come very close to those which would have been obtained when the plant had been continuously in the intensity which is now given during the second period. It should of course be kept in mind that at the low light intensities the period from the switch to flowering varies between about 22 and 25 weeks. This means that plants switched 8 weeks after the beginning of the experiment have been at the second light intensity for a much longer period than at the first. Also, during the second period the photosynthetic apparatus of the plant was much larger than during the first.

3.4.2.2. After flower bud emergence

Experiment 9. – The results of the previous experiment indicate that the number of days between the flower bud emergence, flower colour, and anthesis is not much affected by the light intensity. This experiment was done before the results of the previous experiment were known to test just this aspect. It was done in the phytotron at 16 hours artificial light of two levels of intensities, viz. 50% and 100%. The plants were moved from high to low light intensity and vice versa after the flower bud emergence from the leaves. The temperature was 22°C. Rooted cuttings of the variety 'William Sim' were planted on November 26, 1964, and on December 12, they were stopped back and the treatments started. Sixteen plants were used for each treatment.

Results (Table 14): On the whole these were as could be expected on the basis of the data of the previous experiment. Flower initiation was strongly affected by the light intensity, but of course not by the switch, which was made afterwards. The period between flower bud emergence from the leaves and anthesis was the same in all treatments. The accelerating effect of low light intensity, indicated by the results of experiment 8, was not observed here.

The dry weight of the 100%/50% and 50%/100% plants lay in between that of the 50% and 100% groups but was closest to the group corresponding to the second light intensity given. As far as internode length, stem diameter, flower size and petal number were concerned, however, the opposite holds true: here the values lay closer to those of the group corresponding to the light intensity during the first period.

TABLE 14. Experiment 9 – Effects of changing the light intensity after the flower bud emergence. Daylength 16 hours AL. Averages of 7 plants.

	50%	100%	50%/100%	100%/50%
Number of internodes	24.5	17.0	24.2	18.3
Mean internode length (mm)	47.9	55.1	46.3	52.4
Stem diameter (mm)	3.1	3.7	3.3	3.6
Flower diameter (mm)	54.7	63.0	58.5	57.0
Number of petals	64.0	66.3	64.5	68.3
Total dry weight of plant (g)	5.9	6.5	6.6	5.6

3.5. Discussion

The experimental results described here have confirmed that light (photoperiod as well as light intensity) greatly affects growth, flower bud initiation and development of the flowers. In all experiments, flowers not only were initiated sooner, but also were formed after a smaller number of leaf pairs when the photoperiod was longer.

This confirms the results of Blake (1955) and subsequent workers. Why Post (1952) and Rünger (1957) found no effect of the photoperiod on initiation but only on flower development remains unexplained.

The effect of light intensity on flower bud initiation is also very pronounced: low light intensity retards initiation both in terms of leaf pairs below the flower as in terms of number of days. This is a very general phenomenon, occurring in many plants (see e.g. Liverman, 1955). It had been found before in the carnation by Harris and Harris (1962). Usually the effect of light intensity is not regarded as a specific effect on floral initiation but as an indirect effect via photosynthesis.

The development of the flower primordia is also enhanced by long photoperiods and high light intensity. The data presented here show that these environmental factors affect only the initial stages of bud development, i.e. from flower initiation to the emergence of the bud from the leaves.

In later stages (from bud emergence to visible flower colour and from visible colour to anthesis) were not only unaffected by the various daylengths and light intensities given, but there was even a slight indication of a promotive effect. This can perhaps be explained by the promotive (etiolating) effect of low light intensity on elongation (experiment 6).

Stem elongation, measured as mean internode length, was strongly promoted by long photoperiods. As these conditions also promote flower initiation, thereby reducing the number of internodes, the total effect of long days on stem length may differ from one set of conditions to another. In experiments 1 and 3 stems were longer in short day than in long day, while in experiments 2, 4, 6 and 7 it was the other way around. Obviously, in the first case the greater number of internodes in short day more than compensated for the fact that they were shorter, while in the second case the differences in internode length affected total stem length stronger than the differences in internode number.

The greater elongation of the internodes in long photoperiods led to a reduction in stem thickness, except when the extension of daylength was accompanied by a proportional increase in light quantity (experiment 1). When this was not the case, long photoperiods promoted flower initiation and development, reduced the number of internodes, but led to weak stems, smaller and narrower leaves, and a lower flower quality (smaller flowers with a lower number of petals).

There is no evidence of a specific effect of the photoperiod on stem diameter, leaf length and width and flower size. These characteristics are probably primarily affected by the quantity of available photosynthates. When light intensity is low and the photoperiod long, an excessive stimulation occurs which uses up such a large part of these photosynthates that an adverse effect on the other characteristics mentioned results.

4. TEMPERATURE

4.1. Introduction

It is clear from the literature (Chapter 1) that temperature has a great effect on growth and flowering of carnation plants.

It has been found to affect stem strength, stem dry weight, internode length, node number, leaf width, time of flower bud initiation, flower bud development, flower size, flower weight, petal weight, petal number, flower quality, and keeping life of cut flowers. Also a low temperature treatment has been shown to promote flower initiation and to reduce the number of leaves formed below the flower.

The present experiments were undertaken to investigate the effect of temperature on plant growth, and flower formation from initiation to anthesis, in an effort to separate the temperature effects on each phase. Also, the effect of low temperature (5 °C) on growth and flowering will be discussed, as well as the effect of different conditions during and after the low temperature treatment.

4.2. Effects on initiation and flowering

4.2.1. *Effects of photoperiod and temperature*

Experiment 10. – This experiment was designed to establish the effect of six different constant temperatures on the various phases of development of the carnation plant. It was carried out in the artificial light rooms and the greenhouses of the phytotron. In the former, the plants received fluorescent light for 16 hours per day. In the greenhouses both daylength and light intensity varied with the season. The temperatures in the greenhouses were 12°, 15°, 18°, 21° and 24 °C. In the artificial light rooms, 9 °C was added to this series. Rooted cuttings of the variety 'William Sim' were planted on May 24, 1964. On July 1, the cuttings were stopped back, and one week later the treatments started. There were 16 plants in each treatment.

Results (Tables 15 and 16): As the plants in the artificial light rooms were under identical conditions throughout the experiment, the results of these groups are the easiest to interpret. The most fundamental datum is the number of leaf pairs, as this is determined by the initiation of the terminal flower and in

Table 15. Experiment 10 – Effect of temperature under two light conditions on the number of leaf pairs. Averages of 8 plants.

	16 hrs artificial light (AL)						Natural light (NL)				
	9 °C	12 °C	15 °C	18 °C	21 °C	24 °C	12 °C	15 °C	18 °C	21 °C	24 °C
Number of leaf pairs below the flower	15.7	15.7	18.1	19.5	19.8	19.8	17.5	20.2	20.7	21.4	18.2

its turn is to a large extent decisive for stem length, total dry weight and other characteristics of the plant. The lowest number of leaf pairs, i.e. the earliest flower initiation, was found in the groups at 9° and 12°C; at higher temperatures it was retarded, the maximum difference being 4 leaf pairs.

Under the microscope, the first stage of flower initiation could be detected after 155 days at 9°C, and after 115 days at 24°C. This shows that even the very first stages of flower bud growth depend on the temperature in quite a different way than the actual flower induction: while the latter is promoted by low temperature, actual flower formation is promoted by high temperature. The total process of the formation of the flower primordium took 49 days at 9°C but only 14 days at 24°C. Then the differences became even greater: the phase from complete flower primordium to anthesis took 82 days at 12°C and 35 days at 24°C. If one studies the detailed figures (Table 16) it appears that only the very last phase, from visible flower colour to flower maturity (anthesis) is not dependent on temperature (13 days at 12°C, 12 days at 24°C).

Internode length was greatest (52 mm) at 9°C, and smallest at 15° and 18°C (36 mm); at higher temperature, the internodes were somewhat longer again.

Stem length is the result of internode number and mean internode length. The longest stems were found at 9°C (78 cm), 21°C (75 cm) and 24°C (74 cm). At 9°C, they were caused by the greatest internode length, at 21° and 24°C, by the greatest number of internodes. The shortest stems (67.5 cm) occurred at 15°C where both internode number and length were intermediate.

The diameter of the stem differed from 3.3 mm to 4.0 mm. The thinnest stems occurred at 24°C. It looks as if there is a relation with stem length, the shortest stems being the thickest, but the figures are not very regular.

The groups in natural light are more difficult to interpret, as both daylength and light intensity decreased during the experiment.

The number of leaf pairs is on the whole about 2 more than in the plants under artificial light: it varies from 17.5 at the low temperature to 21.4 at 21°C. This means that the trend is the same as under artificial light. Why flower initiation occurs at a higher leaf number in natural light is no clear, but it should be considered that at the time of initiation natural light intensity was higher, but daylength was shorter than under the lamps. The plants at 24°C form an exception. They initiated flowers after only 18 leaf pairs, which means faster than the plants at 21°C and also faster than those at 24°C under the lamps. The reason remains obscure.

The first stage of the calyx primordia was detected later in natural light than in artificial light, which could be expected as more leaves were formed in the greenhouse. At 21°C, the flower primordia appeared a week earlier, in spite of the 2 additional pairs of leaves, while at 24°C the primordia appeared much (17 days) earlier.

In the course of flower development, the group at 24°C remained 17 days ahead; anthesis occurred 147 days after planting (164 days under the lamps). The plants at 21°C, however, fell behind. Although they started to initiate their flowers only 16 days after those at 24°C, and a week ahead of those plants

at 21 °C under the lamps, they ended up 45 days behind the former and 21 days behind the latter at anthesis. Similar retardations occurred at lower temperatures.

TABLE 16. Experiment 10 – Effects of temperature under two light conditions on flowering. Averages of 8 plants.

	16 hrs artificial light (AL)						Natural light (NL)				
	9 °C	12 °C	15 °C	18 °C	21 °C	24 °C	12 °C	15 °C	18 °C	21 °C	24 °C
First stage of calyx	155	136	134	123	121	115	155	145	135	114	98
Second stage of calyx	175	146	140	128	124	118	165	155	145	120	101
Last stage of calyx	185	155	145	133	127	121	175	165	155	126	104
Styles initiation	196	165	150	138	129	124	186	175	165	131	107
Styles development	200	175	155	143	132	127	196	182	175	137	109
Flower bud maturity	204	184	160	148	135	129	206	188	179	143	112
Flower bud emergence from the leaves	209	194	164	153	138	133	216	195	183	149	115
Colour	–	(253)	208	188	160	152	296	260	239	178	134
Flower maturity (anthesis)	–	(266)	(227)	203	171	164	312	280	259	192	147

No doubt this slowing down of flower development during late stages in natural day is due to the gradual shortening of the days and the decrease of light intensity. The question arises, if the lack of retardation at 24 °C is perhaps due to the fact that at this high temperature the whole development was completed so fast that the plant where already past the sensitive stage before the diminishing light duration and intensity could have their effect.

The data about flower characteristics show that in artificial light, the diameter of the flower is greatest at 15 °C (87 mm); at lower and higher temperatures it is smaller (75 mm at 9 °C and 70 mm at 24 °C). The number of petals, however, shows the opposite trend: there were 60 petals at 15 °C, against 66 at 9 °C and 69 at 24 °C.

A different trend is shown by the number of stamens: this increased regularly with temperature, from about 9 at 9 °C to about 16 at 24 °C.

In natural light, this trend in the number of stamens was the same. There was also some similarity in the relation between temperature and flower diameter: the largest flowers (88 mm) at 15 °C, the smallest (71 mm) at 24 °C. The flowers at 12 °C, however are not significantly smaller than those at 15 °C. The trend in

the number of petals is also somewhat less clear than in artificial light, although the largest number coincides with the smallest flowers.

Flower weight is proportional to flower diameter: the heaviest flowers are those with the greatest width, i.e. those formed at 15°C, the lightest are those at 24°C. Flower weight can be considered as a good measure for the flower quality. The best quality are those flowers with the heaviest weight, i.e. those formed at 15°C, the lightest flowers are the poorest quality, i.e. those formed at 24°C.

Another important characteristic is calyx splitting. This occurred in natural light at all temperatures, especially at the lowest, no doubt because here flowers matured at the lowest light intensity. The rise at 24°C may be due to the greater number of petals.

In artificial light, there is no calyx splitting at 15°, 18°, 21° and 24°C, but at 12°C 25% of the calyxes were split. The absence of calyx splitting at 9°C is due to the fact that after 224 days from planting or 39 days before the appearance of flower colours, the temperature control in this room broke down and the temperature rose from 9°C to 18°C.

4.2.2. *Effects of low temperature followed by high temperature*

Experiment 11. – In experiment 10 it was observed that low temperature promoted flower initiation while actual flower formation is promoted by high temperature. In addition, high temperature increased the quality of the flower. This experiment was carried out to investigate the possibility of getting early flowers of high quality by changing the temperature from low to high at the time of initiation.

The experiment started on 24 May 1964. Plants of the variety 'William Sim' were grown at 9° and 24°C in the artificial light rooms (16 hours of fluorescent light daily). However, in the greenhouses they were grown at 12° and 24°C. Half from 9° and 12°C groups was moved to 24°C at the first sign of flower formation. The treatments were given in the phytotron. There were 16 plants per treatment.

Results (Table 17): Under constant light conditions, the plants in 24°C initiated flowers after four more leaf pairs than those in 9°C. Nevertheless, the flower primordia became visible forty days earlier in 24°C than in 9°C. Plant moved from 9°C to 24°C at this moment needed 57 days to anthesis; as plants that had been at 24°C all the time needed 49 days, the difference in flowering time between the two groups was 48 days (the plants left at 9°C flowered another 65 days later). Therefore, although low temperature reduced the number of leaves laid down before the flower, no time was gained with regards to the plants kept at 24° throughout.

In natural light, the difference in flower time was even greater, because the delay by low temperature led to a further delay caused by the decrease in light intensity and daylength as the season advanced. Moreover, the difference in leaf pair number was very small, presumably for the same reasons as in the previous experiment.

TABLE 17. Experiment 11 – Effects of low temperature followed by high temperature. Averages of 8 plants.

	16 hours artificial light (AL)			Natural light (NL)		
	9°C	9°/24°C	24°C	12°C	12°/24°C	24°C
Number of leaf pairs below the flower	15.7	15.5	19.8	17.9	17.5	18.7

As to the quality of the flower, the heaviest flowers were formed at 9°C under both light regimes. As in the previous experiment, the weight was correlated with the size of the flower, not with the number of petals.

Stem length and stem diameter did not vary significantly in artificial light. In natural day, the plants moved from 12°C to 24°C had longer stems than those left in 24°C (70.5 against 54 cm), but the latter were thicker (3.0 mm in 12°C, 3.8 mm in 24°C).

In conclusion, flowering was not earlier, and flowers were not of better quality, when plants were given 9° or 12°C to initiation and 24°C afterwards. Plants left at 9° or 12°C flowered much later, but had better flowers, while plants kept at 24°C throughout flowered much earlier with flowers of similar quality (in artificial light) or better quality (in natural light).

4.2.3. *Effects of day and night temperature*

Experiment 12. – This experiment was carried out in the greenhouses of the phytotron at temperatures of: 12°, 15°, 18°, 21° and 24°C. Using a factorial arrangement of all possible combinations of day and night temperatures, 25 temperature treatments were obtained. The plants were moved to day temperature at 8.30 A.M. and to night temperature at 4.30 P.M. The day temperature, therefore, was given during 8 hours (which about coincided with the natural daylength) and the night temperature during 16 hours. On November 19, 1965 rooted cuttings of the variety 'William Sim' were planted; after two weeks they were stopped back, and the treatments started. Eight plants were used for each treatment. The treatments were terminated after 7 months after planting. Due to mechanical difficulties the plants were kept under the controlled day and night temperature for the first four and a half months only; for an additional month the night temperatures were controlled but the day temperature was about 22°C for all groups. During the last six weeks of the experiment all plants received a day and night temperature of about 22°C in one greenhouse.

Results (Table 18): Physiologically, the best way to determine the moment of flower initiation is to establish the number of leaves laid down below the flower bud. In the present series of treatments this number varied between 19 and 25–26. The lowest number, i.e. the earliest flower initiation, was found at the lowest temperature. If the treatments in which day and night temperature were the same are compared, flowers were initiated after 19 leaf pairs at 12°/12°C and after about 26 leaf pairs at 24°/24°C.

If the different night temperatures combined with one given day temperature are compared, the same trend becomes apparent, and a similar conclusion can be drawn when the day temperatures combined with one night temperature are compared. In the latter case the differences are larger than in the former, in other words, the night temperatures have a more pronounced effect on flower initiation than the day temperatures. Now the day temperatures lasted for only 8 hours in one 24-hour cycle while the night temperatures lasted for 16 hours. When this is taken into consideration, e.g. when the treatments 24°/12°, 18°/15° and 12°/18°C are compared, which have the same daily 'heat sum' (hours × temperature), the differences are found to be slight or non-existent (21, 21 and 21 leaf pairs in the example given).

The conclusion may therefore be drawn that flower initiation depends on the average daily temperature, and that day and night temperature have no specific effect, while within the range of temperatures of the experiment, the lowest temperature, i.e. 12°C, is the most promotive.

TABLE 18. Experiment 12 – Effects of day and night temperature. Averages of 7 plants.

	Day temperature				
Night temp.	12°C	15°C	18°C	21°C	24°C
(A) Number of leaf pairs (including bracts).					
12°C	19.0	19.3	19.0	20.5	21.0
15°C	21.3	21.8	21.3	23.5	23.0
18°C	21.0	22.0	22.8	23.8	23.0
21°C	24.0	23.8	25.5	25.5	25.8
24°C	25.3	23.3	24.8	25.5	25.8
(B) Microscopical flower bud initiation (days)					
12°C	98.0	91.0	87.0	84.0	74.0
15°C	100.0	95.0	93.0	86.0	80.0
18°C	103.0	97.0	94.0	89.0	84.0
21°C	106.0	100.0	97.0	91.0	86.0
24°C	108.0	103.0	98.0	95.0	88.0
(C) Internode length (mm)					
12°C	47	43	45	46	46
15°C	42	43	41	46	42
18°C	37	37	43	39	41
21°C	35	32	31	35	34
24°C	30	31	32	36	34
(D) Stem length (cm)					
12°C	86.0	80.0	81.8	90.3	92.5
15°C	85.5	90.3	83.5	103.0	93.8
18°C	75.8	80.0	94.0	90.8	91.3
21°C	81.8	74.5	78.5	86.8	85.5
24°C	75.8	72.0	77.5	89.0	84.5

Quite a different trend becomes apparent, when the number of days to microscopically flower bud initiation is taken as a measure, i.e. when the growth rate enters the picture (Table 18 B). From the figures it is evident that:

a. when night and day temperature are the same, bud growth is promoted by high temperatures: buds could be noted after 98 days at 12°/12°C and after 88 days at 24°/24°C;
b. with a given day temperature, low night temperature promotes bud growth;
c. with a given night temperature, high day temperature promotes bud growth. Consequently, flower buds became noticeable after 74 days at 24°/12°C but only after 108 days 12°/24°C.

The question arises, whether this might also be due to the fact that the day temperature was given for only 8 hours and the night temperature for 16 hours. This, however, is not the case. If one compares e.g. the treatments 24°/15°, 18°/18° and 12°/21°C, which all have the same daily 'heat sum', it appears that the number of days to flower initiation is 80, 94 and 106, respectively.

Bud growth therefore, is influenced in a specific and differential way by day and night temperature.

Throughout the development of the flower, from microscopical visible initiation to anthesis, this effect remains noticeable. The differences became even more pronounced; in the group at 24°/12°C flower buds emerged from the leaves after 112 days, and the one at 12°/24°C at 170 days, i.e. 58 days later. At the time of flowering this difference was reduced to 45 days, probably because the temperature control had broken down and all plants had to be kept at a high temperature.

As bud growth is affected both by day and night temperature one might expect that this would also hold true for internode growth. Examination of the data (Table 18 C) reveals, however, that this process is mainly affected by night temperature, and hardly at all by day temperature.

Stem length is the product of number of internodes and internode length. The former is dependent on the moment of initiation of the flower, which is determined by the mean daily temperature, while internode length is determined by the night temperature. The relation of stem length and temperature must therefore be rather complicated. As the number of internodes is smaller at low temperatures, while internode length is increased by low temperature, these tendencies are opposite and the differences in stem length are not as great as might be expected from the data for internode number or internode length alone (Table 18 D).

The longest stems (90–103 cm) are mostly found at high day temperatures (21°–24°C) and low night temperatures (12°–18°C), while the shortest stems (72–80 cm) occurred at low day temperatures (12°–18°C) and high night temperatures (18°–24°C). In the middle region of the temperature range the stems are intermediate in length. At the constant temperatures they vary from 84.5 to 94.0 cm, with the maximum length at 18°/18°C and lower values at both lower and higher temperatures.

The length of the leaves varied between 6.9 and 9.2 cm. There was no signif-

icant effect of the night temperature, but high day temperatures (15°, 21° or 24°C) tended to decrease leaf length, especially in combination with low night temperatures. The shortest leaves were found at 15°/12°, 21°/12°, 24°/12°, 24°/15° and 24°/18°C; the longest leaves at 12°/21°, 12°/24° and 15°/18°C.

Leaf width showed the opposite response; there was little effect of the day temperature, but high night temperatures tended to give narrower leaves. The lowest values (8.9 to 9.7 mm) were found at 24°/12°, 21°/21°, 21°/24°C and all combinations with a night temperature of 24°C. The broader leaves (width 11.2 to 11.6 mm) are spread over all day temperatures with a night temperatures in the 12°–18°C range.

With regard to dry weight of leaves, three variables come into play: leaf number, leaf length and leaf width. As leaf number increases strongly with increasing night temperature, one would expect to see the same tendency in total leaf weight. This does indeed hold true, but not for the highest night temperature, apparently because this reduces leaf width too much. Leaf number also tends to increase with increasing day temperature; however, this tendency is not found in the figures for total leaf dry weight. Here, apparently the adverse effect of high temperature on leaf length comes into play.

The interesting thing about stem dry weight is that it only partly reflects the differences in stem length. The lowest dry weight values were found at high night temperatures, which in many cases also gave short stems. The combination of high day temperatures with low night temperatures, however, which gave the longest stems, in some cases (21°/12°, 24°/12°, 24°/15°C) gave rather low dry weight values.

The weight of the flower was rather uniform and the variation that occur shows no regular pattern. This is easily explained by the fact that during the later phases of flower formation the temperature control had broken down and all groups were at about 22°C.

The total dry weight of the plant is the sum of the dry weights of the stems, the leaves and the flowers. It has been shown that stem dry weight is decreased by high night temperatures and to a lesser extent by the combination of high day temperatures and low night temperatures. Leaf dry weight is lowest at low night temperatures and is also decreased by high day temperatures. The total dry weight follows these trends. It was lowest (about 8.7 gram) at the highest night temperature and only slightly higher (about 8.9 gram) at the lowest night temperature. The highest weights were found at a night temperature of 18° or 21°C. Apart from the fact that the dry weights at 24°/15° and 24°/18°C were rather low, day temperature did not have a significant effect.

In conclusion, this experiment showed that:

– Flower bud initiation depends on the average daily temperature, and that day and night temperatures have no specific effect; the lowest temperature i.e. 12°C is the most promotive.

– Flower bud growth is influenced in a specific and differential way by day and night temperature: a. when night and day temperature are the same, bud growth is promoted by high temperatures (24°/24°C); b. with a given day tem-

perature, low night temperature (12°C) promotes bud growth; c. with a given night temperature, high day temperature (24°C) promotes bud growth.
– Development of flower from microscopical initiation to anthesis is promoted by a combination of high day temperature with low night temperature (24°/12°C).
– Internode length is determined by the night temperature; day temperature had no effect.
– The greatest stem length was usually found at high day temperatures (21°–24°C) and low night temperatures (12°–18°C) while the shortest stems occurred at low day temperatures (12–18°) and high night temperatures (18°–24°C). The lower and higher constant temperatures (12°/12°, and 24°/24°C) gave the lowest values of stem length.
– Leaf length was not significantly affected by night temperature, but high day temperatures (15°, 21° or 24°C) tended to decrease it especially in combination with low night temperatures.
– Leaf width was not much affected by day temperature, but high night temperature tended to give narrower leaves.
– Total dry weight reached its highest value at night temperatures of 18° and 24°C. Day temperature did not have a significant effect.

4.3. Effect of low temperature (5°C)

4.3.1. *Effects of duration of 5°C and interaction with the photoperiod*

Experiment 13. – On February 19, 1965, rooted cuttings of the variety 'Keefer's Cheri Sim' were planted in the greeenhouse at about 20°C and on March 8, they were stopped back. After 94 days from planting – when the plants had 8 pairs of expanded leaves –, they were moved to 5°C. Here they received about 250 mW/sec. cm² fluorescent light for either 8 or 16 hours per day (short day and long day). The treatment lasted for 3, 4 or 5 weeks. Subsequently the plants were put back in the greenhouse, were half of each group was given 8 hours of natural light, and the other half 8 hours natural light + 8 hours supplementary illumination by incandescent lamps. Each treatment consisted of 10 plants.

The results (Tables 19 and 20): The data show that flower initiation was promoted by 3 weeks of 5°C to the extent that only 16 leaf pairs were formed below the flower, against 20 (in LD) or 26 (in SD) leaf pairs in the controls. As 4 or 5 weeks 5°C did not cause an additional reduction, this was the maximum effect attained.

There was no difference in this respect between 3, 4 and 5 weeks of 5°C. On microscopic examination, the explantation for this proved to be simple: in the third week of the low temperature, visible initiation of flower primordia had already taken place. This means that this experiment has given no proof for an indirect effect of low temperature on flower initiation, so that the application of the term vernalisation in its generally accepted sense (e.g. Chouard, 1960) is not yet justified.

There is, however, a true after-effect of low temperature with respect to inter-

node length. In a long day after-treatment, the internodes measure about 37 mm in the controls, about 48 mm after 3 weeks 5 °C and about 53 mm after 4 or 5 weeks 5 °C. In a short day after treatment there is a similar effect, but no difference between 3, 4 or 5 weeks 5 °C (Table 19).

The stem length, i.e. the product of number of internodes and average internode length, gave the following picture. In long day, the shortest stems (73 cm) were formed by the controls; the longest (83 cm) after 5 weeks 5 °C. In short day, the control group had the longest stems (95 cm); the stems of the 'vernalised' plants varied between 68 and 80 cm without a consistent pattern. Stem diameter was also measured, but the differences were too slight to permit conclusions. The same holds true for length and width of the leaves.

TABLE 19. Experiment 13 – Effects of duration of 5 °C and interaction with photoperiod on growth. Averages of 8 plants.

	During 5 °C						
	3 weeks 5 °C		4 weeks 5 °C		5 weeks 5 °C		Control
	SD	LD	SD	LD	SD	LD	
Long day (16 hours) after 5 °C							
Number of leaf pairs	16.0	16.0	16.0	16.0	16.0	16.0	20.0
Internode length (mm)	48.0	49.0	53.0	53.0	55.0	52.0	37.0
Stem length (cm)	77.0	79.0	83.0	81.0	84.0	83.0	73.0
Stem diameter (mm)	3.5	3.5	3.5	3.2	3.0	3.1	3.1
Number of petals	66.3	69.3	69.9	69.7	63.4	67.0	56.8
Total fresh weight of plant (g)	25.6	27.0	26.1	24.6	24.6	25.7	28.2
Short day (8 hours) after 5 °C							
Number of leaf pairs	18.0	17.0	17.0	17.0	17.0	17.0	26.0
Internode length (mm)	47.0	46.0	46.0	43.0	44.0	46.0	37.0
Stem length (cm)	80.0	77.0	77.0	68.0	71.0	73.0	95.0
Stem diameter (mm)	3.1	3.1	3.1	3.1	3.1	3.0	3.5
Number of petals	55.8	59.8	57.5	58.7	55.0	57.0	53.5
Total fresh weight of plant (g)	23.9	24.7	24.3	22.3	22.4	22.1	38.7

In long day flower buds emerged from the leaves about 3 weeks after the end of the cold treatment, which means that this stage of development was reached by plants that received 3 weeks of 5 °C a week before those that received 4 weeks, while these were again one week ahead of the groups that received 5 weeks of cold. These differences were maintained until anthesis, although at that time they were not as regular anymore.

The plants in long day flowered 60 to 65 days after termination of the low temperature treatment; the controls needed 100 days (Table 20).

In short day, development was slower, as could be expected from previous experiments. Here for the first time differences were observed between plants which received short day and those which received long day during their stay at 5 °C, although only when the cold treatment lasted 3 or 4 weeks.

In these cases the plants which received long day developed more rapid in

subsequent long day than those which received short day and flowered about 10 days ahead of these. Plants treated with 3 or 4 weeks 5 °C flowered about 82 days after the cold when they had received short day, and about 73 days when they had received long day during the 5 °C. After 5 weeks 5 °C this period was about 69 days in both cases. The controls required 200 days.

When the figures are grouped in a slightly different way, it emerges that the plants in a short day aftertreatment flowered 8 days later than those in long day, provided they were subjected to low temperature in long day, but irrespective of the length of their stay in the cold. Plants subjected to 5 weeks of 5 °C in SD flowered also 8 days earlier in subsequent LD than in SD. However, when the 'vernalisation' in SD had lasted only 4 or 3 weeks, the differences in flowering were 19 and 21 days respectively. This means that five weeks 5 °C have a stronger effect than 3 or 4 weeks 5 °C, leading to a further acceleration of flower development, which, however, only becomes apparent when the plants have been subjected to SD both during and after the low temperature treatment.

TABLE 20. Experiment 13 – Effects of duration of 5 °C and interaction with photoperiod. Averages of 8 plants.

	During 5 °C						Control
	3 weeks		4 weeks		5 weeks		
	SD	LD	SD	LD	SD	LD	
Long day (16 hours) after 5 °C							
Days from planting until the end of 5 °C treatment	94	94	101	101	109	109	–
Days from planting until flower bud emergence from the leaves	116	116	123	124	130	128	151
Days from planting until colour	145	147	154	156	163	160	184
Days from planting until anthesis	155	158	165	167	172	170	194
Short day (8 hours) after 5 °C							
Days from planting until the end of 5 °C treatment	94	94	101	101	109	109	–
Days from planting until flower bud emergence from the leaves	131	124	137	127	135	131	200
Days from planting until colour	165	156	173	164	170	167	237
Days from planting until anthesis	175	166	184	175	179	177	249

Fresh weight of the whole plant varied between 24.6 and 27.0 grams in the cold treated plants in long day and between 22.1 and 24.7 grams in those in SD. The controls in LD reached 28.2 grams while the controls in SD attained the heaviest weight, i.e. 38.7 grams.

There were no significant or consistent differences in length and diameter of the flower, although it looked as if on the whole those formed in SD after 'vernalisation' were slightly smaller than those in other treatments. This is born out by the data concerning the number of petals: in short day, 55–60 petals were formed against 63–70 in long day. The plants that received no cold formed

54 petals in SD and 57 in LD. It looks therefore as if the low temperature also led to slight increase in petals number.

In conclusion, this experiment has shown:

1. plants with 8 pairs of expanded leaves initiate flowers during the third week in 5 °C;
2. extension of the low temperature treatment beyond 3 weeks leads to slight acceleration of flower bud development, but only when the cold is followed by short day, not in long day;
3. in subsequent long day, no effect is seen of the daylength during the 5 °C treatment, but in subsequent short day plants which received LD during the cold flowered earlier than those which received SD, provided the cold treatment lasted only 3 or 4 weeks;
4. the low temperature pretreatment led to a slight increase in petal number;
5. it led to a clear increase in internode length, which at least in LD was proportional to the duration of the cold.

4.3.2. *The optimum period of low temperature*

Experiment 14. – In experiment 13 it was shown that 3 weeks 5 °C led to earlier flowering than 4 or 5 weeks low temperature. The present experiment was designed to establish the effect of still shorter periods of 5 °C.

On January 18, 1966, rooted cuttings of the variety 'Keefer's Cheri Sim' were planted in the greenhouse at 20 °C. On January 29, they were stopped back, and after 51 days from planting – or after the expansion of 8 to 9 pairs of leaves – they were moved to 5 °C. Here they received fluorescent light of about 250 mW/sec. cm² for 16 hours per day. The plants received 5 °C for 0, 3, 6, 9, 12, 15, 18, 21, 24, 27, 30 or 36 days. After this they were moved to the greenhouse where they received natural day but short photoperiods (8 hours). Each treatment comprised 8 plants.

Results (Table 21): The control group initiated flowers after 22.4 leaf pairs. Up to 15 days of low temperature this number decreased slightly (to 20.8 at 15 days 5 °C) but the differences are not significant. The plants that received more cold, however, initiated flowers earlier: the number of leaf pairs markedly decreases from 20.8 after 15 days 5 °C to 16.0 after 24 days 5 °C. A longer period of 5 °C showed a slight further decrease (to 15.3 after 36 days 5 °C) but this is again not significant. The critical duration of treatment low temperature therefore, is about 24 days.

If one considers the number of days between the end of the cold treatment and flowering, the following trend is observed. Even 3 days of 5 °C promotes flowering by 3.5 days, and a further promotion of 3 to 7 days is found for every 3 days of 5 °C up to 18 days. As the difference in leaf number of these groups does not differ significantly, this effect must be due to an (indirect) promotion of bud formation and elongation by low temperature.

Above 18 days there is a sudden increase in the promotion of flowering by 3 further days of 5 °C. This can easily be explained by the fact that here lies the critical duration of the cold for flower initiation, so that one gets a double effect:

TABLE 21. Experiment 14 – Effects of different periods of 5 °C. Averages of 8 plants.

	Periods of 5 °C (days)											
	0	3	6	9	12	15	18	21	24	27	30	36
Number of leaf pairs	22.4	23.0	22.0	21.8	20.2	20.8	18.8	17.2	16.0	16.1	15.6	15.3
Days from the end of 5 °C to anthesis	133.5	130.0	124.0	120.0	113.2	109.5	105.6	79.0	74.8	70.5	78.5	71.5
Days from planting to anthesis	184.5	184.0	181.0	180.0	176.2	175.5	174.6	151.0	149.8	148.5	159.5	158.5

TABLE 22. Experiment 15 – The relation between size and response to low temperature. Averages of 8 plants.

	Pairs of expanded leaves before 5 °C											
	3 p.l.		5 p.l.		6 p.l.		7 p.l.		8 p.l.		9 p.l.	
	0 w.v.	3 w.v.	0 w.v.	3 w.v.	0 w.v.	3 w.v.	0 w.v.	3 w.v.	0 w.v.	3 w.v.	0 w.v.	3 w.v.
Number of internodes	15.60	15.87	16.20	16.00	16.00	14.00	16.00	12.00	17.00	13.00	17.00	14.00
Days from the end of 5 °C to flowering	100.00	120.00	83.00	97.00	79.00	82.00	76.00	60.00	80.00	58.00	71.00	56.00
Total dry weight (g)	6.95	6.85	6.68	5.89	6.94	5.55	7.49	4.84	7.19	4.42	6.81	4.53

reduction of the number of leaf pairs and promotion of elongation. Above 27 days, there is no effect of additional cold; apparently, neither initiation nor elongation can be stimulated further.

If the number of days from planting is taken as a measure of flowering time, earliest flowering occurred after 21 to 27 days of 5°C. When more cold was given, the retardation caused by the stay at low temperature was not compensated by a further acceleration of initiation or elongation, so that the total number of days increased again.

In conclusion, this experiment has shown that:

a. flower initiation is promoted by 18–24 days of 5°C, shorter periods having no significant effect, and longer periods being no more effective than 24 days;
b. the phase from initiation to anthesis is accelerated by any period of 5°C up to 27 days, longer periods having no additional effect.

4.3.3. *The optimum size for 5°C*

Experiment 15. – This experiment was carried out to investigate the relation between size and response to low temperature. On May 20, and June 15, 1965, rooted cuttings of the variety 'William Sim' were planted in the greenhouse at 20°C. After 10 days they were stopped back. On June 30, some plants which had formed 3, 5, 6 and 7 pairs of expanded leaves were moved to 5°C for 3 weeks. On July 19, some plants which had formed 8 and 9 pairs of expanded leaves were moved also to 5°C for the same period. The controls had the same number of leaf pairs as the treated ones, but without low temperature treatment.

Results (Table 22): It is clear that plants with 3 or 5 pairs of leaves did not respond to 5°C with flower initiation: they formed the same number of leaves below the flower as the controls. Plants with 6 pairs of leaves showed a response: they formed 2 internodes less than the controls, while plants with 7 leaf pairs formed 4 internodes less than the controls. With this the optimal reaction was reached. Plants with 8 or 9 leaf pairs did not show a greater response with regard to flower initiation than those with 7 leaf pairs.

It should be noted that the light conditions during the experiment affected the results. In the first group, i.e. those with 3 to 7 leaf pairs the plants initiated flowers without cold treatment after about the same number of internodes (15.6–16.2). The plants with 8 and 9 leaf pairs initiated flowers without cold treatment one internode later than the first group, presumably because the treatments started 19 days later in a slightly shorter daylength.

The number of days between the end of the 5°C treatment and anthesis shows that plants treated with 5°C when they had formed 3 and 5 pairs of leaves were delayed in comparison to the controls. This can be explained by the fact that in these plants flower initiation was not accelerated by the low temperature, which only retarded growth. Plants treated when they had formed 6 pairs of leaves flowered almost simultaneously with the untreated ones. This means that the promotive effect of low temperature on initiation just equaled the inhibiting effect on growth. Plants treated when they had formed 7 to 9 leaf pairs flowered about two weeks earlier than the controls.

The low temperature decreased the total dry weight of the plants as a result of the decrease of the number of internodes and the inhibition of growth.

4.3.4. *Effects of daylength and light quality during 5 °C*

Experiment 16. – As the low temperature has to last at least 18 days to be effective (experiment 14) the plants have to be supplied with light during this period. The present experiment was undertaken to establish if there is any effect of light quality or photoperiod. Three light treatments were given: (1) 8 hours of fluorescent light (one tube Philips TL 40 W/29 per 0.5 m^2); (2) 16 hours of fluorescent light (same source); (3) 24 hours of incandescent light (one Philinea tube 120 W per 0.45 m^2). The treatment lasted for 3 weeks; the temperature was 5 °C. The treatments started when the plants of the variety 'William Sim' had formed 8 to 9 pairs of expanded leaves. After the low temperature they were moved either to natural short day (November 1965) or to natural day extended to 20 hours by incandescent light. The control plants were in these daylengths throughout.

Results (Table 23): All groups that had been subjected to low temperature initiated flowers after 12 leaf pairs; the control in short day formed about 21 leaf pairs (Table 23). This shows that there was no effect of daylength during the low temperature treatment on flower induction. In subsequent short day, the groups that had been subjected to 16 hours of fluorescent light flowered about 10 days in advance of the others (the difference at the moment the bud became visible was already nearly 8 days). This may be due to a higher light intensity; the visible light was 13.600 erg/cm^2. sec. under fluorescent light against 5.700 erg/cm^2. sec. under incandescent light. This effect is also apparent in the groups moved to long day. Here the difference at anthesis between the plants subjected to 16 hours of fluorescent light and other 'vernalised' ones was 12 days.

TABLE 23. Experiment 16 – Effects of light quality and day length (fluorescent light = FL and incandescent light = Inc). Averages of 10 plants.

	SD (NL + 0) after 5 °C				LD (20 hours) after 5 °C			
	Treatments during 5 °C							
	8 hrs FL	16 hrs FL	24 hrs Inc	0 5 °C	8 hrs FL	16 hrs FL	24 hrs Inc	0 5 °C
Number of leaf pairs	12.0	12.0	12.0	20.9	12.0	12.0	12.6	12.6
Days from planting to flower bud emergence from the leaves	95.4	86.7	94.3	157.0	89.6	77.0	89.3	77.7
Days from planting to colour	150.7	146.4	149.1	192.0	149.4	142.7	147.7	147.3
Days from planting to anthesis	165.5	155.8	164.1	207.5	162.6	151.1	163.0	157.8

The difference between the control groups in short day and long day is very pronounced: in short day the plants flowered after 207 days, or 43 to 52 days

after the cold-treated ones, but in long day they flowered after 158 days, i.e. at about the same time as the 'vernalised' plants. This means that in this case three weeks long day (20 hours) has had the same effect as three weeks 5°C. This also holds true for the number of leaf pairs.

4.3.5. *Effects of temperature after 5°C*

Experiment 17. – The object of this experiment was to study the effect of temperature after the low temperature treatment on the development of the flower. The cuttings of the variety 'William Sim' were stopped back on November 10, 1965, and moved to low temperature 54 days after planting when they had formed 8 to 9 pairs of expanded leaves. During the 3 weeks at 5° they were irradiated by fluorescent light of about 250 mW/sec. cm^2 during 8 or 16 hours per day (short and long day, respectively). On January 3, 1966, the plants were moved to the greenhouses of the phytotron where the temperature kept at 12°, 15°, 18°, 21° or 24°C NL. Each treatment comprised 7 plants.

Results: All plants initiated flowers after 13 leaf pairs. This is in accordance with the previous observation that initiation already starts in the third week of the 5°C treatment. The subsequent temperature therefore only affects bud development. This process is apparently accelerated by high temperature: plants at 12°C required 97 days from the end of the 5°C to anthesis, while plants at higher temperatures required fewer days, those at 24°C needing only 52. This is in accordance with the results of experiments 10, 11 and 12. It is also a confirmation of the results of these experiments that the stems were shorter and thinner and the flowers smaller at the higher temperatures (21° and 24°C) with a corresponding difference in the dry weights, not only of stems and flowers but also of leaves and, consequently, of the whole plant.

There is a notable difference in the date of flowering of plants that received long day during the low temperature and those which received short day. The number of days required by the former from end of the cold treatment to flowering varied from 97 at 12°C to 52 at 24°C; those which received short days during the 5°C required more days. The difference was reversedly proportional to the subsequent temperature and decreased from 13.6 at 12°C to 2.2 at 24°C. This effect of the daylength during low temperature had been noted in experiment 13, but only in a short day after-treatment. In the present experiment, the days were of natural length, i.e. short (about 8 hours).

The difference is not due to the additional photosynthesis caused by the extra light during the cold, as the figures show neither an after-effect of the light quantity during the cold on dry weight of the plant, nor any correlation between dry weight and flowering time. There remains, of course, a theoretical possibility that there are differences in dry weight at the moment the plants are taken from the cold and that these differences at this particular stage of the development of the plant do affect flower bud formation.

4.3.6. *Effects interruption of 5°C with high temperature*

Experiment 18. – Under natural conditions, plants are rarely subjected to a

long period of uninterrupted cool temperatures; usually there are occasional rises in the temperature. To see if these have a specific effect, the following experiment was made. Plants were exposed to a total of 3 weeks of low temperature (5 °C), and this period was interrupted by seven days of relatively high temperature (20 °C) under natural light. The interruptions of 2, 3, 4 or 7 days were given to the plants 5, 7, 10 or 14 days from beginning of the low temperature period.

On January 18, 1966, rooted cuttings of the variety 'Keefer's Cheri Sim' were planted, and after ten days they were stopped back. When the plants had 8 to 9 pairs of expanded leaves, they were moved to 5 °C. After the treatments all plants received long day: 8 hours NL + 8 hours incandescent light (40 Watt bulbs). Eight plants were used for each treatment.

Results (Table 24): An interruption of the 'vernalisation' period by high temperature did not promote flower induction. In fact, it looks as if the uninterrupted period of 5 °C was the most effective: 14.4 leaf pairs in the plants of this group against 15 in the interrupted treatments and 18 leaf pairs in the controls. With regards to number of days to anthesis this tendency is even stronger: 137 days after uninterrupted 5 °C, 143 days after the various interrupted treatments, and 153 days in the controls.

In other respects (stem length, stem diameter, dry weight of stem, leaves and flowers) there were no differences between the plants of the uninterrrupted and the interrupted low temperature treatments. The controls had slightly larger stems and a significantly higher dry weight, which could be expected because they had formed more internodes.

TABLE 24. Experiment 18 – Effects of interruption of 5 °C with high temperature. Averages of 8 plants.

	control (no-cold)	A	B	C	D	E	F
Number of leaf pairs	18.00	14.40	15.40	15.00	15.00	15.00	15.00
Days from planting to anthesis	153.00	137.00	143.00	143.00	143.00	143.00	143.00
Stem length (cm)	91.00	83.00	91.00	88.00	86.00	90.00	89.00
Stem diameter (mm)	3.30	3.30	3.20	3.10	3.10	3.20	2.90
Dry weight of flower (g)	1.05	1.11	1.09	1.11	1.19	1.13	1.16
Dry weight of leaves (g)	2.18	1.48	1.47	1.41	1.51	1.43	1.49
Dry weight of stem (g)	3.13	2.36	2.43	2.29	2.45	2.31	2.26
Total dry weight (g)	6.36	4.95	4.99	4.81	5.15	4.87	4.91

A = 3 weeks 5 °C
B = 1 week 5 °C + 4 days 20 °C + 1 week 5 °C + 3 days 20 °C + 1 week 5 °C.
C = 1 week 5 °C + 1 week 20 °C + 2 weeks 5 °C.
D = 2 weeks 5 °C + 1 week 20 °C + 1 week 5 °C.
E = 5 days 5 °C + 2 days 20 °C + 5 days 5 °C + 2 days 20 °C + 5 days 5 °C + 3 days 20 °C + 6 days 5 °C.
F = 10 days 5 °C + 1 week 20 °C + 11 days 5 °C.

4.4. Discussion

The time of floral initiation depends on the rate of the preceding vegetative growth, and conditions which influence this rate may cause differences in the time of flower formation without having effected initiation in a specific manner. It therefore becomes important to use a criterion which permits clear separation between specific effects in floral initiation. Such a criterion is the relative amount of the preceding vegetative growth, as expressed by the number of leaves (or leaf pairs or whorls) preceding the first flower (Lang, 1952). Therefore, presence or absence of differences in the leaf numbers tells us whether initiation has been affected specifically or not, regardless of whether or not there are differences in the time of appearance of flower primordia, buds or open flowers. In tomato plants, the number of nodes below the first inflorescence has been considered the most objective criterion for measuring earliness of flowering (Honma et al., 1963).

In carnation plants the experiments showed that the low temperature decreased the number of leaves. This means that floral induction is promoted by low temperature. However, under the microscope visible flower bud initiation was observed first at high temperature; this means that the actual flower formation is not promoted by low, but by high temperature. The development of the flower from the primordial stage to anthesis is also enhanced by high temperature, except the very last phase from visible flower colour to anthesis which does not seem to be dependent on temperature. These conclusions are in accordance with Post (1942), Rünger (1957) and Blake and Spencer (1958) who noted that relatively high temperature may retard flower initiation, but promoted the development of the flower subsequent to initiation.

The experiment on day and night temperature showed that the moment of flower bud initiation depends on the average daily temperature, and that the lowest temperature is the most promotive. Day and night temperature had no specific effect. These finds are an extension of the conclusions of Halliday and Watson (1953); Hanan (1959); Harris and Harris (1962) and Schmidt and Holley (1957) who found that low night temperature causes flower initiation to occur after a smaller number of leaves. With regards to flower formation, however, the data shows that with a given day temperature, low night temperature promotes bud growth, while with a given night temperature, high day temperature promotes it.

It was shown in experiment 13 that the flower initiation was promoted by 3 weeks 5 °C. This is in accordance with the results of Harris and Harris (1962) who found that low temperature of 4.5 °C during one month promoted subsequent flower initiation and reduced the number of leaves formed below the flower. Promotion of flowering by cold treatment has been reported by Waterschoot (1957) and Chouard (1960) for a number of species of *Dianthus* other than glasshouse carnation.

Blake (1956) reported that low temperature had an indirect promotive effect on flowering of carnation, but in the present experiments there was no promotion of flower initiation when the plants were removed from the cold before

visible initiation of flower primordia had taken place. Therefore, this experiment has given no proof for an indirect effect of low temperature. As CHOUARD (1960) restricts the term vernalisation to cases where the main effect of low temperature is to prepare the plant for flower initiation at subsequent higher temperatures, the data presented here do not justify the use of the term vernalisation in the case of the carnation.

Although periods of 5°C shorter than 18–24 days have no effect on flower initiation (measured as the number of leaf pairs), flower development was accelerated by any period of cold. Another difference was that while the optimal effect on initiation was reached after 24 days 5°C, longer periods of cold still had an additional effect on development.

The daylength during the low temperature treatment had no effect on the flower induction (experiments 13, 16 and 18), but flower development was accelerated by long day during the 5°C, provided the cold treatment lasted only 3 or 4 weeks and the plants were subsequently grown under short day.

In the extensive literature cereals and perennial grasses, some authors claimed a favourable effect of short day during plant vernalisation, while others found a favourable effect of long day. Considering the data in the literature more closely, it appears that favourable effects of short day during vernalisation were generally found under field conditions, whereas favourable effects of long day were found under artificial light conditions where a weak illumination was applied. Such a case has been explicitly reported by KREKULE (1961). He also reported that daylength effect under artificial light of low intensity disappeared with increasing light intensity. In plants other than cereals or grasses such as *Beta vulgaris* (CHROBOCZEK, 1934), *Raphanus sativus* (KIMURA, 1961) and *Silene armeria* (WELLENSIEK, 1964), promotive effect of long days during plant vernalisation has generally been reported. BARENDSE (1964) found in *Cheiranthus allionii* that the effect of daylength during plant vernalisation depended on light quality and the duration of the vernalisation period.

Young plants of carnation cannot be 'vernalised'. The sensitivity starts when a certain size has been reached and then increases with size until the optimum is reached at about 7 to 8 pairs of expanded leaves. A similar relation between 'vernalisability' and size has been reported for several biennial plants, but in the cases seedlings were used so that apart from size, juvenility may have played a role. According to PIERIK (1967) juvenility (i.e.: insensitivity to low temperature with regards to flower formation) is localized in the buds. It is possible, that the meristems have to reach a certain size before they are able to react to the low temperature.

An interruption of the cold period by high temperature did not promote flower induction, nor did it diminish the effect of the low temperature. This result is in agreement with results with several other plants, e.g. cereals (GREGORY and PURVIS, 1938; PURVIS and GREGORY, 1952) and lettuce (RAPPAPORT et al., 1956; CHOUARD, 1960).

Short day after the low temperature treatment caused a slower development of the flower in comparison to long day. Short day did not substitute for low

temperature as reported by WELLENSIEK (1953) for *Campanula medium* and subsequently by others for some other species (CHOUARD, 1960).

The carnation resembles many species requiring vernalisation in that long day accelerates flowering. However, the conclusion of BLAKE (1956) that the effect of a cold treatment is reduced or disappeared when the plants are subsequently grown in short day was not confirmed.

Temperature had an effect on calyx splitting (experiment 10). In natural light both low (12°C) and high (24°C) temperature increased the percentage of calyx splitting, at 12°C probably because the flower matured at the lowest light intensity, at 24°C possibly because of the greater number of petals. SZENDEL (1938) reported that the colder the environment, the higher was the percentage of 'splits'. According to HOLLEY and BAKER (1963), both high and low temperature can cause calyx splitting. In the present experiments there was no calyx splitting at high temperature (15°–24°C) in artificial light.

The present results show that light has an important effect on calyx splitting. It may be that under natural conditions, where the light varies strongly, the development of the flower is not regular and that this irregular growth leads to calyx splitting.

The temperature also affects the quality of the flower measured as dry weight. As a rule, the best flowers were formed at low temperature, while high temperature gave a poor quality flowers, probably due to the rapid development of the flowers under these conditions.

Stem length is also an important measure for quality. Internode length is promoted by low temperature. Experiment 12 has revealed that the effect is largely due to night temperature and that day temperature has little influence. The combination between high day temperature and low night temperature gave the longest stems, while the shortest stems occurred at low day temperature and high night temperature. The longer stems are usually thinner than the shorter ones. For the rest stem diameter is proportional to light intensity. No specific effect of temperature was found.

5. EFFECTS OF GIBBERELLIC ACID

5.1. EFFECTS OF GIBBERELLIC ACID (GA_3)

Experiment 19. – Interactions of GA_3 and daylength. On January 18, 1966, rooted cuttings of the variety 'Keefer's Cheri Sim' were planted, and after 10 days they were stopped back. When the plants had formed 7 to 8 pairs of expanded leaves, 51 days from planting, they were sprayed until runoff with 0, 50, 100, 250 and 500 p.p.m. GA_3 in water with a hand-compressed air sprayer. This application was made once, twice or three times at weekly intervals. These treatments were given under short day (8 hours NL) and under long day conditions (8 hours NL + 8 hours weak incandescent light). The greenhouse temperature averaged 20°C. Seven plants were used for each treatment.

Results (Tables 25 and 26): The data show that plants in LD formed 18 leaf pairs before initiating a flower, while those in SD formed more leaf pairs, viz. 23, as could be expected. The effect of GA_3 is rather unexpected. In LD, it accelerated flower initiation by two leaf pairs (and even three at the very highest dose). In SD, however, there was no accelerating effect, but a slight retarding effect of 1 or 2 leaf pairs and as much as 3 at the highest dose.

These differences are reflected in the number of days from planting to flower bud emergence: in LD 104 days without GA_3, but 87 to 78 days with GA_3, dependent on the dose; in SD 129 days without GA_3 and about 135 to 141 with GA_3, apparently independent of the dose (Table 25).

The time between flower bud emergence and anthesis in LD was 45 days without GA_3 and about 47 days with GA_3, a difference which is not significant. In SD, however, the untreated group needed 48 days to complete this phase, while the time required by the treated plants increased fairly regularly with the dose to 78 days at 3 × 500 p.p.m.

Another difference between the LD and SD groups was the stem elongation after GA application (Table 25). In LD, the stems of the control group averaged 91 cm whereas those of the treated plants varied between 96 and 103 cm. There appeared to be no difference between the plants treated with different quantities of GA. In SD, however, there was a clear tendency for longer stems after more GA: the controls had stems of 102 cm, while those of the plants treated with the highest dose were 127 cm. However, owing to the fact that GA in LD reduced the number of internodes, but in SD slightly increased it, these tendencies are reversed when the mean internode length is taken into consideration. In LD this was 54 mm in the controls and up to 67 mm in treated plants, a difference of about 20%; but in SD these figures where 47 and 52 mm, a difference of only 10%, and this, in contrast to the situation in LD, only at the highest doses.

Stem thickness, flower diameter, and number of petals did not seem to be affected by GA. The dry weight, however, showed significant differences. In LD, total dry weight was 6.4 g in the controls, about the same (6.0 to 6.4 g) after applications of 50 or 100 p.p.m. GA, perhaps somewhat less (5.8 to 6.1 g) after 250 p.p.m. but clearly less (5.4–5.6 g) after applications of 500 p.p.m. In SD,

TABLE 25. Experiment 19 – Effects of GA_3 sprays during long and short days. Averages of 7 plants.

	photoperiod	GA_3 0 p.p.m.	50 p.p.m. 1×	50 p.p.m. 2×	50 p.p.m. 3×	100 p.p.m. 1×	100 p.p.m. 2×	100 p.p.m. 3×	250 p.p.m. 1×	250 p.p.m. 2×	250 p.p.m. 3×	500 p.p.m. 1×	500 p.p.m. 2×	500 p.p.m. 3×
Flower bud emergence from the leaves (days)	LD	104	85	85	84	87	83	83	83	84	82	80	79	78
	SD	129	136	136	141	133	136	138	138	135	137	138	135	136
Colour (days)	LD	140	121	120	122	122	121	121	121	121	119	119	117	117
	SD	163	171	174	192	186	190	184	183	176	188	187	190	202
Anthesis (days)	LD	149	132	130	133	134	131	130	131	130	129	127	126	127
	SD	177	189	190	205	199	202	197	197	188	204	198	205	214
Stem length (cm)	LD	91	99	96	103	97	99	98	101	98	101	96	101	102
	SD	102	100	108	105	113	111	118	108	129	117	115	123	127
Stem diameter (mm)	LD	3.3	3.5	3.6	3.4	3.5	3.5	3.5	3.4	3.4	3.3	3.5	3.5	3.8
	SD	3.9	4.0	3.6	4.1	3.4	3.3	3.6	3.4	3.7	3.5	3.5	4.1	3.9
Number of leaf pairs	LD	18	16	16	16	16	16	16	16	16	16	16	16	15
	SD	23	24	24	25	25	24	24	24	23	24	24	24	26
Mean internode length (mm)	LD	54	65	63	66	63	66	65	67	66	66	60	67	67
	SD	47	44	48	44	47	47	51	47	59	50	49	53	52
Flower diameter (mm)	LD	67	71	71	70	74	72	69	67	68	72	65	72	69
	SD	69	71	70	72	70	73	69	72	72	72	72	72	74
Number of petals	LD	61	53	54	55	56	57	58	58	55	58	54	59	70
	SD	52	52	54	48	46	50	49	50	54	49	48	46	49

TABLE 26. Experiment 19 – Effects of GA_3 sprays during long and short days on dry weight. Averages of 7 plants.

	photoperiod	GA_3											
		0 p.p.m.	50 p.p.m.			100 p.p.m.			250 p.p.m.			500 p.p.m.	
			1×	2×	3×	1×	2×	3×	1×	2×	3×	1×	2×	3×
Flower (g)	LD	1.1	1.1	1.2	1.1	1.3	1.2	1.1	1.2	1.1	1.1	1.0	1.1	1.1
	SD	1.3	1.2	1.3	1.1	1.1	1.1	1.2	1.1	1.2	1.1	1.1	1.2	1.3
Leaves (g)	LD	2.2	1.9	1.9	1.7	1.9	1.8	1.8	1.8	1.7	1.8	1.7	1.6	1.6
	SD	3.2	3.2	3.1	3.5	3.1	3.1	3.2	3.0	3.1	3.3	3.2	3.4	3.7
Stem (g)	LD	3.1	3.1	3.1	3.2	3.2	3.1	3.1	3.1	3.0	3.1	2.7	2.9	2.9
	SD	3.8	3.9	4.0	3.7	4.2	4.0	4.4	3.9	4.5	4.6	4.4	4.9	5.4
Total weight (g)	LD	6.4	6.1	6.2	6.0	6.4	6.1	6.0	6.1	5.8	6.0	5.4	5.6	5.6
	SD	8.3	8.3	8.4	8.3	8.4	8.2	8.8	8.0	8.8	9.0	8.7	9.5	10.4

the tendency was reversed: at the highest doses, the dry weight (10.4 g) was clearly higher than that of the controls (8.3 g). A closer study of the figures (Table 26) reveals that this is caused in LD mainly by the dry weights of the leaves and in SD primarily by the dry weight of the stems. The dry weight of the flower does not show significant differences.

In conclusion, GA promotes flower initiation, accelerates flower development, increases internode length but reduces total dry weight in LD. In SD, GA slightly inhibits flower initiation, retards flower development, slightly increases internode length (only at high doses) and increases total dry weight.

Experiment 20. – The purpose of this experiment was to compare the effect of GA_3 applications and 3 weeks 5 °C.

This experiment was started at the same date and under the same conditions as experiment 19. When the plants had formed 7 to 8 pairs of expanded leaves, i.e. at the moment the plants of the previous experiment were given their first spraying of GA_3 in the concentrations of 0, 50, 100, 250 or 500 p.p.m., a group of plants was moved to low temperature (5 °C) for 3 weeks. Seven plants were subsequently placed in short days (8 hours NL) and seven in long days (8 hours NL + 8 hours incandescent light).

Results (Table 27): When plants which were sprayed once with one of the five GA concentrations are compared to the 'vernalised' plants (Table 27) the following fact emerges: low temperature reduces the number of leaf pairs from 18 to 14 in LD and from 23 to 15 in SD. It therefore has a similar effect as GA in LD, although not as strong, and a completely different effect from GA in SD. Unlike GA, low temperature did not affect internode length. In LD it did not affect the diameter of stems and flowers, but in SD the plants that had received 3 weeks of 5 °C had thin stems and small flowers.

TABLE 27. Experiment 20 – Comparison between GA_3 applications and 3 weeks 5 °C in long and short days. Averages of 7 plants.

	photo-period	GA_3					3 weeks 5 °C
		0 p.p.m.	50 p.p.m.	100 p.p.m.	250 p.p.m.	500 p.p.m.	
Stem length (cm)	LD	91	99	97	101	96	83
	SD	102	100	113	108	115	81
Stem diameter (mm)	LD	3.3	3.5	3.5	3.4	3.5	3.3
	SD	3.9	4.0	3.4	3.4	3.5	3.0
Number of leaf pairs	LD	18	16	16	16	16	14
	SD	23	24	25	24	24	15
Mean internode length (mm)	LD	54	65	63	65	60	52
	SD	47	44	47	47	49	46
Flower diameter (mm)	LD	67	71	74	67	65	71
	SD	70	69	72	69	72	60

5.2. Discussion

According to the results of these experiments, GA promotes flowering of carnation in long days but not in short days. From this fact one could conclude that GA substituted for temperature requirement but not for photoperiodic requirement. This has been described for *Oenothera biennis* by Chouard (1960) with the difference that in this species the low temperature has an indirect effect and GA repeatedly applied to nonvernalised rosettes causes shooting to a height of 20 to 30 cm under long days. *Oenothera lamarckiana* and *O. parviflora*, on the other hand, even though their chilling and long-day requirements are also obligate, are much easier to satisfy. Repeated gibberellin applications to nonvernalised plants induce shooting and finally quite rapid flowering under long days and sometimes even under short days, but then much more slowly. Carr et al., 1957 found in *Centaurium minus* the same effect as in the present experiments. They observed that in plants in short days, stem elongation ceases shortly after cessation of GA application, but in long days stem elongation continues without an exogenous supply of GA. They suggested that if the rosette habit is due to a genetic block in the synthesis of gibberellin – a block which is removed by cold treatment – then the applied GA may act as a 'starter' and comparatively small amounts will enable further synthesis to take place. This synthesis takes place only under long-day conditions in *C. minus*.

In the present experiments it was observed that in short day GA slightly inhibits flower initiation. The inhibition effects of GA also were observed by other authors. Poleg and Aspinall (1958) stated that the development of flowering spikes in barley can be also inhibited by heavy doses of GA. Also, the inhibition of flowering of *Kalanchoë* by GA_3 was observed by Harder and Bünsow (1958).

It has been commonly supposed that control of flowering is based on a single hormone (the hypothetical 'florigen'), and that this hormone induces flowering both in long day plants and short day plants. Quite clearly, from the results presented above, the gibberellins are not 'florigen'. There may be a close relationship between gibberellin and 'vernalin', the hypothetical hormone produced in response to vernalisation, because GA often substitutes for low temperature.

The data showed that in long and short days GA increased internode length; this was due to the fact that gibberellin induces stem extension in caulescent plants is a consequence both of increased cell multiplication and of increase in cell size (Brian et al., 1960). Bukovac and Wittwer (1956) observed that GA applied to peas, beans, tomatoes, peppers, sweet corn, summer squash, cucumbers, lettuce, and cabbage induced marked elongation of internodes and often caused the leaves to broader or elongate. They also found that there were some accompanying increases in fresh and dry weights of tops, but root growth decreased correspondingly. In carnation plants, however, GA reduced the total dry weight under long day conditions, due to the fact that GA promotes flower initiation and reduces the number of leaves. As a result of the inhibitive effects of GA during SD, the number of leaves and internodes were increased. Consequently, the total dry weight of the plants was also increased.

6. TIMING OF CARNATION CROP

6.1. Introduction

Knowledge of the time required for a crop to come into flower allows the grower to judge when to plant and when to pinch in order to produce flowers at a moment when the market may be expected to be favorable. In addition it may be important to know which time interval may be expected between the first and the second (return) crop. These problems have already been studied from various angles in some countries, particularly in the USA, but not in the Netherlands.

In the present chapter an attempt will be made to answer the following questions:

1. What is the time required to the first crop for plants planted at various times of the year?
2. What is the effect of a low temperature treatment during the various times of the year?
3. What is the time required for the return crop?
4. Is there a residual effect of the low temperature treatment on the return crop?

6.2. Timing of carnation crops by planting date and low temperature treatment

Experiment 21. – From May 1965 until April 1966 every two weeks 50 rooted cuttings of the variety 'William Sim' were potted into 14 cm plastic pots. The plants were pinched as soon as possible after planting. After stopping, 25 plants were planted in steam-sterilized greenhouse soil. The distance between each plant was 20 cm. The other 25 plants remained in the pots, beside those planted in the soil, until they reached the stage in which they could be considered sensitive to low temperature, i.e. after the plants had formed 8 pairs of expanded leaves. The plants were then moved to 5 °C under long day conditions (16 hours AL). After a 3 weeks period the plants were moved to the greenhouse and planted in the soil.

From the shoots which developed after stopping only two were retained, the others were removed at an early stage. The greenhouse was heated during the winter months but it was not cooled in summer. The temperature was recorded on thermograph papers. The following data were collected: plant growth, date of flowering of the first crop, quality of the flowers, and the number of days between the first crop and the return crop.

Results (Tables 28, 29, 30, 31, 32, 33, 34 and Fig. 5): This experiment in fact consisted of two pairs: the relation between planting date and flowering date, and the effect of a pretreatment at low temperature. The easiest way is to discuss each part separately.

Planting date had a great influence on the number of leaf pairs (Table 28). The maximum, i.e. 23, was found in the October planting, the minimum, i.e.

15, in the March and April plantings. This means that the plants of the October planting were the last to initiate flowers, while those planted in March and April were the earliest. Between April and October the number of leaf pairs gradually increased. The number of days from planting to flowering shows the same trend: it increases from a minimum of 125 in the April plantings to 253 in the September plantings. The result was that carnations planted in April flowered after 4 months, while those planted in September required 8 months.

It is obvious that light is the environmental factor responsible for the differences in flower initiation and development. Plants started in April were grown under favourable daylength and light intensity conditions, promotive to flower bud initiation. Plants started in September developed under short day and low light intensity which retarded flower bud formation.

Under these conditions of natural light, light intensity varied in concomitance with the photoperiod. It is impossible to separate the effects of these two factors, but from previous experiments (see experiments 2 and 6) it is evident that these effects are similar; both retard flower initiation and development.

One may, however, separate to some extent the effect of light on flower initiation and flower development. The plants started in August and those in January initiated flowers after the same number of leaf pairs, i.e. 18, but the former flowered after 220 and the latter after 168 days. This clearly is due to an effect of the different light conditions during flower development. In the other hand, plants started in August flowered after the same number of days as those started in November but the latter formed three more pairs of leaves: apparently the light was different during initiation, and not so much during development.

TABLE 28. Experiment 21 – Effects of planting date on flower initiation and development. Averages of 10 plants.

	Planting date											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Number of leaf pairs	16	17	16	18	22	23	21	19	18	17	15	15
Number of days from planting until flowering	129	131	163	220	253	243	219	192	168	143	131	125

Internode length was greatest (65 mm) after planting in July and smallest (46 mm) after planting in October (Table 29). From October until March there were only slight differences but after planting from April onwards the internode length increased rapidly.

Stem length results from internode number and internode length. The longest stems (121 cm) were found after planting in September; these were caused by the greater number of internodes (20). Planting in July, August and October gave also rather long stems (99.5 to 102.5 cm); in July these were caused by the great internode length, in August by both number and length of the internodes, and

in October by the great internode number (20.5). The shortest stem length (72 cm) occurred after planting in March; in this case both internode number and internode length were smaller.

The stem diameter varied from 3.2 to 5.6 mm. The thinnest stems occurred after planting in August; these plants had a rather long stem. Planting from October to January gave the thickest stems (5.4 to 5.6 mm). Later plantings led to thinner stems until stem diameter reached its minimum after planting in August.

The data show no correlation between stem length and stem diameter: the long stems (121 cm) after planting in September were 4.7 mm and the short stems (72 cm) after planting in March were 4.3 mm in diameter.

The flower diameter varied without much regularity between 60 and 77 mm. The flowers after planting from May 15th to August were relatively small (60–72 mm), evidently because these plants flowered in autumn and winter under poor light conditions. All other plantings gave flowers with a diameter of more than 70 mm.

The number of petals formed after planting from 15 July–15 September was relatively small (47–53); in the other plantings it varied without regularity between 55 and 73.

From the foregoing observations it was only to be expected that the dry weight of the flower (0.9–1.2 g) was found after planting between 15 July and 15 August as those flowers had both a small diameter and a small number of petals. High dry weights (1.7 to 2.0 g) were found after planting between September and February.

TABLE 29. Experiment 21 – Effect of planting date on different characteristics of carnation plants. Averages of 10 plants.

	Planting date											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Internode number	14.0	14.5	14.5	17.0	20.0	20.5	18.5	17.0	15.5	14.5	13.5	13.0
Mean internode length (mm)	53.0	60.0	65.0	57.0	57.0	46.0	48.0	49.0	49.0	50.0	49.0	56.0
Stem length (cm)	80.0	90.0	99.5	102.5	121.0	99.5	95.0	88.5	81.5	79.0	72.0	77.0
Stem diameter (mm)	4.5	4.5	4.2	3.2	4.7	5.5	5.5	5.6	5.4	4.8	4.3	4.6
Flower diameter (mm)	72.0	70.0	66.0	68.0	76.0	74.0	74.0	73.0	73.0	74.0	74.0	76.0
Number of petals	58.0	58.0	56.0	49.0	52.0	66.0	60.0	60.0	58.0	57.0	64.0	54.0
Dry weight of flower (g)	1.6	1.7	1.4	1.1	1.7	1.9	1.8	1.8	1.9	1.8	1.6	1.6
Dry weight of leaves (g)	2.6	2.9	2.7	2.3	3.5	4.2	4.2	3.8	3.7	3.2	2.5	2.5
Dry weight of stem (g)	3.4	3.7	3.0	2.0	4.7	6.6	7.0	6.2	5.9	4.4	3.7	3.5
Total dry weight (g)	7.6	8.3	7.1	5.4	9.9	12.7	13.0	11.8	11.5	9.4	7.8	7.6

Flower weight is a measure for flower quality. Therefore, the poorest quality was found after planting in August. The best flower quality resulted from planting from September until February.

The dry weight of the leaves is determined by leaf number and by the meas-

urements of the leaves. The heaviest leaf mass (4.2 g) was found after planting in October and coincided with the greatest number of leaves. The fact that planting in October gave 2 more pairs of leaves than planting in November but the same dry weight, while planting in September gave the same number of leaf pairs as October but a smaller dry weight, shows the effect of leaf size, which was not measured in this experiment. The August planting gave the smallest leaf weight (2.3 g). This did not coincide with the minimum leaf pair number, as this occurred after planting in March or April (15) but not in August when 19 leaf pairs were formed.

One would expect stem dry weight to be closely correlated to stem length and diameter. Generally speaking, this is the case, but although the lowest dry weights found after planting in August coincided with the shortest, thinnest stems, the highest stem dry weight (7.0 g) from plants started in November did not coincide with the longest stems; those from September planting were much longer, although thinner, and those of October plantings were longer and just as thick. Apparently, still another variable enters the picture, viz. the content of dry matter per unit fresh weight. If the figures for fresh weight are compared with the product of stem length $\times$ stem diameter, there is a very close correlation.

After what has been said about the dry weights of flowers, leaves, and stems, it will be clear that the total dry weight shows a similar trend (Table 29): the lowest value (5.4 g) was found after planting in August, the highest weight (13.0 g) after planting in November.

The effect of low temperature was in the first place a reduction of the number of leaf pairs below the flower. This reduction was not the same during the year, however. In plants started in spring the difference was about 1 leaf pair, but this increased to 3–4 leaf pairs in autumn plantings (Table 30).

TABLE 30. Experiment 21 – Effect of planting date and 5 °C pretreatment on flower initiation. Averages of 10 plants.

Number of leaf pairs	Planting date											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Treated plants (5 °C)	15	15	15	15	17	19	18	18	16	15	14	15
Untreated plants	16	17	16	18	22	23	21	19	18	17	15	15

The data on the effect of low temperature on flowering date give another picture (Table 31). When planted between 15 January and 15 June, the untreated plants flowered earlier than the treated ones; when planted between 1 July and 1 November, the treated plants were the first to flower. When planted from 15 November until 1 January there was no difference.

The delaying effect of the low temperature treatment varied from 6 to 36 days. The maximum was reached in plants started on 15 April. The promotive

TABLE 31. Experiment 21 – Effect of planting date and 5 °C pretreatment on flower development. Averages of 10 plants.

Days to flowering	Planting date																							
	May		June		July		Aug.		Sept.		Okt.		Nov.		Dec.		Jan.		Feb.		March		April	
	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15
Treated plants (5 °C)	140	136	137	143	152	166	193	211	190	231	228	226	211	204	192	177	166	166	154	160	144	145	148	152
Untreated plants	129	124	131	126	163	184	220	246	253	244	243	236	219	204	192	178	168	153	143	141	131	134	125	115

FIG. 5. Effect of planting date and a pretreatment of 3 weeks at 5 °C on flowering (experiment 21).

effect of the low temperature varied from 11 to 63 days. It reached its maximum in plants started on 1 September. It should be noted that in this case the treated plants were 96 days ahead at the moment of flower bud emergence from the leaves, but this difference had decreased to 63 days at anthesis.

As to other characteristics, the longest internodes (62–69 mm) were found in the cold treated plants started between 15 May and 15 August; the shortest (48 mm) in plantings of 1 December to 1 January. The mean internode length was greater in the treated plants in 12 plantings, smaller in 3 plantings and about the same ($\pm$ 3 mm) in 9 plantings. The maximum difference in favour of the cold treated plants was 15 mm (1 June planting), the maximum difference in favour of the untreated plants 6 mm (15 April planting). The distribution of these differences over the year was irregular (Table 32).

The stems of cold treated plants were shorter than those of the untreated ones when started between 15 July and 1 February. In the remaining period of the year the difference was slight or in favour of the cold treated plants.

The stem diameter varied in the same way as that of the untreated plants, but in nearly all cases the cold-treated plants had thinner stems. The difference was

TABLE 32. Experiment 21 – Effect of planting date and a pretreatment of 3 weeks at 5 °C on different characteristics of carnation plants. Averages of 10 plants.

	Planting date											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Internode number	13.0	13.0	13.0	13.5	16.0	17.0	16.0	15.0	13.5	13.0	12.5	14.0
Internode length (mm)	58.5	67.0	62.5	63.5	58.5	54.5	52.5	48.0	53.0	52.3	56.0	54.5
Stem length (cm)	81.5	93.0	86.5	91.0	99.5	99.0	90.0	77.5	76.5	73.0	75.0	81.0
Stem diameter (mm)	3.9	4.2	3.7	3.1	3.6	5.2	5.4	5.1	4.9	4.5	4.0	4.0
Flower diameter (mm)	73.0	72.5	66.5	65.5	76.0	75.0	72.0	74.0	72.0	71.0	73.5	75.0
Number of petals	51.0	54.0	52.0	52.5	50.0	62.5	59.0	60.5	57.0	54.0	58.0	47.5
Dry weight of flower (g)	1.4	1.5	1.1	1.0	1.5	1.8	1.8	1.9	1.8	1.5	1.5	1.4
Dry weight of leaves (g)	2.1	2.4	2.0	1.9	2.3	3.1	3.5	2.7	2.7	2.4	2.1	2.8
Dry weight of stem (g)	2.9	3.1	2.2	1.6	2.5	5.1	6.2	4.7	4.4	3.2	2.9	3.5
Total dry weight (g)	6.4	7.0	5.3	4.5	6.3	10.0	11.5	9.3	8.9	7.1	6.5	7.7

greatest (1.4 mm) in the plants started on 1 September; however, this is an irregular group in many ways.

The data about the flower characteristics showed that the cold treatment had no effect on flower diameter. The same tendency as observed in the untreated plants was also apparent here. However, it looks as if there might be a slight reduction of the number of petals in treated plants started between 15 March and 15 July. The dry weight of the flower was reduced by 10–20% in the cold treated plants, except in those started between 15 October and 1 January where the flowers had about the same weight as in the untreated plants.

The dry weight of leaves showed the same trend as in untreated plants, but it lay consistently at a lower level. The same holds true for stem dry weight. Total dry weight of course showed a similar difference (Table 33).

TABLE 33. Experiment 21 – Effect on planting date and 5°C pretreatment on total dry weight (g). Averages 10 plants.

Total dry weight (g)	Planting date											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Treated plants (5°C)	6.4	7.0	5.3	4.5	6.3	10.0	11.5	9.3	8.9	7.1	6.5	7.7
Untreated plants	7.6	8.3	7.1	5.4	9.9	12.7	13.0	11.8	11.5	9.4	7.8	7.6

The return crop: After the flowers on the main stem had been cut, the plants were left in place and the number of days until the side shoots came into flowers was observed. The results are shown in Table 34. As can be seen from this table, the time between the first crop and the return crop varied from 64 days for plants cut in August to 230 days for plants cut in October. The number of days between the two crops is correlated with the amount of solar energy at the time the first crop is cut; when it is high, the period is short and vice versa.

The data show that the two crops can always be grown within one year. The minimum period for these two crops is 6 months after planting in April. The maximum period is 11 to 12 months when the plants are started between June and October.

Treating the plants with a period of low temperature affects the moment of flowering and therefore also the period between the first and second crop. The data (Table 34) show that for plants started between 15 January and June 1 the period between the first and second crop was shorter in the treated plants than in the untreated ones, while for plants started between June 15 and August 1 the trend was reversed. These differences can be explained when the conditions at the moment of the first harvest are taken into considerations. There are no indications of a residual effect of the low temperature treatment on the second crop.

The total number of days from planting to the second crop was somewhat affected by the low temperature treatment. After planting between January 15 and April 15 this number was lower for the untreated plants, especially for the

TABLE 34. Experiment 21 – Effect of planting date and a pretreatment of 3 weeks 5C on first and second crop. Averages of 10 plants.

Planting date		Treated plants (5 °C)			Untreated plants		
		Days from planting to flowering First crop	Days from first crop to return crop	Days from planting to flowering the first and the return crop	Days from planting to flowering First crop	Days from first crop to return crop	Days from planting to flowering the first and the return crop
June	1	137	214	351	131	230	361
	15	143	212	355	126	209	335
July	1	152	172	324	163	167	330
	15	166	167	333	184	160	344
Aug.	1	193	153	346	220	126	346
	15	211	129	340	246	90	336
Sept.	1	190	139	329	253	101	354
	15	231	101	332	244	105	349
Oct.	1	228	96	324	243	90	333
	15	226	95	321	236	94	330
Nov.	1	211	93	304	219	94	313
	15	204	91	295	204	91	295
Dec.	1	192	103	295	192	103	295
	15	177	104	281	178	102	281
Jan.	1	166	108	274	168	106	274
	15	166	57	223	153	65	218
Feb.	1	154	69	223	143	70	213
	15	160	66	226	141	72	213
March	1	144	66	210	131	71	202
	15	145	68	213	134	71	205
April	1	148	64	212	125	64	189
	15	152	53	205	115	64	179

April planting where the difference was more than three weeks. After planting between June 1 and November 1 the treated plants were at the time of the second crop as a rule somewhat ahead of the untreated plants, but the difference was never more than 10 days.

6.3. DISCUSSION

From previous experiments it is clear that flowering in the carnation is affected primarily by temperature, daylength, and light intensity. As neither factor was controlled in experiment 21, the results reflect the effect of all factors and do not permit a precise analysis.

The number of leaf pairs is the easiest to interpret; it follows closely the changes in daylength. This holds true also for the number of days to flowering but here also other factors come into play. The consequence is that the correlation between number of leaf pairs, i.e. the physiological moment of flower initiation, and moment of anthesis is not a very strict one. In the plants started between 1 May and 1 July, the number of leaf pairs was 15 but the number of

days to flowering increased with the progressive planting dates from 129 to 163. Plants started between 1 September and 15 October formed 22 leaf pairs but the number of days to flowering decreased from 253 to 236. In general, flowers which developed in a period of decreasing daylength, light intensity and temperature took a greater number of days than those which developed in a period of increasing photoperiod, light intensity and temperature. The result is that plants started in the period from 1 October to 15 February all flower in June. There is of course a striking difference in habit between these plants. Those planted early have relatively long, thick stems with many short internodes; those plants at the end of the period mentioned have short, thin stems with few long internodes. There are no significant differences in flower quality. The drop in flower quality (measured as dry weight) which occurred in plants started between 15 July and 15 August is probably due to the fact that these flowers, which opened in January to March, had developed under the most unfavourable circumstances.

As to the plants kept at 5°C for 3 weeks before planting, those started between 15 January and 1 August all initiated flowers after 15 leaf pairs, i.e. during the time they were at 5°C. Plants started between 15 August and 1 January formed more internodes before they laid down a flower.

As all plants had 8 leaf pairs when they were moved to 5°C, and as the environment in which they were submitted to low temperature was the same throughout the year, this observation leads to two conclusions:

(1) there is an after effect of the conditions before the 5°C; when the light conditions were unfavourable, the plants were slower to react to subsequent low temperature; (2) in these cases the promotive effect of 5°C was not as direct as when plants had been grown under better light conditions: the plants did not initiate flowers in the cold, but later at higher temperature. This means that in this case the effect of the low temperature was persistent, and more similar to a true vernalisation effect.

The number of leaf pairs was always reduced in comparison to that of the controls. Yet, as we have seen, the flowering time was not always earlier: in plants started between 15 November and 1 January it was the same, and in plants started between 15 January and 15 June it was later. The conclusion must be that for plants started in the latter period, the conditions in the greenhouse were more favourable for flower development than for those in cold storage. In other words, the higher temperature and light intensity in the greenhouse accelerated flower initiation and development in time to such an extent that it surpassed the effect of the faster initiation (measured physiologically, i.e. as the number of leaves below the flower) caused by 5°C. (Daylength probably plays no role here as it was long both in the cold room and the greenhouse).

A similar reasoning can be followed for the other plantings. In those between 15 November and 1 January, greenhouse conditions at the time of the cold treatment (i.e. from about 15 February to 1 April) were just as inductive as those in the cold room, while plants started between 15 January and 15 June received a better environment in the greenhouse than in the cold room at the

crucial period (between about 15 April and 1 August). During the latter period the difference in flowering date in favour of the untreated group is enhanced by an unfavourable after-effect of low temperature: the difference at the moment of flower initiation shows a further increase in the subsequent stages. This is no doubt due to the fact that the cold-treated plants are somewhat weaker than the controls. In the plants started in autumn the opposite effect appeared: here the cold-treated plants where much further ahead of the controls at the time of initiation than at anthesis, in other words, the difference got smaller and the controls caught up, to some extent, with the treated plants. Perhaps here also the explanation is that the latter were somewhat weaker.

If one compare the data of this experiment with the others which were made in different places in USA (Table 35). It is clear that the results from the Netherlands are practically identical with those from Long Island and Ohio with regards to January, February, March, October, November and December plantings. However, April, May, June and July plantings flowered one month later in the Netherlands than in Long Island and Ohio, but were similar to the plants in Colorado. August planting flowered in the Netherlands two months later than in Long Island and Ohio and one month later than in Colorado. From this table it is also apparent that a July planting gives the best winter production in the Netherlands. In Long Island, Ohio and Colorado this was the August planting.

TABLE 35. Relation between time of pinch and time of flowering of 'William Sim' carnations grown at four locations.

Time of pinch	Time of flowering			
	Netherlands[1])	Long Island[2])	Ohio[3])	Colorado[4])
January	June-July	June	June	July
February	June-July	June	June	July-Aug.
March	July	July	July	August
April	August	July	July	Aug.-Sept.
May	September	August	August	September
June	October	September	September	October
July	Dec.-Jan.	November	November	November
August	March	January	January	Jan.-Feb.
September	May-June	May-June	April	March-April
October	June	June	June	April-May
November	June	June	June	May-June
December	June	June	June	June

[1] Table 28.
[2] BING, 1960.
[3] NELSON et al., 1957.
[4] HOLLEY, 1959.

The differences in flowering date summarized in the previous table are mainly due to the temperature. The plants in USA were grown under a controlled night temperature of 10°–11 °C and in a cooled greenhouse during the

summer months. Our plants were grown in greenhouse heated during the winter and not cooled during the summer months. Therefore the night temperature in the summer months was much higher in the Netherlands than in USA. Low night temperature promotes flowering (see experiment 12). This means that plants planted in the spring and summer months flowered earlier in the USA than in the Netherlands. On the other hand, plants planted in the autumn and winter months flowered nearly at the same time in the four places. The differences which were found between the plants grown in Long Island, Ohio, and Colorado are probably due to light conditions.

The return crop came into flower 2 to 8 months after the date the flowers were cut. April planting produced 2 crops in the shortest possible time, because solar energy and temperature were optimal for a rapid first crop and for production of maximum sized lateral shoots before the first crop was cut off. Plants started in July required the longest time to produce 2 crops. In this case the first crop matured under decreasing light conditions; the lateral breaks, where present, were small at the time the first crop was cut, and the second crop had to start under the poorest light conditions of the year. HOLLEY and BAKER (1963) reported that the higher the amount of solar energy at the time a crop was cut, the shorter the time between that crop and the next. The results presented here showed the same tendency as these results and the earlier ones of BING and MAIER (1953).

Plants planted between 15 November and 1 January, whether treated with 5°C or not, flowered at the same date. This means that the second crop was grown under the same conditions. One may expect that if the low temperature has a residual effect on the return crop, differences in the flowering date will be observed. However, the treated and untreated plants gave also the return crop at the same date. This shows that the low temperature has no residual effect on the return crop. This may be due to the fact that 5°C has a direct effect, which disappears after the first crop has been cut. If the effect of low temperature were indirect, perhaps some residual effect could have been observed. CEPIKOVA (1935) found that the effect of the vernalisation of *Phleum pratense* and *Alopecurus pratensis* could still be seen in the behaviour of two-year old plants.

7. CONCLUSIONS

It was confirmed that light (photoperiod as well as light intensity) has a strong influence on growth and flower bud initiation and development of the carnation.

Effects of the photoperiod:

1. A long photoperiod leads to a decrease of the number of leaf pairs below the flower and promotes flower bud growth from microscopically visible initiation to bud emergence from the leaves. The subsequent phases (from emergence to visible colour and from colour to anthesis) required about the same number of days in the various daylengths (experiments 2, 3, 4, 6, 7).

2. A long photoperiod markedly increases internode length (experiments 2, 3, 4, 6, 7), decreases leaf length and increases leaf width (experiment 6). The effects on the leaves, however, are not always very pronounced, and sometimes not significant (experiment 2). No specific effects of the photoperiod were found on stem diameter.

3. There is no consistent effect of daylength on flower size, because of the interaction with light intensity. There is a slight but consistent increase in the number of petals in long day (experiments 4, 6, 7).

4. Due to the small number of internodes, dry weight of stems and leaves is lower in long day (experiments 2, 3, 4, 6). Flower dry weight is slightly higher in long day when light intensity is high (experiment 2) but lower when the light intensity is low (experiment 3).

Effects of light intensity:

5. High light intensity has the same effect as a long photoperiod on flower initiation and flower bud development from microscopically visible initiation to bud emergence from the leaves. There is not much influence of light intensity on subsequent phases (experiments 4, 6, 7, 8, 9).

6. In contrast to the photoperiod, light intensity has only a slight effect on internode length but high light intensity increases stem diameter (experiments 6, 7, 8). It also increases leaf length and width.

7. High light intensity increases flower size and the number of petals.

8. High light intensity has no consistent effect on the dry weight stems and leaves, but markedly increases flower dry weight (experiment 6).

Effects of temperature:

9. In the temperature range studied (9 °C to 24 °C) low temperature promoted bud initiation as determined by the number of leaf pairs (i.e. the lowest number was found at 9 °C). There is no specific effect of day and night temperature (experiments 10, 12).

10. The first microscopically visible flower initiation occurred at a high day temperature in combination with a low night temperature. The opposite

combination gives the strongest retardation of initiation (experiment 12). The same holds true for all subsequent stages of flower bud development (experiment 12), except possible the very latest stage from visible flower colour to anthesis, which appears to be little affected by temperature (experiment 10).

11. Internode growth is promoted specifically by low night temperature (experiments 10, 12). There is no consistent effect of temperature on stem length due to interaction with other factors. Leaf length is promoted by low day temperature, leaf width by low night temperature (experiment 12). Flower dry weight is decreased by high temperature (experiments 10, 11, 17).

12. When plants are subjected to 5 °C, flowers are initiated in the third week. There is no effect of 5 °C on flower initiation (a) when the plants have less than 6 leaf pairs (experiment 15) and (b) when the cold treatment lasts less than 18 days (experiment 14).

13. Any period of 5 °C has an aftereffect on flower bud development, which is accelerated, and on internode length, which is increased (experiments 13, 14).

14. A long photoperiod during the 5 °C treatment promotes flower development when the subsequent photoperiods are short (experiments 13, 16).

15. An interruption of the 5 °C treatment by a period of a higher temperature does not enhance the effect of the cold (experiment 18).

Effects of gibberellic acid:

16. In an experiment of a preliminary nature gibberellic acid promoted flower bud initiation in long day, but not in short day. Flower bud development was retarded in short day and unaffected in long day. Internode length was promoted, but more in long day than in short day.

'Timing' of flower crop:

17. Carnations were planted the year around at two weeks intervals. The shortest time between planting and harvest was 4 months after planting in April, the longest 8 months after planting in September. The shortest time required for the growing of two crops from the same plants was 6 months after planting in April, the longest period 11–12 months after planting between June and October (experiment 21).

18. A pretreatment at 5 °C during three weeks reduced the time to the first crop when the plants were started between July and November, and increased it in plantings between January and June. There was no residual effect of the low temperature on the second crop (experiment 21).

ACKNOWLEDGEMENTS

The author is indebted to the Laboratory of Horticulture, Agricultural University, Wageningen, the Netherlands, for making this study possible.

He acknowledges with gratitude and appreciation the encouragement and advice of Prof. Dr. Ir. J. DOORENBOS during the course of this study.

The University of Cairo, U.A.R. kindly granted the author a study leave to do this research in the Netherlands.

SAMENVATTING

DE INVLOED VAN LICHT EN TEMPERATUUR OP GROEI EN BLOEI VAN DE ANJER (*DIANTHUS CARYOPHYLLUS* L.)

De invloed van licht (zowel intensiteit als belichtingsduur) en temperatuur op een aantal voor de praktijk belangrijke vegetatieve en generatieve kenmerken van de Amerikaanse anjer werden bestudeerd, zowel in kassen als in het Fytotron van het Laboratorium voor Tuinbouwplantenteelt van de Landbouwhogeschool. De gebruikte rassen waren 'William Sim' en 'Keefer's Chéri Sim'.

Effecten van de fotoperiode

1. Een lange fotoperiode doet het aantal bladparen onder de bloem afnemen en versnelt de bloemknopvorming van de microscopisch zichtbare aanleg tot het moment waarop de knop uit de bladeren te voorschijn komt. In de verschillende daglengten vereisten de daarna volgende fasen (van het verschijnen van de knop tot het zichtbaar worden van de bloemkleur en van dit moment tot de bloei) ongeveer hetzelfde aantal dagen (proeven 2, 3, 4, 6 en 7).

2. Een lange fotoperiode leidde tot een aanzienlijke strekking van de internodia (proeven 2, 3, 4, 6 en 7), vermindering van de bladlengte en toename van de bladbreedte (proef 6). De effecten op de bladeren zijn echter niet altijd opvallend en soms niet significant (proef 2). Er werd geen specifiek effect van de fotoperiode op de stengeldikte gevonden.

3. Vanwege de interactie met de lichtintensiteit is er geen duidelijk effect van de daglengte op de bloemgrootte. Er is een gering doch duidelijk effect op het aantal bloemblaadjes, n.l. een toename in lange dag (proeven 4, 6 en 7).

4. Door het kleine aantal internodia is het drooggewicht van stengels en bladeren in lange dag kleiner (proeven 2, 3, 4 en 6). Het drooggewicht van de bloem is in lange dag iets groter dan in korte dag wanneer de lichtintensiteit sterk is (proef 2), maar kleiner wanneer de lichtintensiteit laag is (proef 3).

Effecten van de lichtintensiteit

5. Hoge lichtintensiteiten hebben hetzelfde effect als een lange fotoperiode op de bloemknopaanleg en -ontwikkeling tot het moment waarop de knop tussen de bladeren zichtbaar wordt. Er is geen sterke invloed van de lichtintensiteit op de daarna volgende stadia (proeven 4, 6, 7, 8 en 9).

6. In tegenstelling tot de fotoperiode heeft de lichtintensiteit slechts een gering effect op de internodiumlengte, maar hogere lichtintensiteiten doen de stengeldikte toenemen en evenzo bladlengte- en breedte (proeven 6, 7 en 8).

7. Hoge lichtintensiteiten doen de bloemgrootte en het aantal bloemblaadjes toenemen.

8. Hoge lichtintensiteiten hebben weinig invloed op het drooggewicht van stengels en bladeren, maar doen het drooggewicht van de bloem duidelijk toenemen.

Effecten van de temperatuur

9. In het bestudeerde temperatuurgebied van 9° tot 24°C bevorderen lage temperaturen de knopaanleg, gemeten aan het aantal bladparen (het kleinste aantal werd bij 9°C gevonden). Er is geen specifieke invloed van de dag- en nachttemperatuur (proeven 10 en 12).

10. De microscopisch zichtbare bloemaanleg trad het eerst op bij een hoge dagtemperatuur in combinatie met een lage nachttemperatuur. De tegengestelde combinatie geeft de sterkste verlating van de aanleg (proef 12). Hetzelfde geldt voor alle volgende stadia van bloemknopontwikkeling (proef 12) met een mogelijke uitzondering van het allerlaatste stadium van zichtbare bloemkleuring tot het opengaan van de bloem, dat slechts weinig door de temperatuur schijnt te worden beïnvloed (proef 10).

11. Groei van het internodium wordt in het bijzonder bevorderd door lage nachttemperaturen (proeven 10 en 12). Er is geen duidelijk effect van de temperatuur op de stengellengte als gevolg van interacties met andere factoren. De bladlengte wordt bevorderd door lage dagtemperaturen, de bladbreedte door lage nachttemperaturen (proef 12). Het drooggewicht van de bloem vermindert bij hoge temperatuur (proeven 10, 11 en 17).

12. Na een behandeling bij 5°C worden de bloemen in de derde week aangelegd. Er is geen effect van deze 5°C op de bloemknopaanleg (a) wanneer de plant minder dan 6 bladparen heeft (proef 15) en (b) wanneer de koudebehandeling minder dan 18 dagen duurt (proef 14).

13. Iedere periode met 5°C heeft een na-effect op de bloemknopontwikkeling, die hierdoor wordt versneld, en op de internodiumlengte, die toeneemt (proeven 13 en 14).

14. Een lange fotoperiode gedurende de 5°C behandeling bevordert de bloemknopontwikkeling wanneer de daarna volgende fotoperioden kort zijn (proeven 13 en 16).

15. Onderbreking van de 5°C behandeling met een periode van hogere temperatuur versterkt de invloed van de koude niet (proef 18).

Effecten van gibberellazuur

16. In een orienterende proef bevorderde gibberellazuur de bloemknopaanleg in lange dag, doch niet in korte dag. De bloemknopontwikkeling werd in korte dag vertraagd en in lange dag niet beïnvloed. De lengte van het internodium werd bevorderd, doch in lange dag meer dan in korte dag.

'Timing' van de bloemenoogst

17. Anjers werden het hele jaar door twee-wekelijks uitgeplant. De kortste tijd tussen uitplanten en oogst was 4 maanden na uitplanten in april, de langste 8 maanden na uitplanten in september. De kortste tijd, benodigd voor de produktie van 2 oogsten door dezelfde planten, was 6 maanden na uitplanten in april, de langste 11 tot 12 maanden na uitplanten tussen juni en oktober (proef 21).

18. Een voorbehandeling met 5 °C gedurende drie weken vervroegde de oogst bij uitplanten tussen juni en november en verlaatte de oogst bij uitplanten in januari en juni. Er was geen na-effect van de lage temperatuur op de tweede oogst (proef 21).

REFERENCES

ARTHUR, J. M. and HARVILL, E. K.: Heating and lighting greenhouses with intermittent light. Contr. Boyce Thompson Inst. **10**, 1938: 15–44.

BAILEY, L. H.: Cyclopedia of American Horticulture. The MACMILLAN Company, London **1 (A-D)**, 1904: 247–253.

BARENDSE, G. W. M.: Vernalization in *Cheiranthus allionii* HORT. Meded. Landbouwhogeschool Wageningen **64-14** (1964).

BING, A.: Timing your carnation crop. N.Y. State Flow. Grow. Bull. **172**, 1960: 1–4.

BING, A. and MAIER, O.: Carnation return crops 1951–52. N.Y. State Flow. Grow. Bull. **95**, 1953: 4.

BLAKE, J.: Photoperiodism in the perpetual flowering carnation. Rep. 14th Intern. Hort. Congr. **33**, 1955: 1–6.

BLAKE, J.: Quelques effets de la temperature sur l'oeillet à floraison perpétuelle. Bull. Soc. France Physiol. Vég. **2**, 1956: 169–172.

BLAKE, J.: Normal and abnormal development of the stem apex in carnation. Ann. Bot. N.S. **26 (101)**, 1962: 95–104.

BLAKE, J. and HARRIS, G. P.: Effects of nitrogen nutrition on flowering in carnation. Ann. Bot. N.S. **24**, 1960: 247–256.

BLAKE, J. and SPENCER, R.: The influence of temperature during the light and dark periods on the growth and flowering of the carnation. Rep. 15th Intern. Hort. Congr. 1958: 412–421.

BRIAN, P. W., GROVE, J. F. and MACMILLAN, J.: The gibberellins. Fortschritte der Chemie organischer Naturstoffe **18**, 1960: 351–433.

BUKOVAC, M. J. and WITTWER, S. H.: Gibberellin and higher plants. 1. General growth responses. Quart. Bull. Mich. Agr. Exp. Sta. **39**, 1956: 307–320.

BÜNSOW, R. und HARDER, R.: Blütenbildung von *Bryophyllum* durch Gibberellin. Naturwiss. **43**, 1956: 479–480.

CARR, D. J., MCCOMB, A. J. and OSBORNE, L. D.: Replacement of the requirement for vernalization in *Centaurium minus* MOENCH by gibberellic acid. Naturwiss. **44**, 1957: 428–429.

CEPIKOVA, A. R.: Vernalization of various agricultural plants. Imperial Bureau of Plant Genetics Bull. **17**, 1935: 79.

CHITTENDEN, F. J.: Dictionary of gardening. The Royal Hort. Soc. London **1 (A-Co)**, 1951: 394–399.

CHOUARD, P.: Vernalization and its relations to dormancy. Ann. Rev. Plant Physiol. **11**, 1960: 191–238.

CHROBOCZEK, E.: A study of some ecological factors influencing seedstalk development in beets (*Beta vulgaris* L.). Cornell Univ. Agric. Exp. Stat. Mem. **154**, 1934: 1–84.

DAVIDSON, O. W.: Time required to flower single-pinched carnations. N.J. Plant and Flow. Grow. Bull. **3 (5)**, 1953.

DOORENBOS, J.: Gibberellic acid substitutes for low temperature in certain varieties of *Chrysanthemum*. Coll. Intern. sur le photo-thermopériodisme. Publ. **34**, série B, U.I.S.B., Parma, 1957: 51–54.

DOORENBOS, J.: Het fytotron van het Laboratorium voor Tuinbouwplantenteelt der Landbouwhogeschool. Meded. Dir. Tuinb. **27**, 1964: 432–437.

EBBEN, M. H.: Experiments with gibberellic acid on carnations. A. R. Glasshouse crops Res. Inst, 1957, 1959: 128. Hort. Abstr. **29**, 1959: 2723.

FREEMAN, R. N. and LANGHANS, R. W.: Influence of day and night temperature on carnation. N.Y. State Flow. Grow. Bull. **232**, 1965: 1–3.

GREGORY, F. G. and PURVIS, O. N.: Studies in vernalization of cereals. II. The vernalization of excised mature embryos, and developing ears. Ann. Bot. N.S. **1**, 1938: 237–251.

HALLIDAY, W. G. and WATSON, O. P.: Influence of temperature on the flowering and calyx splitting of greenhouse carnations. Proc. Amer. Soc. Hort. Sci. **61**, 1953: 538–542.

HANAN, J. J.: Influence of day temperatures on growth and flowering of carnations. Proc. Amer. Soc. Hort. Sci. **74**, 1959: 692–703.

HARDER, R. und BÜNSOW, R.: Uber die Wirkung von Gibberellin auf Entwicklung und Blütenbildung der Kurztagpflanze *Kalanchoë blossfeldiana*. Planta **51**, 1958: 201–222.
HARRIS, G. P. and GRIFFIN, J. E.: Flower initiation in the carnation in response to photoperiod. Nature **191**, 1961: 614.
HARRIS, G. P. and HARRIS, J. E.: Effects of environment on flower initiation in carnation. J. Hort. Sci. **37**, 1962: 219–234.
HOLLEY, W. D.: Effect of light intensity on photosynthetic efficiency of carnation varieties. Proc. Amer. Soc. Hort. Sci. **40**, 1942: 569–572.
HOLLEY, W. D.: Crop control for carnations. Color. Flow. Grow. Assoc. Bull. **110**, 1959: 1–4.
HOLLEY, W. D. and BAKER, R.: Carnation production. WM.C. BROWN CO. INC. U.S.A. 1963: 142 pp.
HOLLEY, W. D. and HILL, H. E.: Effect of size of winter crop on yield grade of carnations. Color. Flow. Grow. Assoc. Bull. **136**, 1961: 1–4.
HOLLEY, W. D. and WAGNER, D. L.: Carnation timing from a single pinch. Color. Flow. Grow. Assoc. Bull. **38**, 1952: 1–4.
HONMA, S., WITTWER, S. H. and PHATAK, S. C.: Flowering and earliness in the tomato. Inheritance of associated characteristics. J. Hered. **54**, 1963: 212–218.
KIMURA, K.: Effect of temperature and nutrients on flower initiation of *Raphanus sativus* L. in total darkness. Bot. Mag. Tokyo **74**, 1961: 1361–1368.
KORNS, C. H. and HOLLEY, W. D.: Carnation growth rate follows solar energy. Color. Flow. Grow. Assoc. Bull. **146**, 1962: 1–2.
KREKULE, J: The effect of photoperiod regime on vernalization of winter wheat. Biol. Plant. **3**, 1961: 180–191. Cited after Biol. Abstr. **38**, 1962: 23653.
LANG, A.: Physiology of flowering. Ann. Rev. Plant Physiol. **3**, 1952: 265–306.
LANG, A.: Gibberellin and flower formation. Naturwiss. **43**, 1956: 544.
LAURIE, A., KIPLINGER, D. C. and NELSON, K. S.: Commercial flower forcing. McGraw-Hill book Co., Inc. New York 6th ed. 1958: 509 pp
LAURIE, A. and POESCH, G. H.: Photoperiodism. The value of supplementary illumination and reduction of light on flowering plants in the greenhouse. Ohio Agric. Exp. Sta. Bull. **512**, 1932: 1–37.
LIVERMAN, J. L.: The physiology of flowering. Ann. Rev. Plant Physiol. **6**, 1955: 177–210.
MANRING, J. D. and HOLLEY, W. D.: Optimum temperature for carnations in Colorado. Color. Flow. Grow. Assoc. Bull. **128**, 1960: 1–3.
NELSON, K. S. and KIPLINGER, D. C.: Carnation crop control. Ohio Agric. Exp. Sta. Bull. **756**, 1957: 1–51.
PIERIK, R. L. M.: Regeneration, vernalization and flowering in *Lunaria annua* L. in vivo and in vitro. Meded. Landbouwhogeschool Wageningen **67-6** (1967).
POKORNY, F. A. and KAMP, J. R.: Photoperiodic control of growth and flowering of carnations. Ill. State Flow. Assoc. Bull. **202**, 1960: 6–8.
POLEG, L. and ASPINALL, D.: Inhibition of the development of the barley spike by gibberellic acid. Nature **181**, 1958: 1743–1744.
POST, K.: Effects of day-length and temperature on growth and flowering of some florist crops. Cornell Univ. Agric. Exp. Sta. Bull. **787**, 1942: 1–70.
POST, K.: Florist crop production and marketing. New York Orange Judd. Publ. Co. Inc. 1949: 591 pp.
POST, K.: Florist crop production and marketing. New York Orange Judd. Publ. Co. Inc. 1952: 889 pp.
PURI, V.: The role of floral anatomy in the solution of morphological problems. Bot. Rev. **17**, 1951: 471–552.
PURVIS, O. N. and GREGORY, F. G.: Studies in vernalization. XII. The reversibility by high temperature of the vernalized condition in petkus winter rye. Ann. Bot. N.S. **16**, 1952: 1–21.
RAPPAPORT, L., WITTWER, S. H. and TUKEY, H. B.: Seed vernalization and flowering in lettuce (*Lactuca sativa*). Nature **178**, 1956: 51.
RÜNGER, W.: Licht und Temperatur im Zierpflanzenbau. Paul Parey, Berlin 1957: 163 pp.

SCHMIDT, R. G. and HOLLEY, W. D.: Some effects of night temperature on carnations. Color. Flow. Grow. Assoc. Bull. **93**, 1957: 1–4.
SZENDEL, A. L.: Nutritional and temperature studies in splitting of the calyxes of carnation flowers. Thesis Ph.D. Cornell Univ. Ithaca N.Y. 1938: 128 pp.
THOMPSON, J. MCL: Towards a modern physiological interpretation of flowering. Proc. Linn. Soc. Lond. **156**, 1944: 46–69.
WATERSCHOOT, H. F.: Effects of temperature and daylength on flowering in *Dianthus barbatus* L. Proc. Kon. Ned. Akad. Wet. **C 60**, 1957: 318–323.
WELLENSIEK, S. J.: De physiologie der bloemknopvorming in *Campanula medium*. Proc. Acad. Sci. **C 62**, 1953: 115–118.
WELLENSIEK, S. J.: Vernalization and age in *Lunaria biennis*. Proc. Kon. Ned. Akad. Wet. **C 61**, 1958: 561–571.
WELLENSIEK, S. J.: The interchange of long day by low temperature in *Silene armeria*. Proc. Symp. Praha-Nitra 1964: 299–303.
WHITE, H. E.: The effect of supplementary light on growth and flowering of carnation. (*Dianthus caryophyllus* L.). Proc. Amer. Soc. Hort. Sci. **76**, 1960: 594–598.

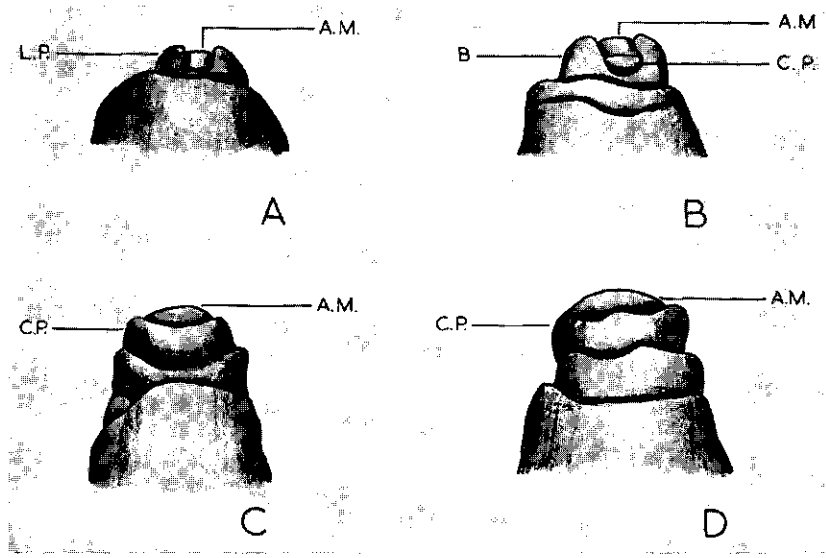

FIG. 1. A. Vegetative apex.
B. Generative apex with calyx primordium.
C. The second stage of calyx initiation, with the teeth becoming visible.
D. A further stage of calyx initiation
A.M. = apical meristem
L.P. = leaf primordium
C.P. = calyx primordium

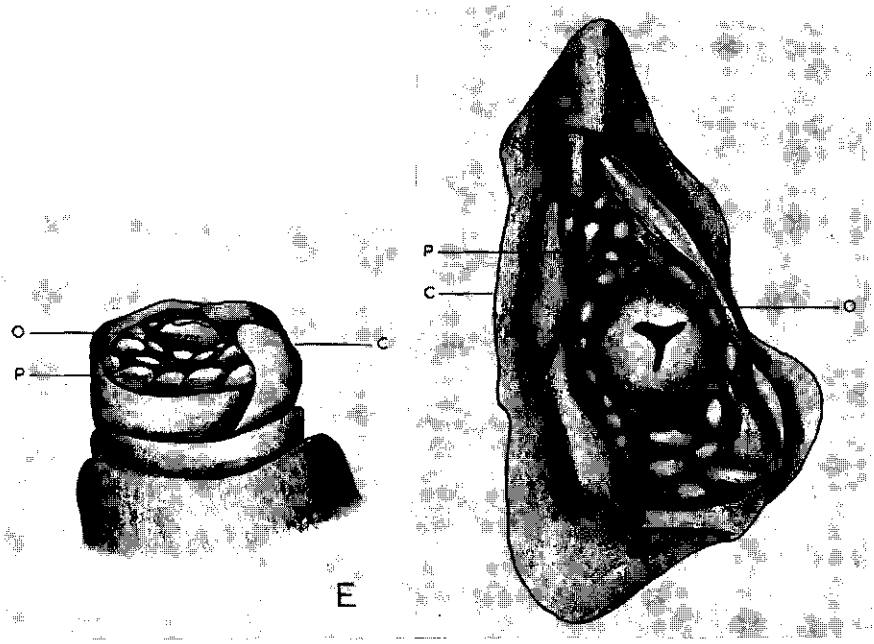

FIG. 2. E. Two apices showing calyx and petal primordia and the beginning of the initiation of the styles.
C = calyx
O = ovary cavity
P = petal primordia

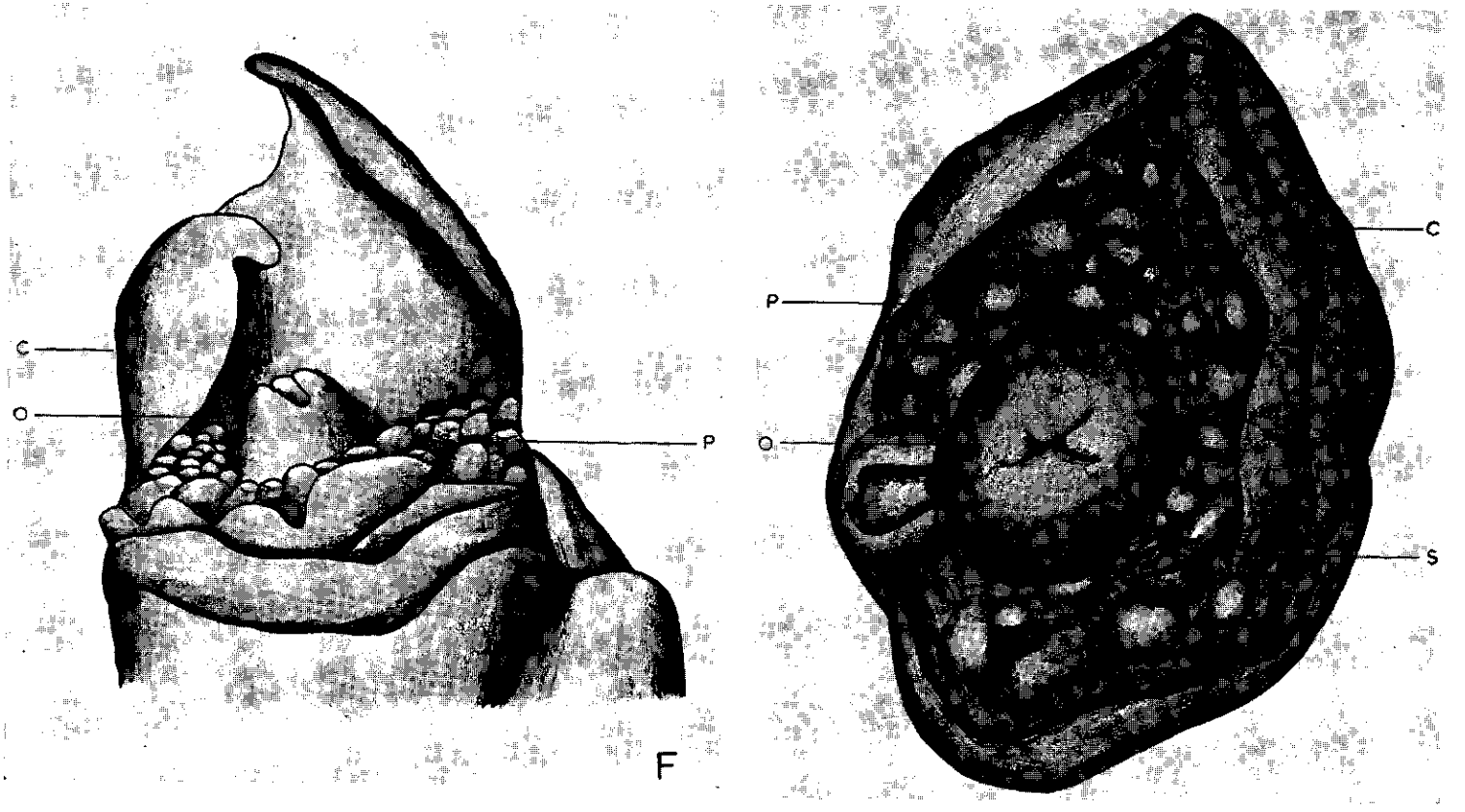

FIG. 3. F. Two apices showing initiation of stamens (S) and styles.

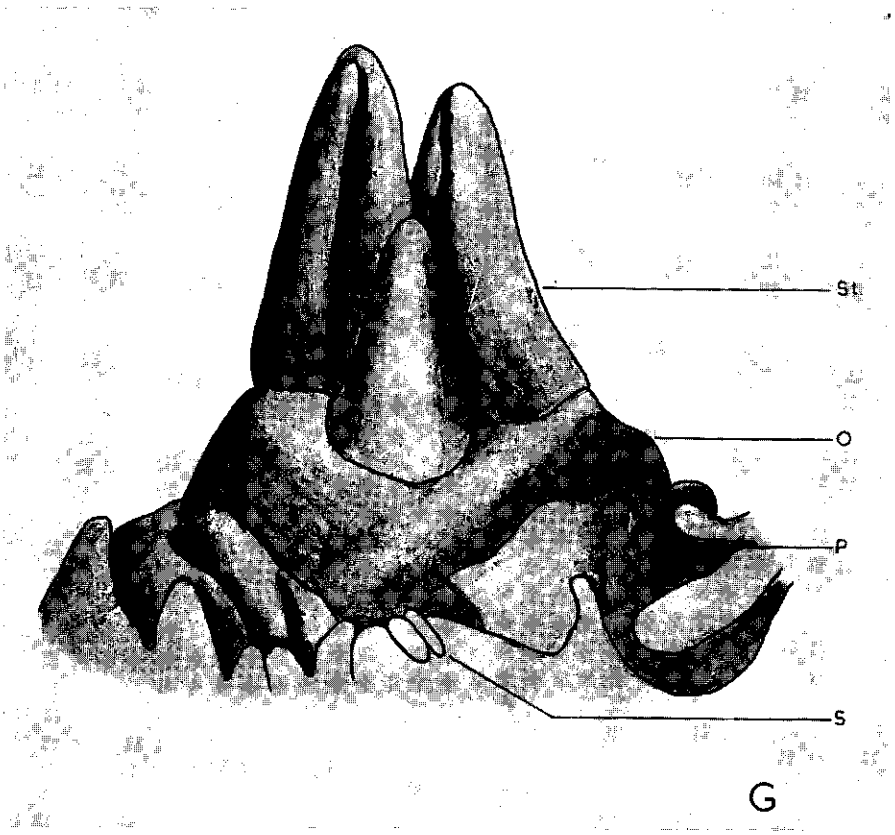

FIG. 4. G. Centre of microscopically visible flower bud, showing style primordia (St).

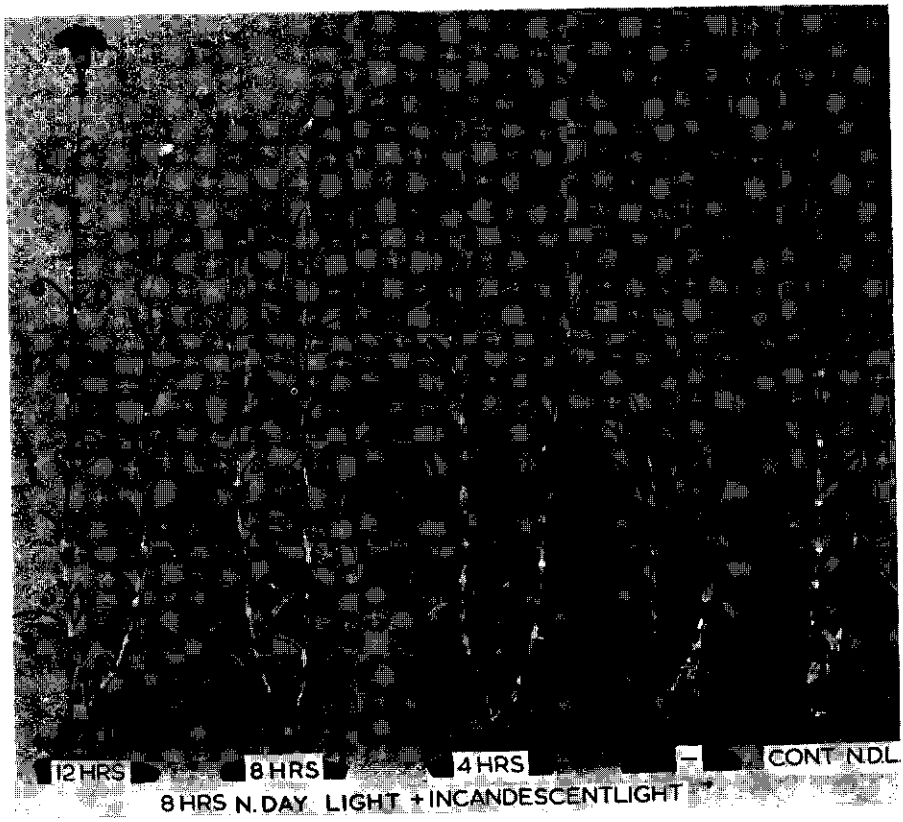

PHOTO 1. Effect of the photoperiod on flowering (experiment 2). In long day (at left) flowering is promoted, the number of leaf pairs is smaller and the internodes are longer.

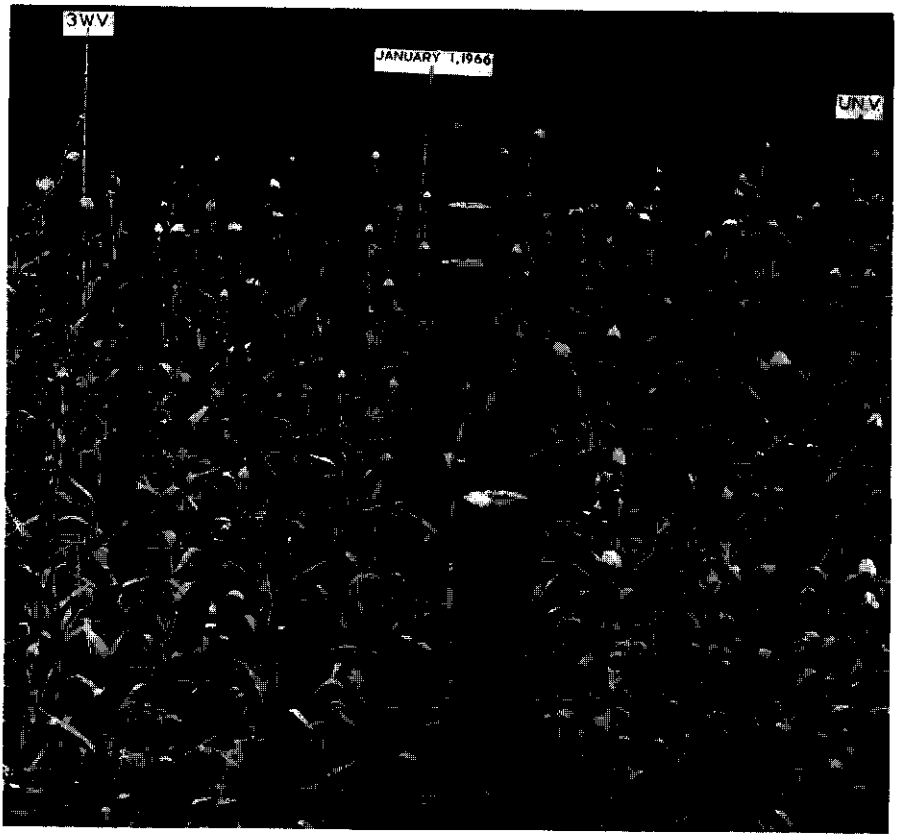

PHOTO 2. Effects of a low temperature pretreatment at various planting dates (experiment 21). After planting on January 1, 'vernalised' and 'unvernalised' plants flower at the same date.

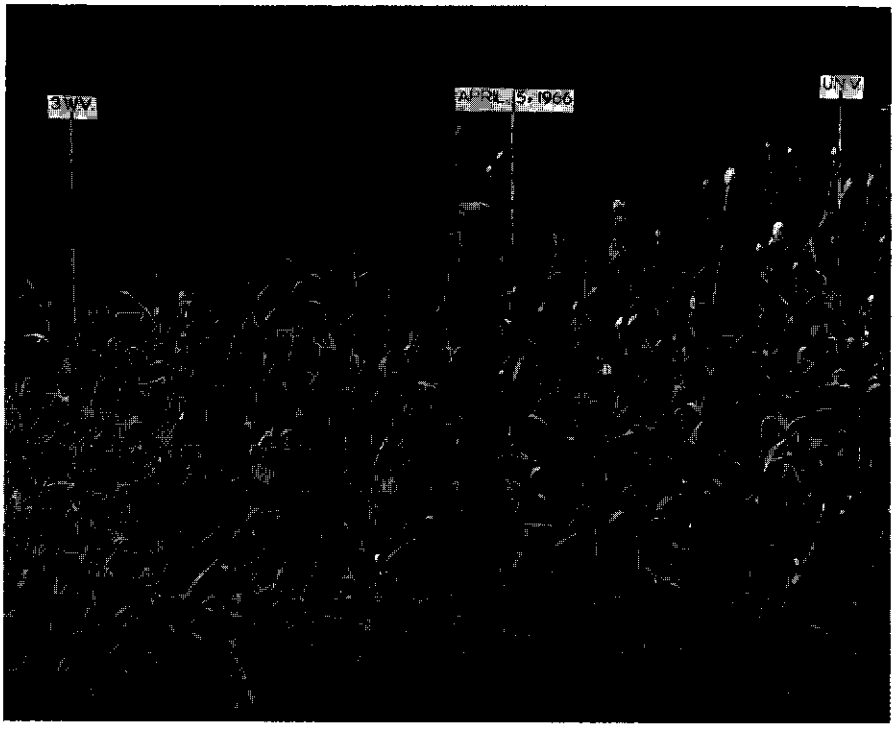

PHOTO 3. As photo 2, but plants started on April 15. The 'unvernalised' plants (at right) are ahead of the 'vernalised' ones.

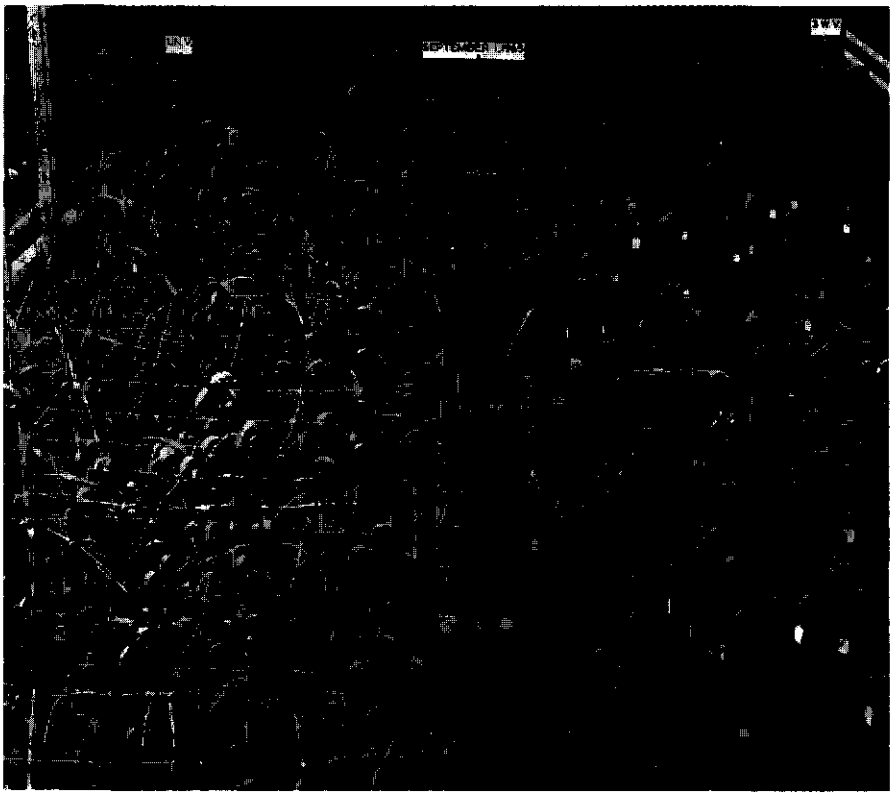

PHOTO 4. As photos 2 and 3, but plants started on September 1. The 'vernalised' plants (at right) flower before the 'unvernalised' ones.