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PHOTOPERIODIC EFFECTS IN *VIGNA UNGUICULATA* (L.) WALP.

(met een samenvatting in het Nederlands)

by / *door*

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CONTENTS

PART I. VEGETATIVE GROWTH

PART II. REPRODUCTIVE DEVELOPMENT

PART III

RELATION BETWEEN VEGETATIVE AND REPRODUCTIVE DEVELOPMENT

CHAPTER I

INTRODUCTION

1. GENERAL OUTLINE

The cowpea [*Vigna unguiculata* (L.) WALP.] is probably one of the most ancient vegetable sources of human food. According to CHEVALIER (17) the plant was first mentioned in Grecian texts 300 B.C., but *Vigna* as a crop plant seems to have existed as early as the neolithic age.

The centre of origin of the cowpea is uncertain. According to BURKILL (14) it is either in Asia or Africa. WIGHT (102) stated that the cultivated cowpea is a native of India, Persia and the southern part of the Trans-Caspian district and that its cultivation extended to China at a very early period. VAVILOV (95) came to nearly the same conclusion as WIGHT (l.c.) in respect of the Asiatic origin of the cultivated cowpeas. He considered India as the primary and China as the secondary centre of origin in Asia; Ethiopia as the centre of origin in Africa. In many papers it is stated, on the authority of PIPER (79), that the cultivated cowpea originated in Central Africa, a statement which is based on a number of wild *Vigna* species from Africa. Wild *Vigna* species are found in Asia as well as in Africa but also in the pastures of Nicaragua (101). Cowpeas may have been carried very early along the ancient coastal and Indian trade routes. At present it is impossible to determine with certainty whether their migration started in Asia, Africa or in both (90).

Although the cultivation of the cowpea in the Old World is of a very early date, the plant was not introduced into the New World before the latter half of the seventeenth century and it probably reached the south of the USA during the first half of the eighteenth century (102). Nowadays cowpeas are grown in New- and Old-World tropics and subtropics where they provide food for millions of people and feed for a vast number of livestock (90).

In Asia and Africa cowpeas are mainly grown in small areas around homesteads, often interplanted with other food crops such as cassava, yam, maize, *Pennisetum* or *Sorghum*. In Africa the most important leguminous crops, in terms of production and food crops, are groundnut, cowpea and Bambarra groundnut (*Voandzeia subterranea*), in that order (90). Not only the dry seeds but also, dependent upon the variety, green pods and seeds or even young leaves may be eaten.

Cultivation on a large scale occurs in the south of the USA, Australia, Southern Rhodesia and South Africa where cowpeas are mainly grown as a fodder crop for domestic animals and also as a cover crop and green manure. Specially selected, edible varieties provide a popular food in Florida and California where freezing and canning have extended their use (63).

The pulse does not enter into international trade and no world production figures are available.

The fact that the cowpea, better than most other leguminous crops (56, 67), succeeds under a great diversity of climatic, soil and cultural conditions, and also its wide use and properties as a human food, make it a principal food crop. Although this was already understood for a long time, little research has been done on the cowpea. Early work on experimental stations consisted mainly in selecting and breeding for improved and disease-resistant varieties.

Later on, foreign introductions have been made for both breeding and propagation purposes. A general improvement of the crop and its cultivation, however, only will be possible through a better understanding of its fundamental requirements for growth and development.

2. REVIEW OF LITERATURE

There is a very limited amount of literature on the physiology of the cowpea. Most of the work done concerns genetics and breeding of improved and disease-resistant varieties. In an article in 1955 on cultural practices in the production of cowpeas LORZ (63) put forth a number of recommendations which were based on commonly adopted cultural methods. He stated that "many of the recommendations doubtless will have to be modified by later research". In fact, one of the most fundamental problems, the choice of suitable climatic conditions for successful crop production, has not been studied yet.

Long before GARNER and ALLARD (28) emphasized the significance of the photoperiod as a factor which may determine the time of flowering, it was already known in the USA that for seed production cowpeas should be sown rather late in the season, *i.e.* towards the shorter days of autumn. When cowpeas were grown for hay, sowing was recommended during the period May 15 to July 15, *i.e.* during the long summer days (3, 72).

Several authors (46, 67, 78) attributed the production of a mass of foliage at the expense of seeds chiefly to rich soils and moist seasons, although the effect of the sowing date was also recognized. Thus, MOOERS (66) at the Tennesee Experiment Station, found that Whippoorwill cowpeas sown at April 15, May 1, May 15, June 4, June 7 and June 29, all became mature on about the same date. The earliest sowing required 183 days to mature whereas the last needed but 101 days. Although factors such as temperature and rainfall may have affected the results, the marked differences in life period must be attributed mainly to daylength effects.

On account of the observation that some tropical varieties did not flower under the prevailing conditions in Virginia, Mississippi or northern Florida PIPER (80) concluded that this was due primarily to the "daylight being too long during the growing season". Even at latitudes where differences in daylength occur of only one hour, an effect of the sowing date was observed. FAULKNER and MACKIE (22), for instance, stated that in Nigeria the right season for sowing cowpeas is July or August, or even September in the south; for if they are planted earlier they produce little or no seed although they may grow very well.

In two publications it has been reported that the growth habit of some varieties may vary with the date of sowing (daylength). This type of varietal behaviour has been reported for the first time by LORZ (*l.c.*). In Florida it was observed that late maturing varieties grown in the greenhouse during winter developed as bunch types. The same varieties sown in the field at the beginning of March produced a few flowers and pods before the onset of the longest day, then stopped flowering, grew vegetatively by producing running vines during the summer and resumed flower and pod production during the shorter autumn days. The second case was reported by LIGON (56). The variety New Era, when sown at the Oklahoma Experimental Station in early May, produced prostrate to semi-prostrate plants, but when planted in late July the plants were of the short-branched bunch type.

In the literature a few experiments have been reported in which cowpeas were exposed to controlled photoperiods. ALLARD and ZAUMEYER (2) exposed plants of the variety Brabham to five photoperiods and obtained a slight short-day response. HEGWOOD and HAMMETT (39), who worked with one variety and two photoperiods, did not obtain any difference in either vegetative growth or flowering. Very marked reactions to the photoperiod have been obtained by NJOKU (75). In his experiments with four Nigerian varieties he observed that in photoperiods of 12 h 45 min or longer no inflorescence primordia became visible within a period of 67 days after sowing, whereas in photoperiods of 11 h 30 min or shorter it was only 30 days before inflorescence primordia appeared. In photoperiods longer than 12 h, however, flower buds never opened and soon abscised. The results obtained in fixed daylengths were compared with those obtained in a date-of-sowing experiment. The results showed clearly that the varieties used were very sensitive to the photoperiod. Only the July to January plantings flowered and fruited. The February and March plantings formed flower buds which did not open. Plants sown in April to June did not initiate inflorescence primordia at all. The observations were done at Ibadan – lat. 7° 26′ N – where the astronomical daylength ranges from 11 h 41 min in December to 12 h 33 min in June.

In spite of the few data available, some preliminary conclusions seem to be justified. The cowpea may be regarded as a short-day plant. The correct sowing date of the crop depends mainly on the plant's sensitivity to the photoperiod, which in some varieties is apparently very high. Inflorescence primordia may be initiated, but further development of the inflorescence does not occur, which suggests a critical daylength for flowering. Some data indicate that both vegetative and reproductive development may be affected by the photoperiod. However, in all these observations of plant behaviour it may well be that non-photoperiodic effects such as photosynthesis and/or temperature have affected the results. Therefore, until results of more extensive experimentation become available, the provisional character of these conclusions has to be emphasized.

3. SCOPE OF THE PRESENT INVESTIGATIONS

In the present work some aspects of the influence of the daylength on flowering and vegetative development have been studied. In some experiments also non-photoperiodic factors such as temperature and light intensity have been considered.

In Part I the experiments on the vegetative growth, mainly stem elongation, are described. Part II deals with the experiments on reproductive development, including inflorescence initiation, inflorescence development and flowering proper. The relation between vegetative and reproductive development and its agricultural implications are discussed in Part III.

CHAPTER II

MATERIAL AND METHODS

1. PLANT MATERIAL

1.1. *Some remarks on the taxonomy*

A brief outline will be presented here of some aspects of the taxonomy of the cowpea which are relevant to the subject dealt with in this work.

Vigna unguiculata (L.) WALP. is a member of the family of the *Papilionaceae*, the largest and most important of the three divisions of the *Leguminosae*.

The genus *Vigna* SAVI, closely related to *Phaseolus* L. and *Dolichos* L., consists of a great many species of which *V. unguiculata* is the main cultivated one. In the literature it has been suggested that the cultivated cowpeas belong to species, sub-species and varieties (see *e.g.* 17, 24, 78, 90). However, it is of little practical importance whether they are considered to belong to one or more species since they can be readily hybridized (78). It is not improbable, therefore, that some (or all) of the cultivated forms are, in fact, hybrids (78).

The classification and nomenclature of cowpeas are very confusing. For example, HALL (32) and FAO (21) list cowpea varieties from different countries partly under the name *Vigna sinensis* (L.) SAVI EX HASSK. and partly under *Vigna unguiculata* (L.) WALP. with as synonym for the latter *Vigna catjang* (L.) WALP. As early as 1912 PIPER (78) stated that since the beginning of the use of binomial nomenclature in botany at least eight specific names had been given to cowpea. Hence the statement of BURKILL (14) "to increase the confusion, other botanists of LINNAEUS' time and immediately after him, added other names". Recently SELLSCHOP (90) traced the taxonomic history of the cowpea. From his study it becomes apparent that the original specimen as described by LINNAEUS has never been found. Therefore, the later taxonomic studies were rejected since all botanists referred to specimens of which it is not known whether they are identical with the type of *Dolichos unguiculatus* as described by LINNAEUS.

SELLSCHOP (*l.c.*) came to the conclusion that "it would be preferable to take as the type LINNAEUS' original description, to admit that a type-specimen had not so far come to light, and that the correct name for the cultivated cowpea is *Vigna unguiculata* (L.) WALP.". According to this author the correctness of this name has been confirmed by the authorities of the Royal Botanic Gardens, Kew (see 90). Therefore, we have used this name to designate the cultivated cowpea. *Vigna sinensis* (L.) SAVI EX HASSK. should be regarded as a synonym.

1.2. *Botanical data*

The cowpea is a rapidly growing, mainly climbing or twining annual herb with a strong tap root which sends out large side roots. The different varieties may show, however, every possible growth habit from perfectly prostrate to tall and bushy forms. With a few exceptions the cowpea continues to grow "indefinitely" provided environmental conditions are favourable.

The smooth stems bear alternating, trifoliate leaves on long petioles subtended by spurred or auricled stipules which protect the young leaves and the apical and axillary meristems of the stem tip. The leaflets are pointed, the terminal one is larger and longer than the asymmetrical lateral leaflets; they are subtended by inconspicuous stipels. Only the two opposite primary leaves of the young seedling are simple.

The "papilionaceous" flowers are arranged in racemose or indeterminate inflorescences at the ends of long stout peduncles which arise in the axils of the leaves. Terminal inflorescences occur but are exceptional. The flowers are borne in alternate pairs, 8 to 12 pairs may occur per inflorescence, but usually only two pairs develop. By preventing the formation of pods, however, each pair of flowers may be forced to bloom in succession. The pedicel of each flower is very short and bears at its base three bracts which are early deciduous. The ten stamens are diadelphous, the vexillar one being free. The sessile ovary is many-ovuled and after fertilization grows out into a pod. The style is longitudinally bearded along the inner side and ends into an oblique stigma. The corollas vary in colour from white or nearly white to pale violet or purple. White flowers are mainly associated with white or partly white seeds. Between the flowers or buds of each pair there is an oblong raised cushion having usually 2 to 8 extra-floral nectaries commonly arranged in a single row and these exude a sweet liquid. The flowers open early in the morning and close before noon. Each flower opens but once, after blooming it wilts and collapses.

Self-fertilization is probably very common among the cowpeas since pollen is shed before the flowers have opened. Inflorescences are often visited by honey bees and bumble-bees which are chiefly attracted by the extra-floral nectaries. During the experiments, however, it was never observed that visiting insects entered the flowers.

The long pods are cylindrical, somewhat curved and usually slightly constricted between the seeds. Most varieties do not shatter their seeds. Some, however, dehisce much more easily than others.

The seeds differ in colour, shape and size. They may be uniformly coloured, spotted, marbled or speckled. Well-known are the types with the second colour concentrated around the hilum such as in the blackeyed and browneyed cowpeas. The shape of the seed may vary from kidney-shaped to globose and is closely correlated with that of the pod. Where the seeds are separate from each other during their development they will become kidney-shaped, whereas in case the seeds are closely crowded they are either globose or compressed when mature. The length of the seeds may vary from 5 to 15 mm but is usually about 9 to 10 mm.

1.3. *Plant material used in the experiments*

A preliminary experiment was carried out with 14 varieties imported from different parts of the world (Table 1, p. 8). Since the plant material supplied by the experiment stations did not always consist of indigenous varieties but sometimes also of foreign varieties, a distinction is made between the origin of each variety and the station from which it was obtained. In addition to the varietal names, their catalogue numbers in the collections of the corresponding experiment stations are also given. In cases where no varietal name is available, the varieties will be indicated by this catalogue number.

2. METHOD OF GROWING COWPEA PLANTS

In the experiments described in this work cowpea plants were grown in the following way.

TABLE 1. Particulars of the varieties used in the experiments

Origin	Variety	Imported from	Cataloguenumber
Nigeria	Ex-Lafia-A	Regional Research Station, Samaru, Zaria, Nigeria.	L 1645
	Ex-Bukuru-A		L 1643
	Banta-B		L 742
	Kananan Wake-A		L 510
India	–	Indian Agricultural Research Institute, New Delhi.	I.C. 2925
	–		I.C. 669
	Kor	USDA, Plant Introduction Section, Beltsville, Maryland.	PI 163142
USA	FC 31705	Landbouwproefstation, Paramaribo, Surinam.	–
	Early Red	Instituto Agronômico do Estado de São Paulo, Campinas, Brazil.	531
Bechuanaland	Going	Mahalapye Experimental Station, Mahalapye, Bechuanaland.	–
	CPM 1		–
Columbia	Ombligo Negro	Estación Agrícola Experimental "Tulio Ospina", Medellin, Columbia.	Tolima 4
	–		Magdalena 9
	–		
South Africa	–	USDA, Plant Introduction Section, Beltsville, Maryland.	PI 221731

Germination of seed and the raising of young seedlings was performed in four stages. Seeds were, if necessary, pretreated, *i.e.* hard seed coats were scarred. Seeds were then placed, with the radicle pointing downwards, in a fine 1/1 sand-soil mixture at a depth of 0.5 cm below the soil surface. The sand-soil mixture was wetted till field capacity and the seed flats were stored for 16 h at 20°C. Subsequently they were transferred to thermostat-controlled cells (temperature 28°C, relative air-humidity 95–100 %). The second day after sowing the seedlings had not yet emerged above the soil surface. Roots of vigorously germinating seeds had already reached a length of 3 to 7 cm at that stage, however. These vigorously germinating seeds were lifted and transplanted into small pots which contained the same soil mixture (the seeds were again covered with 0.5 cm soil, pots were placed in the greenhouse). Two days later the cotyledons were visible. The seedlings were again lifted, soaked in water for about 5 minutes and seed coats were removed. Plantlets were then transplanted in their proper position in pots in the greenhouse.

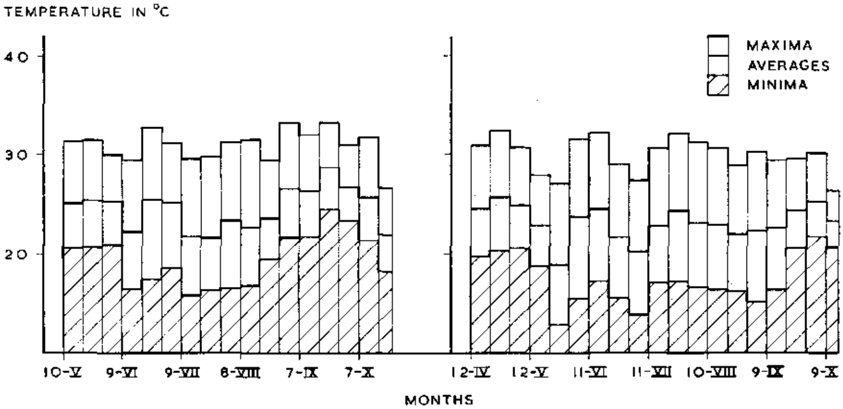
A light sandy soil, thoroughly mixed with some peat, leaf mould and some farmyard manure, was used. Plants were grown individually in pots (contents 2.5 litres) which were dug in cisterns containing the same soil. As a basic dressing one gramme of ammonium nitrate was added to the pots. To prevent roots from growing out of the pots through the drainage hole in the bottom, the pots were frequently lifted during the experiments.

Distances were not kept uniform but depended completely upon the type of experiment and upon the variety used. Usually varieties were grown in rows running north-south but the experiments sometimes made it necessary to deviate from this general practice.

The growth habit of most varieties made it nearly always necessary to support the plants. Plants were either trained along twines hanging from bamboo sticks and tied to the hypocotyl of the plants, or trained along canes.

Photoperiod treatments were applied immediately after the final transplanting. Photoperiods longer than 10 hours consisted of 10 hours natural daylight supplemented with low-intensity light. The supplementary light was partly applied before and partly after the daylight period. Daylight was given from 7 a.m. till 5 p.m. Photoperiods shorter than 10 hours consisted of daylight only. Light treatments were always applied in such a way that 50 % of the photoperiod fell before and 50 % after noon. All photoperiod treatments were based on the 24 h cycle.

All experiments, except those conducted under completely controlled temperature conditions, were carried out in the greenhouse. The temperature in the greenhouse could not be controlled. During spring and autumn minimum temperatures were kept above 15° C by heating. The relative air-humidity was kept above 50 % by means of 6 hygrostat-controlled, centrifugal humidifiers. Temperature and humidity were recorded by a thermo-hygrograph at 40 cm above planting level. For temperature records see Graph 1.



GRAPH 1. Maximum, minimum and average temperatures per 10 days for the seasons 1961 (left) and 1962 (right).

3. THE DARK-ROOM EQUIPMENT

The dark-room equipment consisted of 32 soil-filled metal cisterns mounted on rails for moving them in and out of the eight compartments of a large shed. A different photoperiod treatment could be given to each of the cisterns.

Four strong fans changed the air of the dark rooms twice per minute. The temperature inside the dark rooms was kept at the same level as in the greenhouse.

For controlling the photoperiod supplementary light was used with an intensity of about 6000 erg/sec/cm^2 at 50 cm below the lamps. The light source consisted of two 40 Watt daylight fluorescent tubes (Philips, TLF/55), which were mounted on a panel at 12 cm distance from each other. The tubes could be adjusted for height above the cisterns and were usually kept at about 50 cm from the stem tips. The equipment for supplementary light was operated by electric time switches permitting any combination of photoperiod and nyctoperiod within a cycle of 24 hours.

PART I. VEGETATIVE GROWTH

GENERAL INTRODUCTION

Light may be considered as a decisive factor in plant growth. It supplies the energy required for the assimilation of carbon dioxide in the photosynthetic process. This, however, is not the only function of light in plant growth. Light is also responsible for the normal appearance of plants: it determines, for instance, the height, the size of the leaves, the length of the internodes, and the formation of protochlorophyll.

The effects of light on a green plant can roughly be divided into two groups, which may be distinguished as photo-energetic processes and photo-stimulus processes (97).

Photosynthesis belongs to the first group. The second group consists of a large number of processes, such as tropisms, photoperiodism, stem elongation, leaf expansion, pigment formation, seed germination, which may be subdivided into the movement processes and the formative processes. Generally speaking it can be said that the photo-stimulus processes can be accomplished with relatively low light intensities, whereas photosynthesis requires rather high light intensities in order to obtain measurable responses.

Since GARNER and ALLARD (28) discovered the reaction of plants to the relative length of day and night, photoperiodism in respect of flowering has been one of the most extensively studied formative processes. The term photoperiodism, as used by GARNER and ALLARD (l.c.), covers in addition to flowering, numerous physiological processes which are controlled by the daylength, such as seed germination, pigment and anthocyanin formation, indoleacetic acid oxidase activity, rooting, elongation, leaf expansion, accumulation of food reserves, the onset and breaking of dormancy in perennials, and leaf abscission (see *e.g.* 20, 52, 57, 71, 103).

Although the effect of daylength on vegetative growth was recognized early in the history of photoperiodism (29), this aspect did not receive much attention in later work. The regulation of the vegetative growth of many plants by daylength is clearly demonstrated by the growth of a great many perennials in which the onset of winter dormancy is largely controlled by the photoperiod. There are several more examples. MURNEEK (69), for instance, reported that the growth of the main axis of annuals can be inhibited or retarded by certain photoperiods. He suggested the term photoperiodic inhibition for this phenomenon. Photoperiodic inhibition is, for example, demonstrated in the wild kidney bean, where, under particular daylength conditions, the climbing habit of the bean is changed into a dwarf, bushy growth (1).

These phenomena may be of interest in agricultural and horticultural practice since a promoted vegetative growth may counteract the production of flowers and of seeds, whereas the production capacity of dwarf plants is usually low.

In the present work it has been attempted to investigate the effect of short and long days on growth phenomena of the stem and of individual leaves. In addition, the effects on stem elongation of several other factors, such as light intensity, temperature and gibberellic acid, have been studied.

CHAPTER III

SPECIFIC LIGHT EFFECTS

1. GENERAL OBSERVATIONS

1.1. *Stem elongation*

In a preliminary experiment, in which the 14 varieties mentioned in Table 1, p. 8, were used, plants were exposed to 15 different photoperiods ranging from 6 to 24 h, to investigate varietal differences in photoperiodic response. Per variety and per treatment 6 plants were used. Plant heights were recorded every four to five days from about three weeks after sowing. Stem lengths were measured between the primary leaves and the stem tip. Fifty days from sowing several plants, dependent on photoperiod and variety, had already reached a height of about 2 m and further measurements of stem lengths became impossible. After an additional ten days the experiment was terminated.

Some results on main stem elongation for a number of representative varieties are listed in Table 2. In addition, Table 3 shows some data on internode length for these varieties. These indicate that in general an increase in the length of the photoperiod is associated with an increase in internode elongation until a maximum is reached at photoperiods of 14 to 16 h. At still longer photoperiods internode length remained practically constant. Varietal differences are marked. The variety Ex-Lafia-A formed very short internodes in all photoperiods, but the differences between short and long days were relatively more marked than for the other varieties. Although the internodes of the variety Going are much longer than those of the variety Ex-Lafia-A, yet they can be regarded as rather short. In cowpeas an increase in internode length with increasing photoperiod has been reported earlier by HEGWOOD and HAMMETT (39). It has also been found in sesame (92), *Kalanchoë* (34) and groundnut (23).

TABLE 2. Main stem lengths (in cm) at different photoperiods. Data recorded 46 days (45 days in FC 31705) after sowing. Averages of six plants

Photoperiod *in* hours	Variety				
	Ex-Lafia-A	Going	PI 221731	FC 31705	Kor
7	7.4	29.8	46.6	65.3	64.8
9	12.4	63.6	56.4	117.7	139.3
11	12.3	60.4	60.3	131.5	155.6
13	106.1	99.6	73.2	164.2	156.6
15	114.7	102.8	87.9	170.0	164.1
17½	120.9	110.6	85.6	149.3	162.8
19	116.7	94.3	65.6	145.1	133.9
21½	105.0	102.0	80.0	169.8	142.7
24	108.0	113.6	69.6	161.0	159.4

From the results in Table 2 it appears that in Ex-Lafia-A stem elongation

TABLE 3. Internode length of the main stem in different photoperiods. Total length (in mm) of first 5 internodes. Averages of six plants

Photoperiod in hours	Variety				
	Ex-Lafia-A	Going	PI 221731	FC 31705	Kor
8	48	97	196	218	279
10	46	110	236	269	326
12	69	107	227	250	323
14	69	124	232	293	352
16	68	118	276	309	399
19	71	128	263	326	377
24	86	121	263	326	380

is completely inhibited in short photoperiods. Plants remained very short. The reduced height of PI 221731 in all photoperiods was due to the formation of a terminal inflorescence which prevented further stem elongation. Also in the variety Going the main stem elongation appeared to be controlled by the photoperiod but the plants became much taller than those of the variety Ex-Lafia-A. The two remaining varieties did not show any direct response to the photoperiod. In daylengths shorter than 10 h a reduced height is probably mainly due to a limitation in the photosynthesis which causes a deficiency of assimilates.

The photoperiodic control of stem growth is a well-known phenomenon in many perennials but annuals may also show this behaviour. In the short-day plants Biloxi soybean (68) and *Lespedeza cuneata* (4) stem elongation is abruptly retarded by exposure to a short photoperiod, but the same may occur in long-day plants (27). The opposite response has also been found. DANIELSON (18), for instance, observed that when plants of a day-neutral variety of *Cucumis sativus* were grown in three photoperiods of 8, 12 and 16 h respectively, stem elongation under 16 hours was retarded whereas maximal stem elongation occurred in the 8 h photoperiod.

According to their growth habit the 14 varieties studied in a preliminary experiment (see p. 8) may be classed into four groups, *viz.*:

a. Ex-Lafia-A, Ex-Bukuru-A, Kananan Wake-A and CPM 1.

These varieties are characterized by the phenomenon that in photoperiods of 11 h and shorter, stem elongation is completely inhibited, whereas in longer photoperiods stem elongation continues until fruits are formed and the plants die off. When grown in short photoperiods the plants are of a short-branched bunch type, internodes remain very short (see Table 3) and only 7 to 10 trifoliate leaves are formed on the main stem. In photoperiods of 12 h and longer, however, the plants become twining and produce long winding branches.

A promoted vegetative growth does not necessarily imply non-flowering plants, however. In photoperiods of 12 h plants flowered and fruited although stem elongation only stopped when pods matured. Under our conditions plants of this group never flowered in photoperiods of 13 h and longer.

b. FC 31705, IC 669, Kor, Early Red, Ombligo Negro and Magdalena 9.

Stem elongation is not photoperiodically inhibited but the plants continue to grow until pods mature and the plants die off. In all photoperiods long twining branches are formed and main stems may attain lengths of several metres, while many leaves are produced. The internodes of these varieties are considerably longer than those of the former group (see Table 3).

c. Going and Banta-B.

This group may be regarded as intermediate between the groups (a) and (b). In short photoperiods stem elongation is not completely inhibited, but in comparison with the varieties of group (b) the plants remain much shorter (see Table 2). In short photoperiods the plants are short-branched although the main stem may twine.

d. PI 221731.

The vegetative growth of this variety is limited by the formation of terminal inflorescences. A number of the plants of a different variety, IC 2925, showed a similar behaviour. However, some plants were found in this variety which showed the growth habit of group (b) and did not flower in long days. The apparently genetically very impure variety IC 2925 has not been used in further work. For both varieties it was observed that neither inflorescence initiation, nor the number of trifoliate leaves preceding the initiation of the terminal inflorescence of the main stem, could be affected by any photoperiodic treatment. Both varieties are of the bunch type.

As was already shown for IC 2925, the homogeneity of some varieties left much to be desired. Therefore, further investigations were carried out only with those varieties which were found to be genetically sufficiently homogeneous. For the above groups these varieties are: (a) Ex-Lafia-A and Ex-Bukuru-A, (b) Ombligo Negro, Kor and Early Red, (c) Going, and (d) PI 221731.

The foregoing shows that the varieties belonging to the first group are the most interesting ones in so far as the effect of the photoperiod on stem elongation is concerned. The experiments described in this part will therefore mainly be devoted to the effect of short and/or long days on stem elongation of these particular varieties.

1.2. *Leaf development*

During the preliminary experiment described earlier (p. 11), leaf countings were carried out at regular intervals from about two weeks after sowing. Generally it was found that the rate of leaf production increased with an increase in photoperiod. In daylengths from 6 to 10 h photosynthesis very likely affected growth and thus leaf production. At very short photoperiods growth was probably hampered by a lack of assimilates. From 10 to 14 h the rate of leaf production gradually increased. Thereafter it remained practically constant. In some cases a decrease in leaf number was found in continuous light. This may indicate that continuous illumination is less favourable to the growth of some varieties. However, effects other than the photoperiod may have caused this phenomenon. A few data are presented in Table 4. It seems that, at least to some extent, leaf production is correlated with stem elongation. Without further stem elongation, leaf production becomes impossible. The opposite, *i.e.* further stem elongation without leaf production, has been observed in exceptional cases only.

In Ex-Lafia-A and corresponding varieties, leaf production is limited in photoperiods of 11 h and shorter. As mentioned earlier PI 221731 forms an exception. For the remaining varieties it holds that both leaf production and stem elongation continue until the plants mature.

TABLE 4. The number of leaves on the main stem produced in different photoperiods. Total number of leaves per six plants. Data recorded 44 days after sowing

Photoperiod in hours	Variety				
	Ex-Lafia-A	Going	PI 221731	FC 31705	Kor
7	48	49	49	42	43
9	58	53	50	53	50
11	55	54	53	56	55
13	76	57	49	61	54
15	82	58	54	62	52
17½	81	60	50	61	52
21½	82	58	50	60	51
24	80	58	51	54	50

In order to investigate whether the leaf size was affected by the photoperiod, the area of the fourth trifoliate leaf of plants of the varieties Ex-Lafia-A and Ex-Bukuru-A was measured. The area of the top leaflet and of the entire leaf were determined separately. Since a positive correlation was found between them ($r = 0.97$ and 0.96 for Ex-Lafia-A and Ex-Bukuru-A respectively), only the area of the top leaflet was determined in further work. The number of varieties in which the area of the top leaflet of the fourth trifoliate leaf was determined, was extended with the varieties Going, Kor and Early Red. The results (Table 5) show that daylength exerts a marked influence on leaf expansion. Generally, leaf area increases with increasing photoperiods. In a photoperiod of 24 h, the leaf area decreased in the varieties Kor and Early Red, but increased in the varieties Ex-Lafia-A and Going. Continuous illumination even resulted in a maximum leaf size in the latter two varieties. Leaves were smallest in a photoperiod of 6 h.

TABLE 5. Effect of the photoperiod on the size of the top leaflet of the fourth trifoliate leaf (in cm^2). Averages of six plants

Variety	Photoperiod in hours							
	6	8	10	12	14	16	19	24
Ex-Bukuru-A .	24.2	35.3	41.1	52.4	–	55.0	55.1	54.4
Ex-Lafia-A . .	19.8	24.2	27.3	33.2	33.9	37.4	34.8	41.3
Going.	24.4	35.8	43.4	46.5	53.0	50.6	57.5	61.4
Kor	52.5	68.2	82.2	84.5	89.3	87.7	87.4	83.1
Early Red. . .	53.3	75.1	80.2	96.4	92.8	100.9	100.6	93.8

An increase in leaf area with increasing photoperiods has been reported previously for sesame (92), *Kalanchoë* (34) and other short-day plants (13).

Since photoperiods shorter than 10 h were obtained by using shorter daylight periods, non-photoperiodic effects, probably mainly as a result of a limitation of photosynthesis, may have influenced leaf expansion. The data of Table 5 furthermore indicate that leaves of the varieties Kor and Early Red are much larger than those of the other three varieties. Leaves of Ex-Lafia-A were smallest. It was noticed that varieties belonging to group (b) (see p. 12) are all characterized by large leaves, whereas leaves of the varieties belonging to group (a) and (c) were much smaller.

The effect of the photoperiod on leaf expansion may probably explain the higher rates of leaf production found in long photoperiods. With plants grown in photoperiods of 10 h and longer, all plants received a 10 h daylight period. However, plants grown in "long" photoperiods, 14 h for instance, produced larger leaves than plants grown in *e.g.* a 10 h photoperiod. As a result, the increase in vegetative growth of the "14 h" as compared with the "10 h" plants may be due to differences in photosynthetic output per plant.

In the foregoing it was stated that under exceptional conditions stem elongation proceeded without further leaf development. This phenomenon was only observed in the varieties Ex-Lafia-A and Ex-Bukuru-A in experiments in which stem elongation was promoted either by a long-day treatment prior to short days or by gibberellic acid (see § 2.1 and Chapter IV, § 1). When the variety Ex-Lafia-A was subjected to short days (of 10 h daylight + 1 h supplementary light) following long-day conditions, leafless nodes were formed at the top of the main stem, but unlike with a short-day treatment consisting of 8 h daylight and 3 h supplementary light, the internodes did not elongate. In all other treatments leaves became smaller towards the top of the main stem and finally did not develop any more. Two or three elongated internodes were formed with "bare" nodes.

These observations on the variety Ex-Lafia-A indicate that gibberellic acid has the same effect as a long-day treatment prior to short-day conditions, provided the short days consisted of 8 h daylight only. In both treatments stem elongation was promoted and it continued although further leaf development had stopped. A comparison between the 10 h daylight + 1 h supplementary light and 8 h daylight + 3 h supplementary light treatments shows that the number of leaves decreases with an increase in daylight period, but these differences are negligible when compared with those found for stem elongation (see also Table 11, p. 21). High-intensity light apparently affects stem growth more than leaf growth. Both, however, are inhibited by short days. But with a long-day treatment prior to the short-day condition, stem growth may continue longer than leaf growth.

The above results may be explained in terms of leaf-growth and stem-growth regulators both of which are affected by the photoperiod. Normally short days inhibit stem and leaf growth simultaneously. When short days are preceded by long days apparently leaf-growth regulators are affected more than stem-growth regulators. Leaf growth was always arrested first whereas, dependent on the composition of the light in the short days, stem growth stopped later. This phenomenon, and the formation of longer internodes, are in accordance with the observation that high-intensity light affects stem growth much more than leaf growth. The results obtained with gibberellic acid indicate that stem growth was affected more than leaf growth, which is in accordance with the observation that gibberellic acid could overcome the light inhibition of stem elongation.

In the literature no data were found which could confirm these results on leaf development in the cowpea.

2. ELONGATION OF THE MAIN STEM

2.1. *Effect of short days preceded by long days*

In the preliminary experiment discussed in the preceding section (p. 11) it was found that short days exert an inhibitive and long days a promotive effect on stem elongation. The question may arise whether a short-day treatment will inhibit stem elongation when it is preceded by long days. To investigate this an experiment was conducted with the varieties Ex-Lafia-A and Ex-Bukuru-A. Three lots of plants were sown at 2-week intervals. Immediately after sowing either 0, 14 or 28 long (16 h) days were given. After this treatment the groups, consisting of 20 plants, were placed under short (11 h) days. Main stem lengths and number of leaves were recorded when plants were transferred from long days to short days and when vegetative growth had finally stopped completely under the short-day conditions.

TABLE 6. Effect of a short- (11 h) subsequent to a long- (16 h) day treatment on stem elongation and leaf production. Averages of 20 plants

Variety	Main stem growth in cm and number of leaves produced on the main stem (in brackets) during short days		
	Number of long days prior to short days		
	0	14	28
Ex-Lafia-A	5.4 (7.9)	20.2 (10.4)	17.1 (9.3)
Ex-Bukuru-A	6.9 (6.6)	52.8 (12.1)	60.9 (11.8)

The results (Table 6) indicate that in both varieties a long-day treatment promoted stem elongation during subsequent short days. The first 14 long days were more effective than the following ones. In addition, it should be noted that from sowing it takes at least five days before the young seedlings have unfolded their primary leaves. Therefore, the number of effective long days is smaller than indicated in Table 6, and the actual difference between the first two treatments is only nine days. On the other hand, the data show that short days do exert an inhibitive effect on stem elongation. With an increase in plant age a short-day treatment becomes more effective, in other words, growth stopped more abruptly in short days when the plants were older (*i.e.* when more unfolded leaved were present). This holds in particular for the variety Ex-Lafia-A which proved to be much more sensitive than Ex-Bukuru-A.

The experiment was repeated with the variety Ex-Lafia-A. In this experiment the long-day treatment consisted of 0, 14, 28 and 42 long (16 h) days, given immediately after sowing, and followed by short (11 h) days. Leaf numbers produced in short days were 7.9, 7.0, 4.6 and 3.7 respectively. Although these data do not completely correspond with those obtained earlier, the same trend was found, *i.e.* further vegetative growth decreased with an increase in plant age.

This more abrupt cessation of stem elongation when plants were older may be caused by the fact that the total leaf area of the plants had increased and/or that, at least to some extent, the higher located leaves were much more sensitive to the photoperiod than the lower located ones. No special experiments have been made to separate between these two possibilities, but it seems probable that both contribute to a rapid inhibition of stem elongation.

The differences between the results of the two experiments may probably be attributed to differences in temperature conditions. Temperature can have a marked influence on stem elongation as will be shown in Chapter IV, § 2.

2.2. *Effect of short days preceding long days*

The question may arise whether the inhibitive effect of short days on stem elongation can be overcome by a subsequent long-day treatment. To investigate this an experiment was done with the variety Ex-Bukuru-A. Immediately after sowing plants received 0, 10, 15, 20, 25, 30 and continuous short (11 h) days. After this treatment the plants were transferred to long days (16 h). Each group consisted of 8 plants. Some results are presented in Table 7.

TABLE 7. Effect of a short- (11 h) prior to a long- (16 h) day treatment on stem elongation; variety Ex-Bukuru-A. Averages of eight plants

Number of days after sowing	Main stem length in cm				
	Number of short days prior to long days				
	0	15	20	30	control
23	2.0	1.9	1.6	1.8	1.7
27	3.1	3.0	2.5	2.7	2.6
32	4.9	4.7	4.0	4.1	3.9
35	6.4	6.4	5.1	4.9	4.5
39	15.0	17.2	10.3	9.2	5.4
45	66.5	67.5	46.2	42.2	6.3
49	102.4	100.7	77.8	71.4	6.4

No differences were observed between the treatments with 0, 10 and 15 short days. The treatments with 20, 25 and 30 short days showed a slight retardation in stem elongation which was soon overcome by the subsequent long-day treatment. It appeared that a short-day treatment of 30 days was still too short to inhibit further stem elongation under long-day conditions.

In a second experiment the number of short days prior to long-day conditions was extended to 45. The treatments consisted of 25, 30, 35 and 45 short days given immediately after sowing. At regular intervals leaves on the main stem were counted. The results (Table 8) indicate that, in accordance with the above, further vegetative growth of the main stem was not inhibited after 25 or 30 short days. After 35 short days, however, only three out of eight plants

TABLE 8. Effect of a short- (11 h) prior to a long- (16 h) day treatment on the growth of the main stem. Growth expressed by the number of trifoliate leaves. Variety Ex-Bukuru-A. Averages of eight plants

Number of days after sowing	Number of trifoliate leaves on the main stem				
	Number of short days prior to long days				
	25	30	35	45	control
30	6.1	6.0	6.0	5.8	6.1
55	14.5	10.4	8.6	7.1	8.0
70	26.2	22.5	11.4	7.2	8.0

continued stem elongation, whereas after 45 days further vegetative growth of the main stem was completely inhibited. Within 106 days of sowing no further stem elongation was observed. Removal of either flowers or fruits could not stimulate plants to resume stem elongation.

The effect that after 45 short days growth inhibition could not be reversed by a long-day treatment may be explained by assuming that the leaves formed in short days were photoperiodically induced (see also Chapter V, § 3). Apparently this induction could not, or only very slowly, be reversed by long days. In some treatments growth inhibition even occurred when the transfer from short to long days was made before growth had stopped under short-day conditions. This in spite of the fact that one or two leaves unfolded in long days. Apparently the combined effect of all leaves present remained inhibitive and stem growth was not continued.

2.3. *Leaf sensitivity*

Since stem elongation stops at about 40 days after sowing in short days it was thought that inhibition of stem growth reaches its maximum when the plants have unfolded four or five trifoliate leaves. Leaves produced thereafter apparently do no longer contribute appreciably to the inhibition. To investigate this assumption an experiment was conducted in which the following degrees of defoliation were applied to plants of the variety Ex-Lafia-A:

1. Removal of leaves as soon as they could be distinguished from the buds after the development of the primary leaves.
2. As in 1, but the first trifoliate leaf left intact.
3. As in 1, but four trifoliate leaves left intact.

The number of plants per treatment was 20. The photoperiod was 11 h. Plants were defoliated daily and the number of folded leaves removed was recorded separately for the main axis and the laterals. Although the plants remained very short, leaf production in group (1) and (2) did not stop until the plants flowered and fruited. If flowers and fruits were removed, leaf production continued.

The average number of trifoliate leaves produced on the main axis for group (3) was 9.3, whereas the control plants had formed 8.1 unfolded leaves. In addition, one very young leaf could be removed from the main stems of the control plants. For comparison, however, it is necessary to consider the total of both unfolded and folded leaves. Taking this into consideration, the difference between the plants of group (3) and the control plants is only 0.2 leaves, which is practically negligible. In both treatments vegetative growth had stopped before the plants started flowering and removal of the flowers did not lead to renewed leaf production. From these results and those obtained in the preceding experiments, it seems probable that the leaves are the receptor organs of the short-day effect, which is in accordance with the results reported by NITSCH and NITSCH (74) for perennials.

The inhibition of vegetative growth may be explained by the fact that the inhibitive effect of the leaves increases with the unfolding of each new leaf. Whether this is caused by an increase in total leaf area and/or by an increase in sensitivity of the higher located leaves has not been investigated, but it is likely that both contribute to a rapid cessation of growth.

In all treatments it was observed that defoliation resulted in a complete growth inhibition of the internodes from which the corresponding leaves were removed. In the control plants the internodes which corresponded with the first leaves were fairly long, but in the higher portion of the stem the internodes were short. This may indicate that the leaves exert at least two effects, *viz.* a promotive and an inhibitive effect on stem elongation. With the early formed leaves the promotive effect seems to dominate: the corresponding internodes are relatively long, and when the leaves are removed, internode growth is completely inhibited. With the later formed leaves the inhibitive effect seems to dominate the promotive effect: the internodes corresponding with the later formed leaves are short.

2.4. *Effect of long days on leaf sensitivity*

In the foregoing it was shown that leaves exposed to short days may have been induced to such a degree that induction can be reversed only very slowly or not at all by a long-day treatment. Conversely, leaves exposed to long days may be less readily induced or perhaps completely lose their sensitivity to short days. This would imply that plants with leaves unfolded under long-day conditions (LD-leaves) would stop stem elongation in short days more abruptly when the leaves unfolded in long days were removed than when these leaves were left on the plant. To study this a preliminary experiment was done with ten plants of the variety Ex-Lafia-A, which were grown in 42 long (16 h) days and thereafter transferred to short (11 h) days. From five plants all LD-leaves were removed. After 33 days, when no further stem elongation took place, plants were measured and leaves counted (Table 9).

TABLE 9. Effect of the presence (+) or absence (−) of leaves which have unfolded in long (16 h) days, on stem elongation in subsequent short (11 h) days. "Absence" of "long-day leaves" obtained by removing the leaves at the time of transfer to short days. Variety Ex-Lafia-A. Data recorded 75 days after sowing. Averages of five plants

Experimental data	+	−
Main stem length in cm	80.9	47.5
Total number of leaves produced on main stem .	19.4	20.0

The results show that there was a marked effect of leaf removal on stem elongation. No difference was found in the number of leaves produced. The presence of LD-leaves seems to counteract to some extent the inhibitive effect of a short-day treatment. This might be explained by assuming some or all of the following possibilities:

1. In short days the promotive effect of the leaves unfolded in long days gradually decreases.
2. With an increasing number of induced leaves the inhibitive effect on stem elongation increases.
3. Once leaves have perceived a long-day stimulus they become less sensitive to short days.

The following experiment has been made to investigate the factors mentioned under (1) and (3). Of the variety Ex-Lafia-A three groups of plants, each consisting of 10 plants, were sown at 2-week intervals (see p. 16). After the plants had been exposed to long-day conditions for 14, 28 and 42 days respectively, the groups were placed under short (11 h) days. At the same time five plants of each treatment were defoliated above the last unfolded leaf and newly grown leaves were cut off. Plants were harvested 60 days after the beginning of the short-day treatment. The results (Table 10) indicate that when the plants had been exposed to long days for either 14 or 28 days, removal of leaves formed under short-day conditions could not prevent inhibition of stem elongation. In other words these plants (leaves), were still capable of reacting to short days. Removal of "LD-leaves" did not inhibit leaf production although the newly formed internodes remained very short. This result confirms the data obtained previously, namely that removal of leaves under short-day conditions inhibits internode elongation completely.

TABLE 10. Stem elongation as affected by the removal of leaves formed in short (11 h) days when the latter are preceded by 14, 28 or 42 long (16 h) days. – = leaves formed in short days removed; + = leaves formed in short days not removed. Variety Ex-Lafia-A. Data recorded after 60 short days. Averages of five plants

Recorded data	Number of long days prior to short days					
	14		28		42	
	+	–	+	–	+	–
Number of unfolded leaves on the main stem prior to the short-day treatment	1.0		5.4		9.1	
Total number of leaves formed on the main stem	8.0	25.8	10.0	29.4	12.8	34.0*
Main stem length in cm.	9.7	9.5	21.2	21.0	31.4	85.1*

* Average of two plants.

In the treatment in which the plants were exposed to 42 long days, stem elongation stopped soon after the plants had been transferred to short days. This was not the case with defoliated plants. The latter continued stem elongation for some time but finally also stopped growth.

Considering the plant in its entirety, it will be clear that leaves of different age had been exposed to a different number of long days. Young leaves, exposed to a few long days only, were probably more sensitive to short days than older leaves which had been exposed to more long days. Therefore, it is possible that the youngest leaves exerted an inhibitive, the oldest a promotive effect on stem elongation. Some evidence has been obtained which supports this view. When after 25 short days the two youngest leaves were removed, the remaining leaves appeared to have no inhibitive effect and plants continued stem elongation. After another 35 short days these plants had reached an average height of 213.3 cm against 85.1 cm for the plants which had retained their two youngest leaves. Conversely, removal of the two youngest leaves from plants grown for 28 days under long-day conditions, resulted in an inhibition of stem elongation. In the latter treatment the remaining leaves had apparently retained some sensitivity to short days and could thus inhibit stem elongation under short days.

These results indicate that leaf sensitivity is affected by long days. When plants had been subjected to 42 long days, the oldest leaves had lost their photoperiodic sensitivity or were at least much less sensitive to short-day treatments.

2.5. *Effect of light intensity*

The inhibitive effect on stem elongation of short days subsequent to a long-day treatment may be explained by assuming that short days bring about a lowering of the level of growth-promoting substances and/or a rise of the level of growth inhibitors. It may be questioned whether this inhibitive effect is merely a photoperiodic one, in other words, whether it requires only low light intensities to be accomplished, or whether there is also a high-intensity light reaction. In order to investigate this an experiment was performed in which the effect of two differently composed short-day treatments was investigated.

In the original experiment as described in § 2.1 three lots of 40 plants were grown in a photoperiod of 16 h for 0, 14 and 28 days respectively. After this treatment each lot was divided into two groups: one was placed under short-day conditions of 8 hours daylight and 3 hours supplementary light (8 + 3), the second group received 10 hours daylight and one hour supplementary light (10 + 1). After fruit setting the plants were harvested.

TABLE 11. Effect of the composition of short days on stem elongation and leaf production when the short (11 h) days are preceded by long (16 h) days. Short days based on either 10 hours of daylight (10 + 1) or 8 hours of daylight (8 + 3). Averages of 20 plants

Variety	Recorded data	Number of long days prior to short days					
		0		14		28	
		8 + 3	10 + 1	8 + 3	10 + 1	8 + 3	10 + 1
Ex-Lafia-A	Main stem length in cm	6.2	5.4	59.4	21.2	56.0	21.2
	Number of leaves on the main stem	8.0	7.9	14.2	11.4	15.4	13.5
Ex-Bukuru-A	Main stem length in cm	7.3	6.9	61.5	53.8	68.3	64.9
	Number of leaves on the main stem	7.0	6.6	12.8	13.1	13.7	15.3

For both varieties (Table 11) it was found that plants in (8 + 3) h were always taller than in (10 + 1) h. In the variety Ex-Bukuru-A these differences were small and, proportionally, almost of the same magnitude in all three treatments. In the variety Ex-Lafia-A, plants grown in (8 + 3) h were more than twice as tall as in (10 + 1) h when these short-day treatments were preceded by long days. The differences between the two short-day treatments were small, however, when the short days were not preceded by long days.

It is clearly shown in Table 11 that there is much less inhibition of stem elongation in the variety Ex-Lafia-A if the daylight period of the short-day treatment is decreased with two hours. This effect on stem elongation could not be attributed to an increased number of leaves or postponed flowering and fruiting (*cf.* Chapter VIII, § 1), but was mainly the result of an increased length of the individual internodes. The data suggest that, at least in the variety

Ex-Lafia-A, the inhibitive effect of short subsequent to long days consists of a low-intensity light as well as a high-intensity light reaction. The phenomenon that the latter is very striking only after a preceding long-day treatment, may be explained by assuming that the high-intensity light reaction acts chiefly upon the after-effect of the long days.

The effect of light intensity on stem elongation was also studied in a second experiment. Originally this experiment was carried out to investigate the effect of reduced light intensities on floral initiation (see Chapter VI, § 3). The varieties Ex-Lafia-A and Early Red were used. The photoperiod was 12 h 30 min. This photoperiod is above the optimum for inflorescence initiation in Ex-Lafia-A (*i.e.* inflorescence initiation is markedly retarded as compared with a photoperiod of 11 h). In addition, vegetative growth was much less inhibited. As mentioned earlier (p. 12), stem elongation in the variety Early Red is not inhibited by any photoperiodic treatment.

Light intensities were reduced by using cheese cloth fitted over a metal frame-work. Thus, dependent on weather conditions, the position of the sun and the kind of cloudiness, a reduction in light intensity of 30 to 40 % was obtained. Immediately after sowing three groups, of 12 plants each, were subjected to the following treatments:

1. Shade during the entire daylight period.
2. Shade from 7.00 until 9.30 a.m. and from 14.30 until 17.00 p.m., *i.e.* during 50 % of the daylight period.
3. Daylight intensity not reduced (control).

Leaf countings and stem length measurements were carried out at regular intervals from about three weeks after sowing. When in the Early Red control 8 leaves had unfolded, plants were harvested (49 days after sowing). Ex-Lafia-A, however, was harvested when flowering had stopped and fruits had set (90 days after sowing). The data on main stem elongation and leaf production are presented in Table 12.

A reduction of light intensity promoted stem elongation. At early stages leaves were formed more slowly under low than under high light intensity conditions, but when the experiment was terminated the control plants were always shortest. The effect of a reduced light intensity appeared to be greater in the variety Ex-Lafia-A than in the variety Early Red. At 43 days after sowing the plants of Ex-Lafia-A grown permanently under shade were more than four times as tall as those in the control, and in the variety Early Red twice as tall as in the control. At that stage the differences in the number of leaves amounted at most to one which number cannot account for the differences in the total stem length.

From the data for the variety Ex-Lafia-A at 90 days after sowing it appears that, although stem elongation in the control had stopped early, plants grown permanently in diffuse daylight had continued stem elongation and eventually reached much greater heights. The same holds for the leaf production of this variety. Since inflorescence initiation was not markedly affected (*cf.* Chapter VI, § 3), the differences in vegetative growth must have been brought about directly by differences in light intensities, and not indirectly through differences in the time of inflorescence initiation.

TABLE 12. Effect of reduced light intensity during 0% (0), 50% (50) and 100% (100) of the daylight period on main stem elongation and leaf production; varieties Ex-Lafia-A and Early Red. Photoperiod 12 h 30 min. Averages of 12 plants

No. of days after sowing	Main stem length in cm						Number of leaves on the main stem					
	Ex-Lafia-A			Early Red			Ex-Lafia-A			Early Red		
	0	50	100	0	50	100	0	50	100	0	50	100
31	6.8	6.9	9.7	14.0	18.9	24.4	6.2	5.9	5.7	4.0	3.7	3.5
37	13.5	16.7	30.7	35.2	48.3	73.3	7.2	7.1	6.7	5.0	4.9	4.4
43	21.6	48.9	91.3	67.4	110.5	150.1	9.4	9.9	10.5	6.8	7.2	7.4
90	32.3	125.1	217.9	–	–	–	12.9	19.2	22.3	–	–	–

The results of this and the preceding experiment may be explained by assuming that high light intensities cause a lowering of the level of growth-promoting substances. Apparently the effect of short days following a long-day treatment can be divided into a high-intensity light reaction causing the inactivation of growth-promoting substances, and a low-intensity light reaction in which a growth inhibitor is produced. When the effect of short days subsequent to long days is considered, it appears that when the short day is composed of 8 hours daylight only, the plants will reach greater heights than when 10 hours of daylight are used. Under the latter conditions more of the growth-promoting substances will be inactivated while the same amount of inhibitor is produced as in the case of 8 hours daylight with, as a result, shorter plants.

CHAPTER IV

OTHER FACTORS

1. GIBBERELIC ACID

The most striking and immediate effect of gibberellic acid on plants is an acceleration of shoot growth resulting in increased height. In addition, it is known that the light inhibition of stem growth of many dark-grown plant species can be quantitatively reversed by gibberellin treatments. In Pinto beans it was established that when plants were grown in 50% shade, elongation was 2 to 3 times more rapid than under full sunlight conditions in the greenhouse; this decrease in growth rate as a result of high light intensities could be prevented by gibberellin treatments (59).

Since the results obtained in the preceding experiments resemble to some extent those obtained with Pinto beans, the question arose whether the photoperiodic inhibition observed in some cowpea varieties in short days could also be prevented by gibberellic acid applications. Therefore an experiment was started in which, in addition to Ex-Lafia-A, also the varieties Going, Kor and

Early Red were used. Plants were grown in an 11 h photoperiod. The gibberellin treatment consisted in placing one droplet of an aqueous solution of gibberellic acid (GA_3) on the top of the plants (100 drops = 4.2 cc). Control plants were treated simultaneously with a drop of water. When applications to the top of the plants became impossible, the axil of the youngest leaf was used instead. Treatments started ten days after sowing and were repeated on alternate days until 50 days after sowing. The experiment was started with an arbitrary concentration of 100 p.p.m. of GA_3. It appeared that after four applications the leaves of the treated plants remained smaller than those of the controls. The concentration was therefore lowered to 50 p.p.m.

Eight weeks after sowing, when the plants in all treatments and in the control had started flowering, the experiment was terminated. At that stage vegetative growth had stopped completely in the varieties Ex-Lafia-A and Going. Gibberellin applications, either to the plants previously treated with gibberellic acid or to the control plants, had no effect in these varieties any more.

The results compiled in Table 13 show that gibberellic acid had a striking effect on stem elongation in all the varieties. In Ex-Lafia-A stem elongation has been accelerated much more than in any other variety investigated. Also Going showed a considerable response, but much less than Ex-Lafia-A. Both internode number and elongation were increased. Although the varieties Ex-Lafia-A and Going had stopped stem elongation before the data of Table 13 were obtained, there was no difference in the moment of cessation of stem growth between the treated and the control plants. Both groups, apparently affected by the onset of flowering and fruit setting, had stopped further growth simultaneously.

TABLE 13. Effect of gibberellic acid on main stem elongation and leaf production. Photoperiod 11 hours. Data recorded 56 days after sowing. Averages of 12 plants

Variety	Main stem length in cm		Number of leaves on the main stem	
	$+GA_3$	$-GA_3$	$+GA_3$	$-GA_3$
Ex-Lafia-A . . .	76.7	7.1	9.2	7.9
Going	116.8	23.0	10.5	8.1
Kor	177.4	85.6	10.2	8.8
Early Red. . . .	196.0	76.6	10.3	9.3

It may be concluded that light inhibition of stem elongation can be reversed by gibberellin treatment. The stronger the light inhibition of stem growth, the greater the response to gibberellin. This, however, does not necessarily imply that light affects the level of endogenous gibberellin. The results may be explained as well in terms of an inactivation of the inhibitor produced in short days or by a rise of the level of growth-promoting substances.

2. TEMPERATURE

When the results obtained in the preceding experiments are compared, it becomes apparent that in the variety Ex-Lafia-A stem elongation is not only affected by the photoperiod. Generally the plants became taller, *i.e.* the internodes were longer and more leaves were produced, when night temperatures were high. To give an example, plants grown in spring in a photoperiod of 11 h attained heights of 10 to 12 cm and produced about 10 trifoliate leaves (see

Table 2, p. 11 and Table 4, p. 14). Plants grown in the same photoperiod in summer, when night temperatures were usually lower (*cf.* Graph 1, p. 9), reached heights of only 5 to 6 cm with at most 8 trifoliate leaves (see Table 6, p. 16). In other experiments differences in stem elongation for plants grown under the same photoperiodic conditions were also observed.

To test the influence of different day and night temperatures on stem elongation in a short photoperiod the following experiment was conducted. Plants were grown in cabinets in which light and temperature were controlled. The light source consisted of two high pressure mercury vapour lamps (HO/2000, 450 Watt) and one 150 Watt incandescent lamp. The heat radiation of the lamps was reduced by a 4 cm layer of continuously running water on the top of a glass panel, which forms the ceiling of the cabinet. The average light intensity at 20 cm below the glass panel was about 50,000 erg/sec/cm^2. The light equipment was operated by electrical time switches. The photoperiod used was 11 h. Temperature was thermostatically controlled between 15° and 45°C within 1°C. Different day and night temperatures were obtained by transferring the plants from one cabinet to the other.

Immediately after germination the plants were subjected to the following temperature treatments:

1. A constant temperature of 30°C.
2. A day temperature of 30° and a night temperature of 20°C.
3. A day temperature of 30° and a night temperature of 15°C.

TABLE 14. Effect of different day and night temperatures on main stem elongation and leaf production; variety Ex-Lafia-A. Photoperiod 11 hours

Recorded data	Day/night temperature in °C		
	30/15	30/20	30/30
Number of plants	11	8	12
Main stem length in cm	14.4	37.5	3.0
Number of leaves on the main stem	8.7	7.4	5.3

When flowering started the plants were harvested. The results (Table 14) show that there is a very marked influence of temperature on stem elongation. In plants grown at a constant high temperature stem elongation soon stopped. When the night temperature was lowered to 20°C stem elongation was promoted which could already be noticed before the first trifoliate leaf unfolded. The rate of stem elongation at a night temperature of 15°C was low but plants eventually reached greater heights and produced more leaves than plants grown at a constant high temperature. Leaf production in this case even surpassed the 30/20 treatment. It should be kept in mind that at these relatively low light intensities a constant temperature of 30°C was less favourable for plant growth. It would have been better to use a temperature of about 26°C instead. Nevertheless it can be concluded that stem elongation is favoured by a change in day and night temperature. When night temperatures become too low, the vegetative growth is hampered and the plants remain small.

Although the conditions of this experiment cannot be compared with those prevailing in the greenhouse, the results are in accordance with the observations made during the experiments under greenhouse conditions.

DISCUSSION OF VEGETATIVE GROWTH

The effect of different photoperiods on vegetative growth of a number of cowpea varieties has been studied. In all varieties investigated internode length and leaf area increase in long photoperiods as compared with short ones. Photoperiodically controlled vegetative growth has been found in some varieties. In these varieties short days inhibit vegetative growth completely, whereas in long days plant growth is indeterminate.

Evidence has been obtained that the leaves perceive the photoperiodic impression. Leaves exposed to long days exerted a promotive, leaves exposed to short days an inhibitive effect on stem elongation.

The sensitivity of the plant to short-day conditions increases with the age of the plant, which can be explained by an increase in leaf area and/or by an increase in the sensitivity of the individual leaves. When the plants were exposed to long days prior to a short-day treatment the sensitivity of the leaves had either been lost completely or was very much reduced. In short days leaves could attain a state of induction which was not reversible in subsequent long days.

Reduction of light intensity causes an accelerated stem elongation and plants continued growth longer than those grown in full sunlight in the greenhouse. This light inhibition could be overcome by gibberellic acid, provided it was applied before growth was inhibited. When plants had stopped growth the application of gibberellic acid could not induce renewed growth.

The effect of different day and night temperatures on stem elongation has been studied. The results indicate that a diurnal fluctuation in temperature favoured stem elongation.

Our results suggest that the balance between growth-promoting substances and growth inhibitors plays a role in the growth of certain cowpea varieties. NITSCH (73), who studied the biochemical aspects of photoperiod controlled growth inhibition in the perennial *Rhus typhina*, came to the conclusion that in the shoot tips of this plant both growth promotors and growth inhibitors were present. In short days there occurred a lowering of the level of growth-promoting substances and an increase in the concentration of inhibitors. NITSCH (l.c.) stated that cessation of growth under short days could not be caused by a deficiency in some gibberellin-like substance. Evidence for the presence of growth promotors has been reported by GARAY *et al.* (27). From their experiments with *Lupinus albus* they concluded that IAA*) oxidase activity was high under short-day conditions. In long days an inhibitor would be produced which would affect the enzyme activity, with, as a result, a rise of the native auxin level. The enzyme IAA oxidase inactivates IAA by oxidation (94, 96). Moreover, its activity is known to be controlled by a low energy photoreaction (44) which is apparently typical of the photoreaction controlling photoperiodism and other processes (see 42). Contrary to the view of NITSCH (l.c.) and GARAY *et al.* (l.c.), SHIBAOKA (91) states that the growth-inhibiting effect of light is caused by the direct effect of a growth inhibitor on growth and by its inhibiting effect on the transport of IAA from leaf to stem. The physiological role of gibberellic acid in stem elongation may be visualized as a neutralization

*) IAA = indoleacetic acid

of an inhibitor system which otherwise restricts growth rates to a level below that made possible by the available auxin (11). NITSCH (l.c.) found, however, that when *Rhus typhina* was treated with gibberellic acid under short or long days the level of growth-promoting substances was higher than in untreated plants. These results were confirmed by the findings of PHILIPS *et al.* (77). SÁGI and GARAY (88), who continued the experiments of GARAY *et al.* (l.c.), found no effect of gibberellic acid on the level of the inhibitor or on the activity of IAA oxidase under both short and long days.

Neither our results nor the data in the literature provide convincing evidence for a control of vegetative growth by either growth-inhibiting or growth-promoting substances. A photoperiodic control of the level of inhibitors as well as promotors seems the most likely. A few points may be mentioned. (1) The observation that defoliation under continuous short-day conditions results in a complete growth inhibition of the internodes from which the leaves are removed, whereas non-defoliated plants show at least some elongated internodes, indicates that the leaves produce some growth-promoting substances. These substances are either neutralized or counteracted by growth inhibitors produced in higher located leaves with a higher sensitivity to the photoperiod. (2) The effect of the composition of short days subsequent to a long-day treatment suggests that the high-energy light inactivates more of the growth-promoting substances than the low-energy light. Apparently the short photoperiod has two effects, *viz.* a high-energy light reaction (discussed in the foregoing) and a low-energy light reaction in which an inhibitor is produced.

Summarizing it may be concluded that the photoperiodically controlled growth of some cowpea varieties seems to be caused by a balance between growth promotors and growth inhibitors. The main effect of a short-day treatment seems to be the production of growth inhibitors, whereas in long days the level of growth promotors is raised. The high-energy light effect is present in both short and long days, but its effect is relatively more marked in short than in long days as a result of a low level of growth promotors in short days.

PART II. REPRODUCTIVE DEVELOPMENT

GENERAL INTRODUCTION

In horticultural and agricultural crops which are grown for their fruits or seeds, flowering is a crucial process. But this also applies to the products of market gardening, such as lettuce, spinach and beets, which have commercial value only in the vegetative state. These simple examples demonstrate that the control of flowering may be of extreme importance in agriculture and horticulture.

Flowering as influenced by external factors has since long attracted the attention of many plant physiologists. The extensive experimental work so far done on the physiology of flowering has supplied methods to alter at will floral initiation and the number of flowers produced. Of the external factors governing the transition from a vegetatively growing plant to a flowering one, daylength and temperature are the most important ones.

Prior to the discovery of photoperiodism (see 71), the effect of the duration of the light period on plant development had already been observed by several investigators. It was not until 1920, however, that GARNER and ALLARD (28) obtained conclusive evidence that daylength is a factor of primary importance in flowering. They suggested the term photoperiodism to designate the response of plants to the relative length of day and night. According to the photoperiodic responses three groups of plants were distinguished, *viz.* long-day plants, short-day plants and day-neutral plants.

KNOTT (50), who studied the long-day plant spinach, was the first to establish that green leaves perceive the light-dark stimulus. This finding has been confirmed in later work with other plant species, *e.g.* *Chrysanthemum* (15), *Soya* (81), *Perilla* (58) and many others (see 71).

SACHS (87) postulated the idea that leaves in light produce "flower-forming substances". Many workers have followed this hypothesis. CAJLACHJAN (15), for instance, claimed that a flower-forming hormone, called "florigen" would regulate the flowering process in plants. Nowadays it is generally assumed that the leaves of photoperiodically induced plants produce a flower-inducing stimulus (see *e.g.* 20, 60, 71, 89, 107). Until a few years ago attempts to isolate such a compound had failed or yielded irreproducible results. This led some investigators to postulate a different view, that of the flower inhibition hypothesis, which has been clearly defined by VON DENFFER (19). He suggested that a plant is always capable of flowering, but that flowering may be inhibited by a particular factor which in plants sensitive to the photoperiod would be produced under an unfavourable photoperiod. VON DENFFER (l.c.) further suggested that the flower-inhibiting factor is identical with auxin. WELLENSIEK *et al.* (99) also suggested that the photoperiodic induction would remove an inhibition, but they believe that flower formation is determined by a certain balance between products of photosynthesis and auxin. Studying photoperiodism in plants by means of response curves, BEST (6) came to the conclusion that a combination of the flower-inhibition hypothesis and the flower-hormone hypothesis would be most acceptable.

These hypotheses will not be discussed here in more detail. In our experiments we have thought in general terms of a floral stimulus produced in the leaves of photoperiodically induced plants and transported with the stream of assimilates to the growing point of the plant where it could exert its morphogenetic effect.

In the following chapters an attempt has been made to investigate some aspects of the photoperiodic control of reproductive development in a number of cowpea varieties. The study of reproductive development has been confined to floral initiation and development and some observations on the opening of the flowers.

CHAPTER V

STAGES IN PLANT DEVELOPMENT

1. GENERAL OUTLINE

In Chapter III, § 1, some results of a preliminary experiment in which 14 varieties were exposed to photoperiods ranging from 6 to 24 h have been briefly discussed. In the same experiment data on flowering were recorded. All plants were examined for inflorescence primordia and inflorescences. The average node number where the first inflorescence was found on the main stem was used to express differences in infloresence initiation. For example, when the first inflorescence was borne in the axil of the fourth trifoliate leaf, the node number was four.

The data on inflorescence initiation for eight selected varieties (Table 15) show that responses to the photoperiod may differ greatly. Generally speaking the cowpea may be regarded as a short-day plant, which is in accordance with the data reported in the literature (see Chapter I, § 2).

In the varieties PI 221731, FC 31705 and Ombligo Negro, inflorescence initiation (Table 15) and time of flowering (Table 16) were hardly if at all affected by the photoperiod, but flowering intensity was affected by photoperiods exceeding 13 to 15 h. During the first 10 days of flowering the number of flowers formed decreased in long photoperiods as compared with short photoperiods.

In the varieties Ex-Lafia-A and Ex-Bukuru-A (Table 15) no inflorescence primordia could be detected in photoperiods of 13 h or longer. In a 13 h photoperiod the plants were grown until at least 30 leaves had unfolded. These two varieties apparently are very sensitive to the photoperiod. This could be confirmed in later experiments. The variety Going was slightly less sensitive to the photoperiod than the former two varieties. Throughout the experiment no inflorescence primordia were initiated in photoperiods of 14 h or longer. In the variety Kor inflorescences were initiated in all the photoperiods used, but initiation was markedly delayed in long days.

A completely different reaction was found in the variety Early Red. Floral initiation was markedly delayed by a 15 and a 16 h photoperiod and promoted by both a 10 h and a 24 h photoperiod. These results were confirmed in a second experiment in which 12 plants per treatment were used. This type of photoperiodic response, the so-called ambi-photoperiodic reaction, has been

TABLE 15. Effect of the photoperiod on floral initiation. Averages of six plants

Photoperiod in hours	Average number of the first node with an inflorescence on the main stem							
	Variety							
	Ex-Lafia-A	Ex-Bukuru-A	Going	PI 221731	FC 31705	Ombligo Negro	Kor	Early Red
6	4.7	3.5	4.0	2.7	5.4	9.6	5.0	10.0
7	4.5	3.5	4.2	3.0	4.2	8.8	5.0	9.7
8	4.0	3.2	4.0	2.5	4.0	6.5	4.2	7.7
9	4.8	4.0	3.7	2.5	4.0	3.8	4.3	4.5
10	4.5	3.6	3.8	2.3	4.0	4.2	4.0	4.2
11	4.5	4.0	4.0	2.7	4.0	4.0	4.0	4.8
12	5.8	4.8	3.8	2.8	4.0	4.2	4.0	5.7
13	–	–	5.7	2.7	3.8	4.2	5.2	6.8
14	–	–	–	2.7	4.0	4.0	7.8	10.3
15	–	–	–	3.0	4.0	4.0	15.5	16.3
16	–	–	–	3.0	4.0	3.8	15.8	16.5
17½	–	–	–	2.8	4.0	3.8	15.8	15.7
19	–	–	–	2.8	3.8	5.6	16.3	11.7
21½	–	–	–	2.8	4.0	3.8	16.3	9.0
24	–	–	–	2.3	3.8	4.0	15.2	6.7

TABLE 16. Number of days from sowing until flowering and total number of flowers during the first 10 days of flowering (intensity of flowering) at different photoperiods. Averages of six plants

Photoperiod in hours	Variety					
	PI 221731		FC 31705		Ombligo Negro	
	Number of days until flowering	Intensity of flowering	Number of days until flowering	Intensity of flowering	Number of days until flowering	Intensity of flowering
7	43.7	74	50.6	97	–	–
9	40.5	109	46.7	154	48.4	58
11	41.0	117	44.5	134	47.6	60
13	40.3	116	42.7	125	46.4	61
15	40.0	108	43.8	134	48.5	52
17½	40.7	98	45.2	115	47.7	50
21½	40.0	106	43.3	113	47.8	47

reported earlier by LEWIS and WENT (55) in *Madia elegans* and by MATHON and STROUN (64) in *Setaria verticillata.*

Floral initiation in the varieties Early Red and Ombligo Negro was markedly retarded in very short photoperiods. This delay in initiation may partly be caused by non-photoperiodic effects. In particular photosynthesis, which supplies the plant with energy substrate for normal growth and development, is likely to be deficient in short days. Other non-photoperiodic effects, temperature for instance, may also have affected the results. Apart from the behaviour in the varieties Early Red and Ombligo Negro, differences in inflorescence initiation in photoperiods of 8 to 11 h were rather small which made it impossible to find the exact optimum photoperiod for floral initiation. In the following experiments an 11 h photoperiod was used as a short (inductive) daylength, and a 16 h photoperiod as a long (non-inductive) daylength.

In Chapter III, § 1.2 it was shown that leaf size was markedly affected by photoperiodically active light of low intensities. For an accurate interpretation of the various light treatments it would thus have been necessary to correct the obtained data for non-photoperiodic effects. Such corrections have not been made, however.

Summarizing it can be said that four types of reactions were found, *viz.* (1) varieties which did not flower in long days (Ex-Lafia-A, Ex-Bukuru-A and Going), (2) varieties in which flowering was retarded in long days (Kor), (3) varieties which were practically insensitive to the photoperiod (FC 31705, PI 221731 and Ombligo Negro) and (4) a variety with an ambi-photoperiodic reaction (Early Red).

2. THE JUVENILE PHASE

2.1. *Review of literature*

The life cycle of most plants sensitive to the photoperiod starts with a stage in which the plant is either insensitive or less sensitive to the photoperiod than in later stages. In some plants it is not possible to distinguish such a juvenile phase clearly. A specific type of behaviour is found in a strain of popcorn in which an inflorescence primordium is distinguishable in the embryo before germination (51). Another exception has also been reported for *Arachis hypogaea* L. cv. Schwarz 21, where flower primordia can be detected in the axils of the cotyledons shortly after germination (85). Normally, however, floral initiation is preceded by an initial period of vegetative growth. This apparent necessity for plants to reach a certain size before flower primordia can be formed has already been described by KLEBS (49). He suggested the term "Blühreife" or "ripeness to flower" for the completion of this early vegetative growth. Several investigators have worked out a quantitative expression for this juvenile phase, *e.g.* PURVIS (82), VON DENFFER (19) and ZIERIACKS (108). ZIERIACKS (l.c.) reasoned that a definite area – the critical leaf area – is required for the production of a sufficient amount of floral stimulus.

More recent investigations showed that cotyledons and primary leaves may have a reduced sensitivity to daylength (92, 107) or do not perceive the photoperiodic stimulus at all (47). In addition, it was established that older plants are more sensitive to inductive conditions than younger ones (10, 35, 45). In his experiments with *Perilla crispa* ZEEVAART (107) presented conclusive evidence that the plant's sensitivity to induction increases with each new pair of leaves appearing until the maximum sensitivity has been reached in the fifth or a higher located pair of leaves. Similar results have been obtained by BEST (7) in his experiments with rice. Both authors assume that the insensitive period of plants is due to little or no floral stimulus being produced by the first leaves. According to BEST (l.c.) the juvenile phase may be considered as terminated when the first leaf of maximum sensitivity to the photoperiod attains its full sensitivity. The plant then enters what is called its adult phase in which only fully sensitive leaves are formed.

No data in the literature are known which point to the existence of an insensitive or a less sensitive period in the life cycle of the cowpea. From the results in Table 15 (p. 29) it appears that apart from the variety PI 221731, inflorescence primordia were never found in the axils of the first two trifoliate leaves. In the following sections some experiments will be described, designed with a view to investigate the presence of a less sensitive juvenile period in *Vigna.*

2.2. *The less sensitive period*

To investigate whether the life cycle of the cowpea begins with a period in which the plants are less sensitive to inductive conditions, an experiment was conducted with three varieties, Ex-Lafia-A, Going and Kor. Six groups of plants were sown every other day. The plants were grown for 5, 7, 9, 11, 13 and 15 days under long-day conditions prior to short days. Control plants were of the same age as those which had been grown under 5 long days. The number of the first node with an inflorescence on the main stem was recorded in this experiment.

The results (Table 17) show that in Kor the first 13 short days were practically ineffective. The data obtained after 11 and 13 long days did not differ from the control. After 15 long days, however, when plants had unfolded one trifoliate leaf (*cf.* Table 18) inflorescence initiation was clearly retarded. This may be explained by assuming that the sensitivity of the primary leaves is so low that an adequate level of induction is not reached before the more sensitive first trifoliate leaf has reached this stage. It may also be that the primary leaves do

TABLE 17. Effect of long (16 h) days prior to short (11 h) days on inflorescence initiation. Averages of 12 plants

Variety	Average number of the first node with an inflorescence						
	Days from sowing until the beginning of the short-day treatment						
	0	5	7	9	11	13	15
Ex-Lafia-A . . .	3.7	4.1	6.2	6.7	6.5	8.7	9.7
Going	3.3	3.3	4.1	4.9	4.5	5.2	6.2
Kor	4.1	4.3	4.1	4.7	4.2	4.3	5.2

not perceive the short-day stimulus or that the lower located axillary meristems cannot react to the floral stimulus.

Floral initiation in the variety Going was already retarded when the plants had been exposed to 7 long days prior to the short-day treatment. No difference was obtained between the control plants and the plants grown for 5 days under non-inductive conditions. From Table 18 it appears that when plants after 5 long days were transferred to inductive conditions, the primary leaves were still folded. Consequently, these plants could not have perceived the long days. After 7 days when the primary leaves had unfolded, inflorescence initiation was retarded. It may be concluded that in this variety the primary leaves are already able to perceive the short-day stimulus. The regular increase in the node number of the first inflorescence may indicate that there is no after-effect of the long-day treatment.

TABLE 18. Plant size expressed by the number of unfolded leaves at the time the plants were transferred to short (11 h) days. Where necessary frequencies are given in brackets. p = primary leaves, p + 1 = primary leaves plus one trifoliate leaf, etc.

Variety	Number of days after sowing					
	5	7	9	11	13	15
Ex-Lafia-A .	p (3/12)	p	p	p + 1	p + 1	p + 2
Going. . . .	–	p	p	p	p + 1	p + 1
Kor	p	p	p	p	p + 1 (9/12)	p + 1

A completely different response was found in the variety Ex-Lafia-A. Inflorescence initiation was retarded in all treatments. This indicates that in this variety the primary leaves are already capable to perceive the short-day stimulus. Differences between the treatments with 7, 9 and 11 long days were rather small. Two additional long days, however, caused a marked delay. At the stage at which the plants were transferred to inductive conditions, only the primary leaves had unfolded yet (see Table 18). The trifoliate leaf present after 11 days had just unfolded. It may, therefore, be expected that this leaf had not yet perceived the long-day stimulus. This seems to indicate that in the variety Ex-Lafia-A leaves exposed to long days, lose their sensitivity or become less sensitive to the photoperiod; in other words, an adequate level of induction to evoke inflorescence initiation will not be reached until the next leaf has unfolded. When this is kept in mind, it will become evident why differences between the treatments with 7, 9 and 11 long days were small, whereas on the other hand, a marked difference was found between the treatments with 11 and 13 and those with 5 and 7 long days.

These results point to the fact that there is no completely insensitive period in the life cycle of the cowpea. As to the data on inflorescence initiation in the variety Kor, it is evident that there is a stage in which this plant is less sensitive to the photoperiod.

In the preliminary experiment described in § 1, the results on inflorescence initiation in the varieties Early Red and Ombligo Negro suggested that the plants were not fully sensitive to the photoperiod until the axillary buds were differentiated at about the ninth or tenth node of the main stem. In short days the first inflorescence was initiated at about the fourth or fifth node in these varieties. However, with much variation among individual plants, axillary buds at the fifth to eleventh node were vegetative. Inflorescence primordia were initiated again at all higher located nodes (see Graphs 4 and 5, p. 47 and 48). Since these results could be reproduced in later experiments, it has been assumed that during the period in which the axillary buds were differentiated at the first 10 or 11 nodes, the maximum induction level could not be reached which resulted in possible interruptions in the inflorescence initiation. This phenomenon will be discussed in more detail in Chapter VI.

From the data of Graph 6, p. 50 it can be calculated that the less sensitive period in these two varieties ends at the unfolding of the fourth or fifth leaf, which usually occurs 28 to 30 days after sowing.

The duration of the juvenile phase may vary from a few days as in sesame (92) to periods of over two months as was observed in rice (7). In annuals, however, such long juvenile phases seem to be rare.

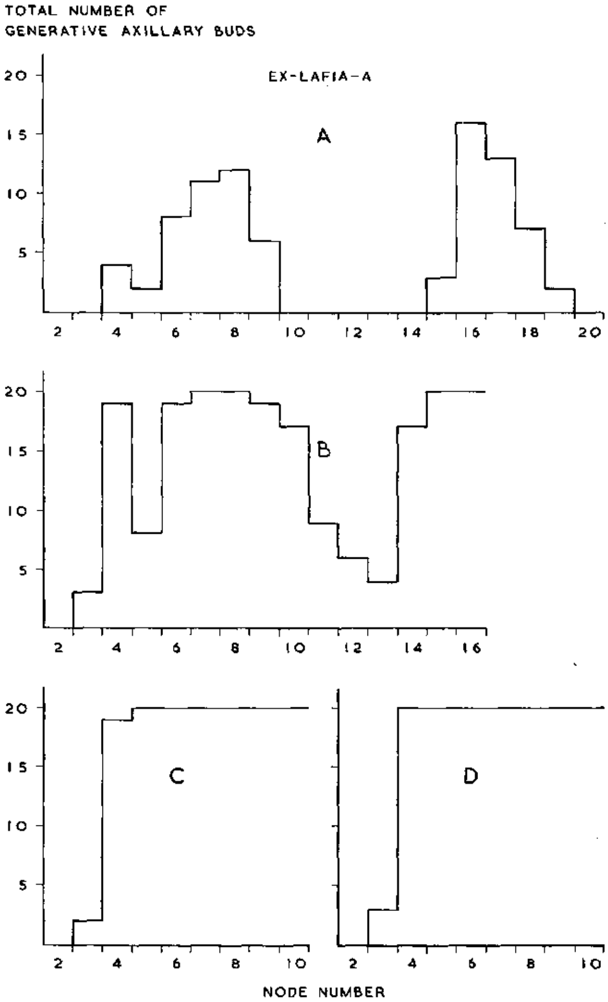
2.3. *The sensitivity of the leaves*

In the foregoing it was concluded that in the varieties Ex-Lafia-A and Going the primary leaves can reach an adequate level of induction for inflorescence initiation. To investigate whether the sensitivity of the plant increases with each new leaf appearing after the primary leaves, plants were grown with increasing numbers of leaves functioning and with all other leaves removed as soon as they became visible. Plants were grown in a photoperiod of 11 h. The following degrees of defoliation were applied to plants of the variety Ex-Lafia-A:

1. The primary leaves left intact and all further leaves removed at their appearance.
2. As in (1) but the first trifoliate leaf also left intact.
3. As in (1) but the first and second trifoliate leaf also left intact.
4. As in (1) but the first three trifoliate leaves also left intact.
5. Control (all leaves left intact).

The number of plants per group was 20.

The leaf axils of the main stem were examined for inflorescence primordia and the results are presented in Graph 2. This graph is obtained by plotting the total number of inflorescence primordia on the ordinate against the node number on the abscissa. For example, a total number of three inflorescence



GRAPH 2. Effect of different degrees of defoliation on inflorescence initiation in plants of the variety Ex-Lafia-A. Inflorescence initiation expressed by the distribution and the number of inflorescence primordia (generative axillary buds) on the main stem. Plants defoliated above the primary leaves (A), or above the first (B), the second (C) or the third (D) trifoliate leaf of the main stem. Data based on 20 plants per treatment.

primordia at node number eight indicates that there were three plants which bore an inflorescence primordium at the eighth node. Consequently, the maximum number of inflorescence primordia (generative axillary buds) in this treatment could never exceed 20 since there were only 20 plants.

When the plants were grown with only the primary leaves left intact (Graph 2/A), inflorescence initiation was very irregular. Inflorescence primordia could be found at the fourth until the ninth node, but the higher located axillary buds were vegetative. Inflorescence primordia could be found also at the 15th node in a few, and at the 16th node in most plants. After this "maximum" at the 16th node, the number of inflorescence primordia decreased rapidly; at higher nodes inflorescence primordia were found in a few plants only. The same tendency was found in plants which had retained the primary leaves plus one trifoliate leaf (Graph 2/B); all plants initiated inflorescences at the nodes 7 and 8 as also at the nodes 15 and 16. However, between the 8th and 15th node, inflorescence primordia were always found in some plants (*cf.* Graph 2). If in addition to the primary leaves two or three trifoliate leaves were left on the plant (Graph 2/C, D), inflorescence initiation did not differ from that obtained in the control plants. The experiment was repeated and yielded similar results.

The interruptions in the sequence of inflorescence primordia may be attributed to non-photoperiodic effects, probably mainly due to high temperatures, which accelerated vegetative growth. This acceleration apparently caused a discrepancy between the rate of development of axillary meristems and the level of floral stimulus, which resulted in vegetative axillary buds. Further examination of these vegetative axillary buds confirmed this supposition. The first axillary bud of these potential laterals was always an inflorescence primordium. Other non-photoperiodic effects, however, such as photosynthesis, may also have affected the results.

Although no investigations were carried out on the sensitivity of individual leaves, it is probably justified to say that the plant's sensitivity to inductive conditions increased with each new leaf appearing until the second trifoliate leaf or even higher located ones. Whether this increase in sensitivity is caused by the increase in total leaf area only or also by the more sensitive trifoliate leaves has not been investigated.

2.4. *Grafting experiments*

It has been reported earlier that, apart from the variety PI 221731, inflorescence primordia were never found at the first two internodes of the plant. This may be explained by assuming that these axillary meristems are already initiated before the plants reach an adequate level of induction. A second possibility is that the lower located axillary meristems could not react to the floral stimulus. To investigate this last point a number of grafting experiments has been carried out. In these experiments seedlings which had just emerged, *i.e.* five days after sowing, were grafted onto stocks obtained from induced plants. Usually the plants to be used as stocks had five to six unfolded trifoliate leaves. Throughout the investigations a modified cleft-grafting was used (see Fig. 1).

In general grafting was carried out as follows. Tops of plants to be used as stocks were removed above the fourth leaf and the scions were inserted in the cleft stems and sealed with self-sealing crepe rubber. Grafting was done in the epicotyl of the seedling. Care was taken that grafting was performed in not too old internodes. Preparation of scions and stocks was done with a razor blade. A high air-humidity around the grafted plants was maintained by means of a wooden frame-work covered with polyethylene, which fitted onto the cisterns. In addition, the pots were placed in the cisterns above a layer of water. When the grafts had taken the pots were placed in soil-filled cisterns where they remained until the experiment was terminated.

In these experiments the primary leaves were left on the scions until grafts had taken. The later developing leaves were removed as soon as they appeared. The grafted plants were grown under inductive conditions until at least 5 or

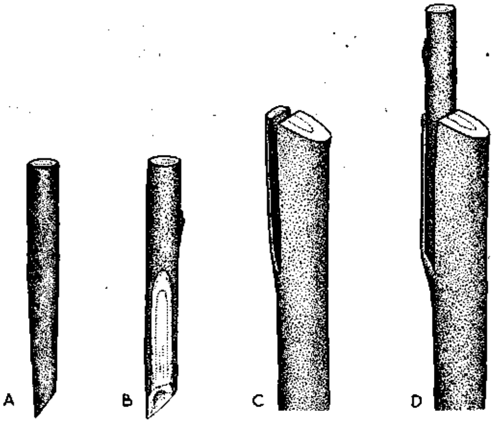


FIGURE 1. Modified cleft-grafting. Schematic drawing of the steps in making the graft-combination. The scions are prepared with long sloping cuts on both sides (A) and a shorter oblique one at the base of the scion (B). The stock is prepared with a short oblique cut at its top. A long shallow, tangential cut is made into one side of the stem (C). The scion is then inserted into the cleft stem so that the cambium layers match at least along one side (D).

6 trifoliate leaves had been removed. The scions were then examined for inflorescence primordia. Two varieties have been used as stocks, *viz.* PI 221731 and Ex-Lafia-A. Seedlings of the varieties PI 221731, Ex-Lafia-A and Kor were grafted onto stocks of PI 221731. For Ex-Lafia-A the scion varieties were PI 221731 and Ex-Lafia-A.

TABLE 19. Grafting of non-induced scions (5-day old seedlings) on inductive stocks. Effect of the graft combination on floral initiation in the scion. Photoperiod 11 hours

Variety		Number of grafts	Number of plants (graft combinations)			
			Node number at which the first inflorescence was found on the scion:			
Scion	Stock		1st	2nd	3rd	4th
Ex-Lafia-A	PI 221731	10	–	1	9	–
Kor		10	2	7	1	–
PI 221731		10	4	6	–	–
PI 221731	Ex-Lafia-A	6	5	1	–	–
Ex-Lafia-A		5	–	–	4	1

The results (Table 19) show that the practically insensitive variety PI 221731 can function as a donor of floral stimulus for photoperiodically sensitive plants. Similar results are known from the literature, *e.g.* day-neutral strains of soybean may induce floral initiation in a short-day strain (40); the same holds for *Gossypium* (52).

Furthermore, the results indicate that the meristems in the axils of the lower located leaves can react to the floral stimulus. Only in a few cases was an inflorescence primordium found in the axil of the first trifoliate leaf. If the variety PI 221731 was grafted onto stocks of either PI 221731 or Ex-Lafia-A a considerable number of scions initiated an inflorescence primordium at the first node. In the variety Ex-Lafia-A, however, it was usually impossible to obtain inflorescence primordia in the axils of the first trifoliate leaves of the scion. In one plant, however, an inflorescence was found in the axil of the second trifoliate leaf. These results may be explained by assuming that the axillary bud of the first trifoliate leaf is already initiated in the seedling before grafting. Microscopical examination of five-day old seedlings confirmed this. In many cases an axillary bud could be observed in the axil of the first trifoliate leaf.

In the variety Ex-Lafia-A it might also be that more floral stimulus is needed to obtain floral initiation in the axils of the lowest leaves than in those of the higher located ones.

As an explanation for the absence of inflorescences in the axils of the first two or three trifoliate leaves in most varieties it may be assumed that it is either due to an inadequate level of floral stimulus at the time of initiation of these meristems or to a lower sensitivity of these meristems to the floral stimulus.

3. PHOTOPERIODIC INDUCTION

3.1. *General*

The term photoperiodic induction covers the changes which take place in plants under the influence of photoperiods and which may lead to floral initiation (52). Photoperiodic induction in plants is thought to involve two processes, both of which are apparently favoured by the same photoperiods in most plants. In some plant species, the so-called short-long-day and long-short-day plants, each stage has a different photoperiodic requirement (6). In many experiments no difference is made between induction and its visible evidence, floral initiation.

In the cowpea the duration of the induction period is usually fairly short in short days. When plants of the varieties Ex-Lafia-A, Ex-Bukuru-A and Going were exposed to short days first and then to long days, it appeared that floral initiation could already be obtained when the plants were transferred to long days 10 days after sowing. In the variety Kor this was 15 days after sowing. When it is considered that the seedlings emerge above the soil about 4 or 5 days after sowing, it follows that the actual induction period in short days does not exceed 5 or 6 days. In the variety Kor this seems to be longer. It has to be kept in mind, however, that Kor has a distinct insensitive period in which the plant does not react to the photoperiod (*cf.* § 2.2). If this insensitive period is also deducted from the 15 short days to which the plant was exposed, it appears that in the variety Kor the induction period is also in the order of 5 or 6 days. Similar short induction periods have also been reported for rice (7). No reference is made in the literature to such a period in cowpea, however.

Under long days the induction takes longer and, provided the variety used is not very sensitive to the photoperiod, inflorescence initiation may take place within a few weeks of sowing. It is not known whether this is achieved by a gradually building up of the induced state in the plant during many cycles or whether the rate of induction becomes more rapid.

3.2. *Effect of long days on subsequent induction in short days*

It was observed in § 2.2 that at least in the early growth stages of the variety Ex-Lafia-A, inflorescence initiation was retarded when the short-day treatment was applied late in the life of the plant. This phenomenon was thought to be brought about by an effect of the long days preceding the short-day treatment. In an experiment to investigate this two groups of plants of the varieties Ex-Lafia-A and Ex-Bukuru-A were grown in a photoperiod of 16 h. The groups, sown at 2-week intervals, were exposed to either 14 or 28 long days prior to the short-day treatment. At the time the plants were transferred to short days, the numbers of unfolded leaves were counted. During the short-day treatment the node number was recorded at which the first generative bud was found.

The data obtained show that the induction period in short days was prolonged when the plants were exposed to long days prior to inductive conditions (the first inflorescence was found higher than would be expected from the differences in vegetative development at the moment inductive conditions started). The experiment was repeated with the varieties Ex-Lafia-A and Going. Plants were exposed to long days for either 14, 28 or 42 days. The data obtained in this and the previous experiment are presented in Table 20. Since the data for the variety Ex-Lafia-A obtained in the first experiment were completely comparable with those obtained in the second one, only those of the latter have been entered in this table.

TABLE 20. Effect of long- (16 h) day treatments (0, 14, 28 and 42 long days) on subsequent induction in short (11 h) days.. Averages of 5 plants (of 20 plants in Ex-Bukuru-A).

Recorded data	Variety										
	Ex-Bukuru-A			Ex-Lafia-A				Going			
	0	14	28	0	14	28	42	0	14	28	42
No. leaves formed prior to the short-day conditions . .	–	1.0	3.5	–	1.0	5.4	9.1	–	1.0	4.0	7.0
No. first node with inflorescence . . .	4.3	9.9	12.4	4.5	10.0	16.0	–	3.0	6.0	11.6	17.0
No. short days until flowering	41.9	34.0	32.7	44.3	37.0	37.4	40.6	44.9	36.2	30.0	28.4

The results, which are in complete accordance with those obtained earlier (see § 2.2), show that the after-effect of long days on subsequent induction in short days is very marked in both varieties, Ex-Lafia-A and Ex-Bukuru-A. In the treatment with 14 long days the plants in all three varieties, Going, Ex-Lafia-A and Ex-Bukuru-A, had unfolded only one trifoliate leaf, but the first inflorescence was found at a much higher located node in the varieties Ex-Lafia-A and Ex-Bukuru-A than in the variety Going. This may indicate that any after-effect of long days in the latter variety is much less marked (the retardation of inflorescence initiation in this variety may be explained by differences in vegetative development when inductive conditions started).

There does not seem to be an effect of the duration of the long-day treatment on induction as the plants flowered almost simultaneously. After 42 long days there was a tendency towards later flowering in the variety Ex-Lafia-A, but this must be attributed mainly to the fact that in this particular treatment vegetative growth was inhibited before an inflorescence could be initiated on the main stem. In the variety Going, however, the plants were the earliest in flowering in the treatment with 42 long days. This seems in accordance with the conclusion that the after-effect of long days is less marked in this variety.

It was assumed in § 2.2 that after an exposure to long days the sensitivity of the leaves to short days was either less or completely lost, but it may also be possible that such leaves are less capable of producing the floral stimulus. An after-effect of long days on induction in short days has been reported earlier for the rice variety Tjina (7). However, no explanation was given for this phenomenon.

To determine more precisely the effect of long days on the duration of the induction period in short days it would have been necessary to determine the number of days to inflorescence initiation. Although microscopical determination of inflorescence initiation is not impossible, this would have met with many difficulties. Inflorescence initiation is not accompanied by macroscopically visible changes in the plant, which implies that a great number of plants would have been required. When the size of the leaves and the growth habit of most *Vigna* plants is taken into consideration, it will be clear that even working with merely one variety would have taken up very much space. Therefore, variation in inflorescence initiation has been expressed by variation in node number. This, however, makes an interpretation of the results more difficult.

4. REPRODUCTIVE DEVELOPMENT

4.1. *General*

In cowpea varieties which do not have a terminal inflorescence, vegetative and reproductive growth may occur side by side. In most cases stem elongation and leaf production continue until maturity. Thus, the same plant may bear pods, flowers and flower buds. In some cases, provided environmental conditions are favourable, even inflorescence initiation may take place although the first pods have already set. When studying the four stages into which the reproductive development may be divided, *viz.* inflorescence initiation, inflorescence development, anthesis and fruit development, one has to take into account the indirect effects from the simultaneously occurring vegetative growth. For example, an apparent effect of the photoperiod on inflorescence development may be brought about indirectly by the vegetative growth which was affected by the photoperiod.

Some experiments have been carried out to investigate the first three stages of the reproductive development. The data obtained on each of these stages will be discussed separately. The fourth stage, pod development, will not be considered here. It should be noted, however, that in our experiments an effect of the photoperiod on pod development has never been observed.

4.2. *Inflorescence initiation*

In the leaf axils buds are borne which may be either vegetative, *i.e.* they represent a lateral branch, or generative, in which case they may develop into an inflorescence. The vegetative buds consist of an apical meristem, 5 or 6 leaf primordia and axillary meristems which are protected by the stipules of the leaf primordia. In a generative bud neither leaves nor stipules are found but bracts protect the first floral structures instead. Outwardly these buds differ greatly from the vegetative ones and both can be distinguished macroscopically. Due to their protective stipules, the vegetative buds have a longer, flatter and more pointed shape than the reproductive ones which are more spherical. Close to the base of both vegetative and generative axillary buds a pair of small, opposite, reduced leaves (prophylls) is found. In the axils of these prophylls buds are present which normally remain dormant but which may be forced to grow out. Usually one of the buds is bigger than the other. These buds – if forced – develop into lateral branches (*cf.* Chapter VII).

In the literature reference has only been made to the above mentioned bud stage (75). However, no published data are available on the inflorescence initiation as determined by microscopic examination.

In order to study the early developmental stages of the axillary meristems, young cowpea plants were dissected under a binocular. The very young axillary meristems were removed by means of dissecting needles and placed on microscope slides. After being heated in a chloral hydrate ($CCl_3COH \cdot H_2O$) solution the meristems were examined microscopically.

Very young axillary meristems are hemispherical in shape. At the base of these structures two small outgrowths soon become visible which are the squamiform prophylls of the bud. The first sign of the initiation of the inflorescence consists of the formation of a shallow groove over the top of the growing point, due to an apparent doubling of the latter. One part – the actual growing point – elongates, whereas at the base of the other part the first bract is initiated. This bract always remains below the top of the growing point. This ostensible doubling of the growing point, together with the formation of the first bract, indicates the initiation of the inflorescence.

In a vegetatively developing axillary bud the doubling does not occur and, instead of a bract, the first trifoliate leaf is differentiated and soon followed by the stipules. At this stage the leaf primordium is always longer than a bract primordium in a generative bud, and extends above the growing point. The growing point elongates, and higher located leaves are subsequently differentiated.

4.3. *Inflorescence development*

Inflorescence development can be defined as the period between inflorescence initiation and the moment at which the first flowers open in the individual inflorescence. Flowering proper and inflorescence development cannot be completely separated, however. The inflorescence of the cowpea is racemose and inflorescence development may continue after the appearance of the first open flowers, provided these flowers are removed (*cf.* Chapter II, § 1.2). Usually only two pairs and at most three pairs of flowers develop before the development of higher located flower buds is arrested. The investigations on inflorescence development are mainly confined to the period between inflorescence initiation and the opening of the first flower.

To study the photoperiodic effects on inflorescence development an experiment was carried out in which plants of the varieties Ex-Bukuru-A and Going were grown for 10, 15, 20, 25 and 30 days under short-day conditions. After this treatment plants were transferred to long days. In all the treatments with both varieties inflorescences had been initiated but they never developed. No peduncle elongation took place and the small flower buds soon aborted (see Photo 1). Sometimes even the entire inflorescence – although small – shrivelled and was abscised. Control plants of the varieties Going and Ex-Bukuru-A flowered after 50 and 44 days respectively. In all treatments vegetative growth had continued (*cf.* Chapter III, § 2.2) which may have caused this failure of inflorescence development.

The experiment was repeated with the same varieties. The short-day treatment consisted of 25, 30, 35 and 45 days prior to long-day conditions. The number of days to flowering and the number of flowers were recorded in each treatment.

TABLE 21. Effect of long (16 h) subsequent to short (11 h) days on inflorescence development. Effect expressed by the number of flowers and the days from sowing until flowering. Averages of eight plants

Number of short days prior to long days	Variety			
	Ex-Bukuru-A		Going	
	Number of flowers	Days from sowing until flowering	Number of flowers	Days from sowing until flowering
25	–	–	4.5*	60.5*
30	–	–	5.3**	63.6**
35	24.5	50.4	3.5**	65.4**
45	50.1	51.0	17.7	58.4
control	49.4	50.4	26.7	57.4

* Average of two plants.
** Average of five plants.

The results (Table 21) show that in the variety Ex-Bukuru-A, flowering was markedly affected by vegetative growth (*cf.* Chapter III, § 2.2). After 25 and 30 short days vegetative growth continued, but inflorescence development was inhibited. However, when further vegetative growth was inhibited, after 45 short days, no difference with the control was found. In the treatment with 35 short days flowering was not retarded but the average number of flowers was much smaller than in the control plants. In this treatment flowering also seemed to have been affected by vegetative growth. The average number of flowers formed on the three plants which had continued stem elongation, was only 14.7 whereas for the remainder an average of 30.4 was found. This is still less than the number of flowers produced in the control. When the location of these flowers was studied, it appeared that only the oldest inflorescences bore open flowers. The subsequently formed ones did not develop and flower buds aborted. This may indicate that the inflorescence development requires inductive conditions until a certain stage of development is reached. Microscopic examination of a number of aborted flower buds showed that all the floral parts had been initiated, but that meiosis had not taken place.

Flowering in the variety Going was very irregular. In the first three treatments only a limited number of plants had flowered, but even in the treatment with 45 short days flowering was markedly affected. This may be attributed to the fact that in the variety Going vegetative growth was promoted in long days in all treatments.

In the variety Going some lateral branches always bore a terminal inflorescence. Closer observation of the flowering plants in the first three treatments revealed that all flowers were borne in terminal inflorescences. From this it was concluded that if vegetative growth would be curtailed by means of shortening and/or removing part of the main stem and the laterals, all the inflorescences could be forced to further development. Some experimental evidence was obtained to support this view. When plants were continuously pruned, all the inflorescences developed and the plants eventually flowered and set fruit. However, these inflorescences differed from those in the control. In the inflorescences of the control plants, the "internodes" of the main axis between the successive flower-bearing "nodes" were usually not longer than about 5 mm. In this treatment, however, they elongated markedly and sometimes attained a length of 75 mm. On the other hand, pruning of the same plants under short days and repeated removal of the flowers did not yield such abnormal inflorescences (see Photo 2).

The same treatments as described above were applied to the variety Ex-Bukuru-A, but as long as new shoots were formed, inflorescences could not be forced to continue their development. After about 90 days the vegetative activity stopped and no further axillary shoots had to be removed. When after 106 days the experiment was terminated, almost all the plants in the treatments with 25 or 30 short days had formed one or two open flowers or some flower buds which would have opened soon. This gives an indication that in the variety Ex-Bukuru-A the inhibition of inflorescence development may have been caused by a high level of growth-promoting substances owing to the long-day conditions (see 105). When after repeated removal of axillary shoots the plants stopped their vegetative activities the flower buds developed but the peduncles did not elongate.

It may also be that inflorescence development is hampered by a lack of floral stimulus, or that the requirement for floral stimulus is higher for development than for initiation of the inflorescence. MURNEEK (70) assumed a quantitative relationship between the production of floral stimulus and flower development. In his experiments with the long-day plant *Rudbeckia* he observed that partial or incomplete photoperiodic induction yielded very short pedicels or sometimes even sessile flowers. A similar relationship has been reported by JOFFE (48) who worked with the long-day plant *Lotus corniculatus*. The appearance of abortive inflorescences, which seems to be characteristic of the latter plant species, as well as the degree of development of the defective buds, as expressed by length of peduncle and size of the buds at abscission, were quantitatively affected by sub-optimal inductive conditions.

To investigate the effect of floral stimulus on the development of inflorescences in the cowpea generative shoots of the varieties Going, Magdalena 9 and PI 221731 were grafted onto vegetative stocks of Ex-Lafia-A. For details of the grafting technique used see p. 35. Part of the grafted plants was grown in long days and part in short days. Scions were kept defoliated. In long days the same phenomena were observed in all combinations: no inflorescence ever developed, whereas in short days inflorescences developed normally. These results may indicate that for inflorescence development floral stimulus is required. The question remains, however, why in the variety Going inflorescences can be forced to develop under long-day conditions, whereas in the variety Ex-Bukuru-A the same technique did not result in the production of open flowers.

A quantitative effect of the floral stimulus on inflorescence development in the cowpea seems likely from the findings of NJOKU (75). In his experiments he observed that the plants flowered only when grown in photoperiods of 12 h and shorter. When the plants were grown in photoperiods of 12 h 15 min and 12 h 30 min they never flowered although inflorescences had been initiated. Inflorescence initiation was inhibited in photoperiods of 12 h 45 min and longer. Similar results were obtained in our experiments when the varieties Ex-Lafia-A and Ex-Bukuru-A were grown in a photoperiod of 12 h 30 min or the variety Going in a photoperiod of 13 h 30 min (see Chapter VI, § 1). The plants of Ex-Lafia-A and Ex-Bukuru-A grown in 12 h and 12 h 15 min flowered, but their vegetative growth was not inhibited. In a later experiment in which Ex-Lafia-A was also grown in a 12 h 30 min photoperiod, inflorescences developed normally and plants flowered, but in this treatment vegetative growth did not continue. These results indeed suggest that inflorescence development in the cowpea depends both on the vegetative growth and the concentration of the floral stimulus.

Inhibition of inflorescence development has repeatedly been observed in the varieties Ombligo Negro, Kor and Early Red in short days. In these varieties inflorescences initiated in the axils of the lower leaves usually did not develop but aborted. The first flower in these varieties was practically never found below the ninth or tenth node. These observations may indicate once more that inflorescence development is affected by the vegetative growth and/or by the level of floral stimulus. The effect of the vegetative growth appears to be an indirect one, for when plants of the variety Going, grown for 30 days under inductive conditions, were transferred to long days and vegetative growth was reduced by means of a constant low temperature (21° C), inflorescence development was inhibited as well. Therefore, it seems likely that inhibition of inflorescence development in long days is caused by a rise of the level of growth substances and/or a lowering of the level of floral stimulus.

4.4. *Anthesis*

In all treatments and in all varieties used it was noticed in our greenhouse experiments, that in the morning when the plants were brought into daylight the flowers had already opened. In those treatments in which the plants were grown in 10 hours daylight, from 7 a.m. until 5 p.m., the flowers usually closed around 9 a.m. However, when plants were moved back to the dark room earlier in the afternoon and thus brought out later in the morning (*cf.* Chapter II, § 2) the flowers closed earlier. Some observations made early in the morning showed that in photoperiods of 10 h and longer flowers opened at about 5 a.m., thus before plants were brought into daylight. These results seem to indicate that there is no effect of the photoperiod on anthesis, for both plants in continuous light (24 h) and plants in short photoperiods (*e.g.* 10 h) flowered simultaneously. This may indicate that the change from high-intensity light (daylight) to low-intensity light (fluorescent tubes) or darkness starts this process.

To investigate possible effects of light and darkness on anthesis, an experiment was conducted with two varieties, Ex-Lafia-A and PI 221731. The plants were grown in the greenhouse in an 11 h photoperiod. Earlier it was observed that in the greenhouse anthesis could be influenced to some extent by low temperatures. To avoid such an effect the experiment was carried out at a constant temperature of 27° C. When anthesis started, plants were transferred to the cabinets as described in Chapter IV, § 2. Plants were exposed to the following periods of light and darkness:

1. Ex-Lafia-A, 10 h high-intensity light (10 p.m. until 8 a.m.).
2. Ex-Lafia-A, 10 h high-intensity light followed by 6 h low-intensity light (10.30 p.m. until 2.30 p.m.).
3. Ex-Lafia-A, 16 h high-intensity light (5 p.m. until 9 a.m.).
4. PI 221731, as in (1).
5. PI 221731, as in (3).

The high-intensity light source consisted of two high pressure mercury vapour lamps (HO/2000, 450 Watt) and one 150 Watt incandescent lamp, yielding a total light intensity of about 50,000 erg/sec/cm^2 at plant level, 20 cm from the glass panel. Low-intensity light was supplied by the incandescent lamp with a light intensity of 4500 erg/sec/cm^2.

The first observations were made five days after the plants had been transferred to the controlled conditions. The plants were examined every hour for open flowers. In the following days observations were made every 15 minutes, if necessary. During the dark period examination was carried out by means of a safe-light (monochromatic green), thus avoiding any other light effect. Open flowers were removed during the light period. The data collected on anthesis during four successive days are presented diagrammatically in Fig. 2. In order to facilitate a comparison between the different treatments the time scales have been chosen in such a way that zero in all treatments represents the moment when plants entered the dark period.

The results indicate that under the prevailing conditions of light and temperature, the change from light to darkness determined the moment of opening of the flowers. In treatments (2) and (3) there was no difference in the effects of high-intensity and low-intensity light. When the light period was 10 h – treatments (1) and (4) – all flowers were open 12 h after the plants had entered darkness. In treatments (2), (3) and (5), where the photoperiod was 16 h, anthesis appeared to be accelerated by 1 h 30 min in the variety Ex-Lafia-A and by 2 h in the variety PI 221731. This is probably due to the fact that the dark period was shorter than 12 h, and consequently the flowers had not yet opened when the plants came into the high-intensity light.

To some extent the results obtained in this experiment correspond with the observations made in the greenhouse. There was one difference, however. In the greenhouse anthesis appeared not to be affected by the supplementary light, whereas in the experiment with the variety Ex-Lafia-A no difference was found between high-intensity and low-intensity light; in the latter case plants only reacted to the change from light to darkness. Anthesis is apparently affected by a very considerable drop in light intensity, *e.g.* in the greenhouse from daylight to low-intensity lamp light, or, as in the experiment under controlled conditions,

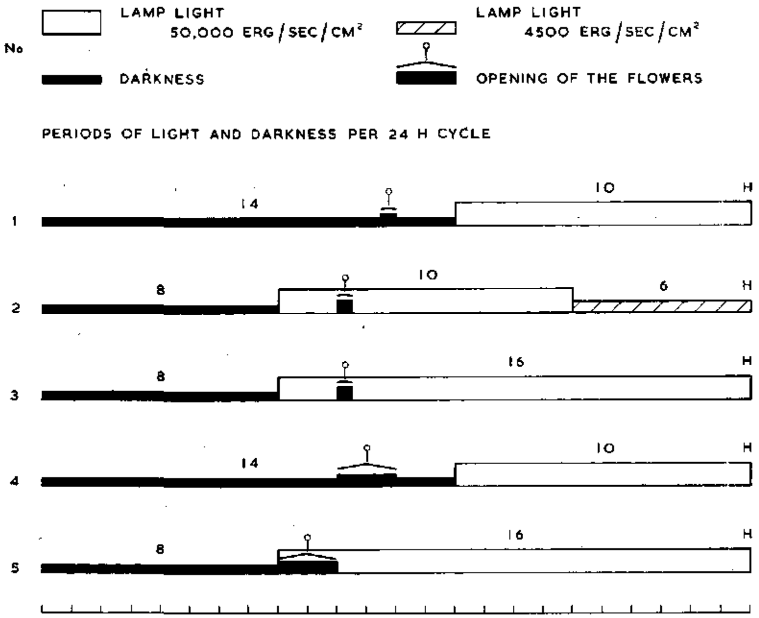


FIGURE 2. Effect of duration and intensity of illumination on the time of anthesis; varieties Ex-Lafia-A (1, 2 and 3) and PI 221731 (4 and 5).

from lamp light to darkness, but not from high-intensity to low-intensity lamp light. It may also be that the different reactions were caused by differences in light quality. The light from an incandescent lamp as compared with that from the fluorescent tubes used in the greenhouse contains more red and infrared. Especially these parts of the spectrum are known to be most effective in photo reactions (see *e.g.* 42).

In *Arachis hypogaea* the opening of the flowers has been reported to be inhibited in continuous light, but flowers opened soon after they had been exposed to a period of darkness (23). In the literature only a few studies on the effect of light on anthesis have been reported. In several plant species morning anthesis was found to be inhibited by illumination during the night (see 43).

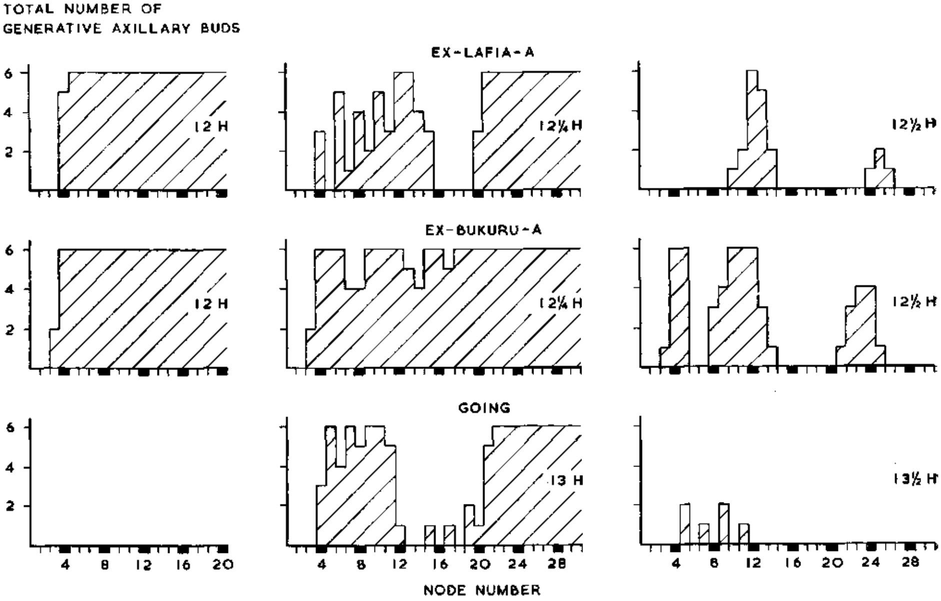
CHAPTER VI

DISTURBANCE IN FLORAL INITIATION

1. GENERAL

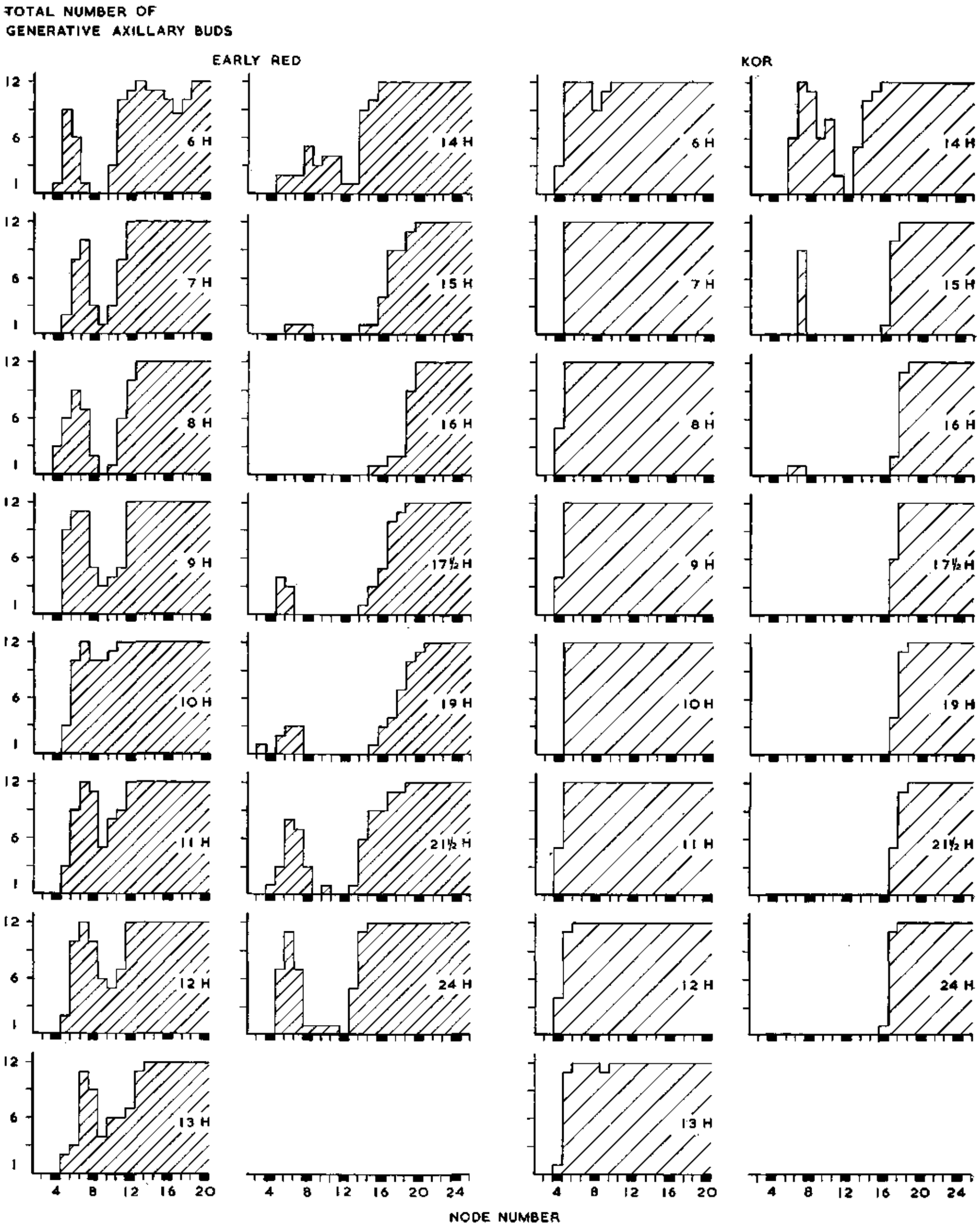
In Chapter V, § 1, some results of a preliminary experiment on floral initiation have been discussed. It was found that in the course of the experiment the varieties Ex-Lafia-A and Ex-Bukuru-A did not initiate inflorescences in a photoperiod of 13 h. The same holds for the variety Going when grown in a photoperiod of 14 h. The question arises whether these varieties will never initiate inflorescences in these photoperiods. To investigate this, six plants of each variety were grown in the photoperiods 12 h, 12 h 15 min and 12 h 30 min for Ex-Lafia-A and Ex-Bukuru-A, and 13 h and 13 h 30 min for Going. Twelve weeks after sowing data on inflorescence initiation were recorded.

The results (Graph 3) show that inflorescence initiation was very irregular. In the varieties Ex-Lafia-A and Ex-Bukuru-A a photoperiod of 12 h 30 min may be regarded as "critical" (*cf.* 6). In the variety Going the same holds for a photoperiod of 13 h 30 min. In these treatments inflorescences had been initiated but they all abscised and never produced open flowers. The results suggest that, dependent on the variety, flowering will be inhibited in a photoperiod of 13 or 14 h.



GRAPH 3. Photoperiodic response of three varieties, Ex-Lafia-A, Ex-Bukuru-A and Going, at super-optimal photoperiods. Response expressed by the number of inflorescence primordia (generative axillary buds) on the main stem. Data based on six plants per treatment.

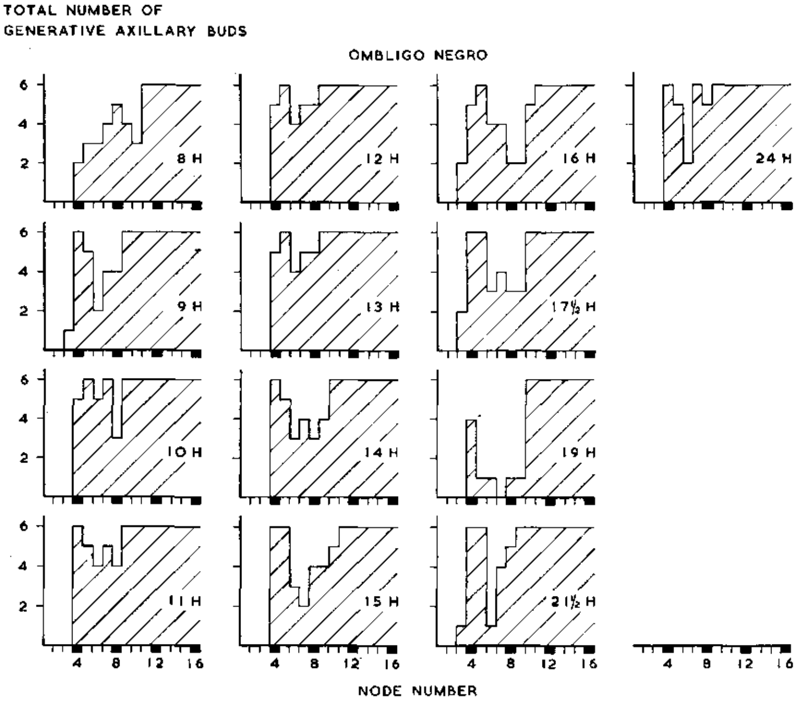
The data as presented in Graph 3 may indicate that in the "critical" photoperiod neither the node number of the first inflorescence nor the time from sowing until inflorescence initiation is a correct criterion as to differences in



GRAPH 4. Photoperiodic response of two varieties, Early Red and Kor, expressed by the distribution and the number of inflorescence primordia (generative axillary buds) on the main stem. Data based on 12 plants per treatment.

photoperiodic behaviour. In the following experiments the data on inflorescence initiation will therefore be presented in the form of graphs such as described on p. 33.

The most striking phenomenon in the experiment discussed above is probably the *interruption in the sequence of inflorescence primordia along the main stem*. Normally, when plants with axillary flowers become generative, flowers are borne in all subsequent leaf axils. In the cowpea this appears to be otherwise since interruptions may be observed in most varieties. Interruptions in floral initiation were, for instance, observed in the variety Ex-Lafia-A in short days when either the primary leaves or the primary leaves plus one trifoliate leaf were left intact and all other leaves were removed at their appearance (see Chapter V, § 2.3). A similar behaviour has been reported previously by MURNEEK (69) for Biloxi soybeans. When these plants were grown with only the cotyledons left intact "flower bud production was weak, irregular and absent in some parts of the plant". In our work with cowpea such interruptions were found in photoperiods which were either sub-optimal or super-optimal as shown in the foregoing for the varieties Ex-Lafia-A, Ex-Bukuru-A and Going. These interruptions also occurred in the variety Kor. The varieties Early Red and Ombligo Negro showed this phenomenon in almost any photoperiod. However, all these responses have one thing in common: the interruptions always occurred when the inductive conditions were sub-optimal.



GRAPH 5. Photoperiodic response of the variety Ombligo Negro expressed by the number of inflorescence primordia (generative axillary buds) on the main stem. Data based on six plants per treatment.

The results on inflorescence initiation in the varieties Kor and Early Red obtained in a second experiment are presented in Graph 4. The data for Ombligo Negro (Graph 5) are from the preliminary experiment. On comparing the results on inflorescence initiation in these three varieties, it becomes clear that the frequency of such interruptions in floral initiation, or the number of inflorescence primordia initiated before the interruption, varies with the photoperiod. The interruptions become greater and the number of inflorescence primordia prior to the interruption becomes smaller as the photoperiod deviates more from the optimum one. This is very clearly shown by the results obtained in the variety Early Red but it is also present in the variety Ombligo Negro. In the variety Kor interruptions were only found in the photoperiods of 6, 13, 14, 15 and 16 h. In the series 13, 14, 15 and 16 h a photoperiodic effect on the inflorescence initiation is clearly demonstrated.

In Chapter V, § 2.3, it was suggested that interruptions in the sequence of inflorescence primordia along the main stem may be attributed to non-photoperiodic effects. It was thought that when vegetative growth was accelerated *e.g.* by a high temperature, a discrepancy could be brought about between the concentration of floral stimulus and the rate of development of axillary buds. However, other factors may also cause a failure of inflorescence initiation, *viz.*:

1. The growth rhythm. The rate of vegetative growth of young cowpea plants is rather high which may cause such discrepancies as suggested above.

2. The carbohydrate status of the plant, which is known to play a role in floral initiation and flowering (see *e.g.* 6, 53, 83). It may well be that 10 hours of natural daylight as used in our experiments are inadequate for the optimal growth of some varieties. When growth rates are high a lack of carbohydrates may be caused in the seedling.

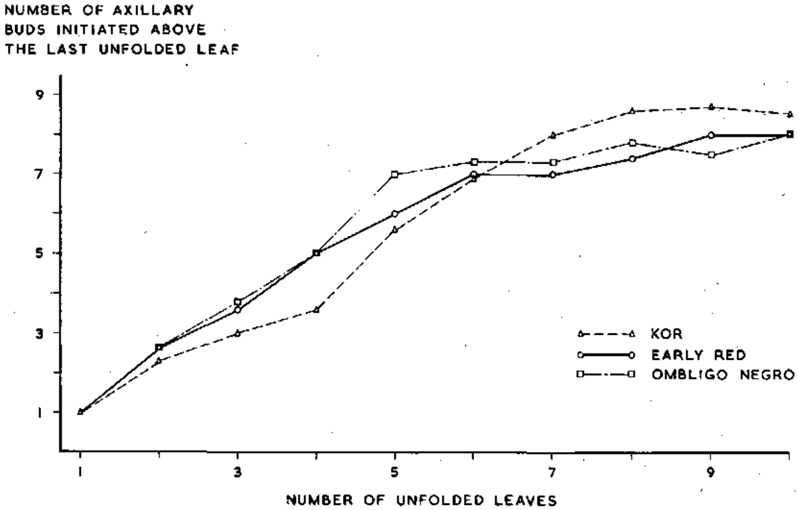
3. Temperature may also affect photoperiodic induction. NAYLOR (71) states that, although there are variations among species, the optimum temperature in short-day plants lies in the region of 20° to 25° C. At low temperatures between 1° and 4° C, or at high temperatures between 30° and 38° C flowering is inhibited provided these temperatures prevail only during the dark period. In short-day plants several cases are known in which the "critical" daylength and/or the number of necessary photoperiodic cycles vary with temperature (33, 62, 76, 86, 100). With *Vigna* a direct temperature effect seems not to be likely since results were reproducible under various temperature conditions.

4. At an early stage of growth the plant is unable to initiate inflorescences. Inflorescence initiation in the axils of the lower located leaves is evoked by flower-promoting substances present in the cotyledons, but these are active for a relatively short time only.

2. VEGETATIVE DEVELOPMENT

Growth rhythm. – In the foregoing it was stated that a temporary failure of inflorescence initiation is a common phenomenon in the varieties Ombligo Negro and Early Red at almost any photoperiodic treatment, whereas in the variety Kor it was found in some daylengths only. The question may arise whether the vegetative development of these varieties differs fundamentally.

At sowing the plumula of the embryo consists of two primary leaves and a growing point. Immediately after germination new leaves are initiated which eventually start unfolding. In the axils of folded leaves and leaf primordia, meristems are formed which are either generative or vegetative. During the early growth stages the number of differentiated axillary buds between the growing point and the last unfolded leaf increases with each new leaf unfolding until about 6 to 8 leaves are present. The rate of increase in this number of axillary buds during the first weeks of growing has been used to express differences in vegetative development between the three varieties mentioned above. In order to establish these differences, plants of the varieties Early Red, Ombligo Negro and Kor were grown in a photoperiod of 16 h. After one, respectively two, three, etc. until ten leaves had unfolded, 6 to 10 plants were examined for axillary buds above the last unfolded leaf. The results (Graph 6) indicate that differences between the varieties are not very striking, but it can be concluded that during the early growth stages the rate of development was higher in the varieties Early Red and Ombligo Negro than in the variety Kor. However, it should be kept in mind that these differences are in fact greater owing to a lower rate of leaf production in Kor. A few data on leaf production may demonstrate this (see Table 22).

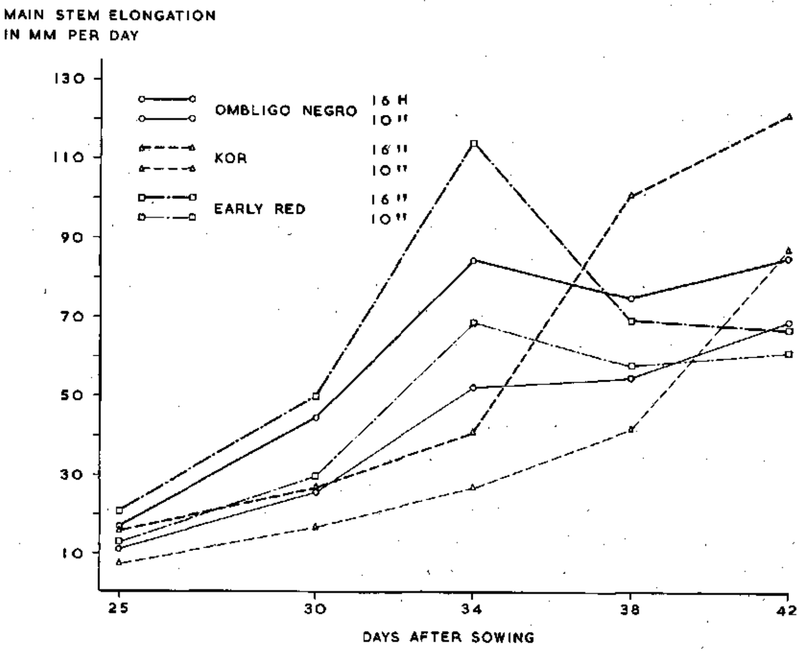


GRAPH 6. Rate of vegetative development in the varieties Kor, Early Red and Ombligo Negro. Vegetative development expressed by the number of differentiated axillary buds initiated above the last unfolded leaf on the main stem.

TABLE 22. Number of trifoliate leaves formed on the main stem in photoperiods of 10 and 16 h. Averages of six plants

Number of days after sowing	Variety					
	Kor		Ombligo Negro		Early Red	
	10 h	16 h	10 h	16 h	10 h	16 h
24	3.0	3.3	3.3	3.7	3.0	3.2
28	4.0	4.7	4.7	4.7	4.2	4.8
32	5.0	5.2	6.0	6.8	5.5	6.0
36	5.8	6.7	7.2	8.0	6.7	7.3
40	6.5	7.3	8.2	9.2	7.7	8.3

From the data on stem elongation in the preliminary experiment average rates of stem growth have been calculated. The results (Graph 7) clearly show that in both a 10 h and a 16 h photoperiod the rate of stem growth in Kor during early growth stages is much lower than in the other two varieties. These results, combined with those discussed above, demonstrate that there are differences in the growth rhythm between the three varieties investigated, and that during early growth stages, *i.e.* up to about five trifoliate leaves, the vegetative development in the variety Kor proceeds more slowly than in the varieties Early Red and Ombligo Negro.



GRAPH 7. Average rate of main stem growth in short (10 h) and long (16 h) days for the varieties Ombligo Negro, Kor and Early Red. Averages of six plants.

In the variety Early Red inflorescence initiation is retarded most when the plants are exposed to a 15 or a 16 h photoperiod. Closer examination of the vegetative axillary buds on the main stem, other than the first one, revealed that the first axillary bud of these potential laterals was always generative. This may suggest that inflorescence initiation is possible, provided vegetative development is reduced. As discussed above, vegetative growth of the main stem is rapid in this variety. The rate of development of vegetative axillary buds, however, is at first fairly low but increases thereafter. For instance, when in a variety sensitive to the photoperiod an inflorescence is initiated at the tenth node, an inflorescence will also be initiated in the first axil of the 5 or 6 vegetative axillary buds located below this node. When in Early Red these axillary buds develop into laterals it appears that inflorescence initiation has been confined to the first, and in some cases also to the second node, which may suggest that as soon as the laterals start to elongate the rate of growth becomes too high for further inflorescence initiation.

On considering the data of Graphs 4 and 5 (p. 47 and 48) it will be clear that temporary failure of inflorescence initiation in the varieties Ombligo Negro and in Early Red in short days mainly occurs from the fifth to the tenth node. The axillary buds corresponding with these nodes are initiated during stages in which the rate of stem growth (Graph 7) and the rate of development (Graph 6) are highest. The fact that these phenomena seem to coincide may suggest that during these particular growth stages a discrepancy is brought about between the concentration of the floral stimulus and the initiation of axillary buds. This may hold particularly if the concentration of the floral stimulus is sub-optimal as may be expected in young plants.

Grafting experiments. – The question may arise whether the differences between the varieties Kor and Early Red in short days are caused only by differences in vegetative development, or whether they are also due to quantitative differences in the level of floral stimulus. It may be that for inflorescence initiation a lower concentration of floral stimulus is required in Kor than in Early Red, or that plants of Early Red with two or three leaves produce less floral stimulus than do similar plants of Kor. In the latter situation even more floral stimulus may be produced than is required for inflorescence initiation. To investigate this, reciprocal graftings have been made between the varieties Kor and Early Red. Plants of both varieties were grown under inductive conditions until 4 or 5 trifoliate leaves had unfolded. In all cases graftings were made above the third trifoliate leaf, thus all stock plants retained three trifoliate plus the primary leaves. The scions consisted of 5- or 6-day old seedlings which had just unfolded their primary leaves. When the grafts had taken, these primary leaves were removed and the scions were kept defoliated. Therefore, the stocks in these grafts were used as donors, whereas the scions functioned as receptors of the floral stimulus. Four graft combinations were made, *viz.* two control grafts (Kor/Kor and ER/ER) and the two reciprocals ER/Kor*) and Kor/ER. Of each of the combinations 15 grafts were made. Of the combinations ER/Kor and Kor/ER respectively only 7 and 8 grafts were successful, whereas 14 grafts of Kor/Kor and 13 of ER/ER had taken. The fact that but 50 % of the reciprocal grafts were successful may be caused by a graft-incompatibility. It was observed that there were differences in chromosome size between the two varieties (25). This matter was not investigated.

When about six leaves had been removed, scions were examined for inflorescence primordia. The results (Graph 8) suggest that the stocks of Early Red were a more favourable donor for floral stimulus than stocks of Kor since in the combinations with Early Red as the donor, scions had initiated more inflorescence primordia than when Kor was used. In the latter combinations inflorescence initiation was very poor. The differences between the combinations Kor/ER and ER/ER may indicate that for floral initiation less floral stimulus is needed in Kor than in Early Red. However, the data obtained in the combinations Kor/Kor and ER/Kor seem to indicate the opposite. In

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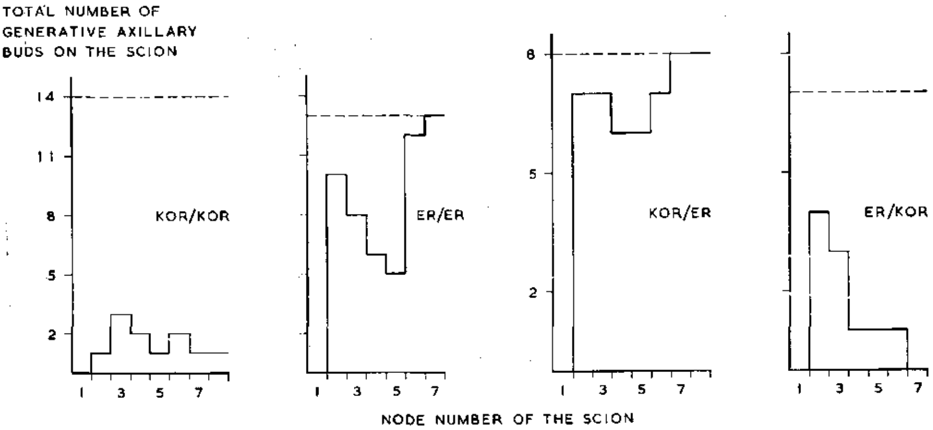
*) ER/Kor = Early Red scion on Kor as a stock



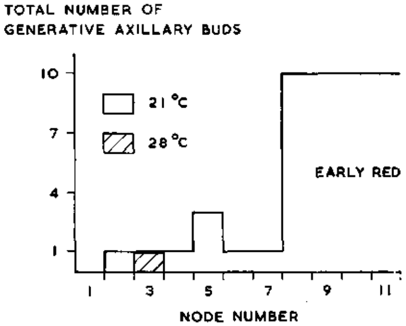
GRAPH 8. Grafting of non-induced scions (5- or 6-day old seedlings) onto inductive stocks. Effect of the graft-combination on floral initiation in the scion. Results of reciprocal grafts between the varieties Kor and Early Red (ER). For instance, Kor/ER = Kor scion on Early Red as a stock.

the latter two combinations growth of the scions was rather poor which is clearly demonstrated by the average numbers of leaves removed per day (Kor/ER: 0.20, ER/ER: 0.16, Kor/Kor: 0.14, ER/Kor: 0.13). These results clearly show that there is a positive correlation between the growth of the scion and inflorescence initiation in this scion. This may be explained by the assumption that in the case of poor growth very small amounts of assimilates were transported to the scion and subsequently no adequate level of floral stimulus could be reached to evoke inflorescence initiation.

Summarizing it can be stated that the experiment did not yield any evidence for a possible explanation of the differences in inflorescence initiation between the varieties Kor and Early Red.

Temperature. – Normally the rate of node production decreases when temperature is lowered and increases with increasing temperatures. The question may arise as to what extent slow growth also means earlier inflorescence initiation. To investigate this point plants of the variety Early Red were grown at constant temperatures of 21° and 28° C respectively. Per treatment 10 plants were grown in controlled-environment rooms in a photoperiod of 16 h. The light source consisted of twenty-four 40 Watt daylight fluorescent tubes (Philips, TLF/55) with an average light intensity of 50,000 erg/sec/cm^2 at 15 cm below the lamps. In both treatments the photoperiod consisted of high-intensity light only. At 60 days after sowing, the plants were examined for inflorescence primordia. Vegetative growth at these two temperatures differed greatly. Whereas the plants at 28° C had unfolded 15.3 leaves, this number was only 6.7 at 21° C.

The results (Graph 9) show that temperature, directly or indirectly through vegetative growth, had a marked effect on inflorescence initiation. At a temperature of 21° C, at which vegetative growth was retarded, inflorescence initiation was promoted and took place at nodes lower than was ever found under greenhouse conditions. However, in spite of the fact that plants had grown at a constant temperature, in a few plants inflorescence initiation was again interrupted. At 28° C in only one plant an inflorescence had been initiated on the main stem. Examination of the vegetative axillary buds and of the laterals from the second node on, again showed that all first axillary buds were generative.



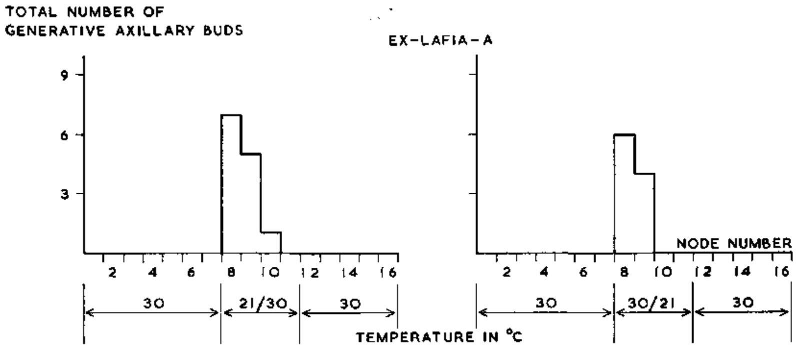
GRAPH 9. Inflorescence initiation on the main stem of plants grown in a constant low (21° C) or a constant high (28° C) temperature; variety Early Red. Photoperiod 16 h. Data based on 10 plants per treatment.

It appears once more that in an early stage of growth inflorescence initiation seems to be determined by the balance between vegetative growth and the concentration of the floral stimulus in this variety. High temperatures may disturb this balance by increasing the vegetative growth and/or lowering the concentration of the floral stimulus. It is not likely that the differences in the experiment were brought about by an effect of temperature on photoperiodic induction, although this possibility cannot be completely ruled out. No experiments were carried out to investigate this. The greater differences were probably partly due to differences in the carbohydrate status of the plants as a result of a high rate of respiration at 28° C.

The results obtained indicate that an effect of the temperature cannot explain the interruptions in inflorescence initiation as observed in the greenhouse.

In Chapter V, § 2.3, it was shown that failure of inflorescence initiation in the variety Ex-Lafia-A also occurred in short days when all leaves above the primary leaves were removed. To investigate the effect of temperature on inflorescence initiation in this treatment, three lots of 9 plants each were grown in cabinets (p. 25) at a constant temperature of 30° C and in a photoperiod of 11 h (high-intensity lamp light). The primary leaves were left intact and all trifoliate leaves were removed at their appearance. When 7 trifoliate leaves had been removed, plants were subjected to different day and night temperatures. One lot of plants was grown at a day temperature of 30° and a night temperature of 21° C, the second lot at a day temperature of 21° and a night temperature of 30° C. After 8 days the plants were transferred to a constant temperature of 30° C. After an additional 10 days the inflorescence primordia on the main stem were counted. The average leaf production in both treatments was one leaf per two days, which rate remained constant throughout the experiment.

The results (Graph 10) show that under the prevailing conditions a diurnal temperature range, either with a low night or a low day temperature, favoured inflorescence initiation only when it was applied after a constant high temperature. The second change, from a different day and night temperature to a



GRAPH 10. Inflorescence initiation on the main stem of plants defoliated above the primary leaves and grown in different temperature treatments. The plants were initially grown in a constant temperature of 30° C. After the removal of the seventh folded trifoliate leaf from the main stem, plants were subjected to either a day temperature of 21° and a night temperature of 30°C (left) or a day temperature of 30° and a night temperature of 21°C (right). When a total of 11 folded trifoliate leaves had been removed from the main stem, plants were transferred to a constant temperature of 30° C. Variety Ex-Lafia-A. Photoperiod 11 h. Data based on nine plants per treatment.

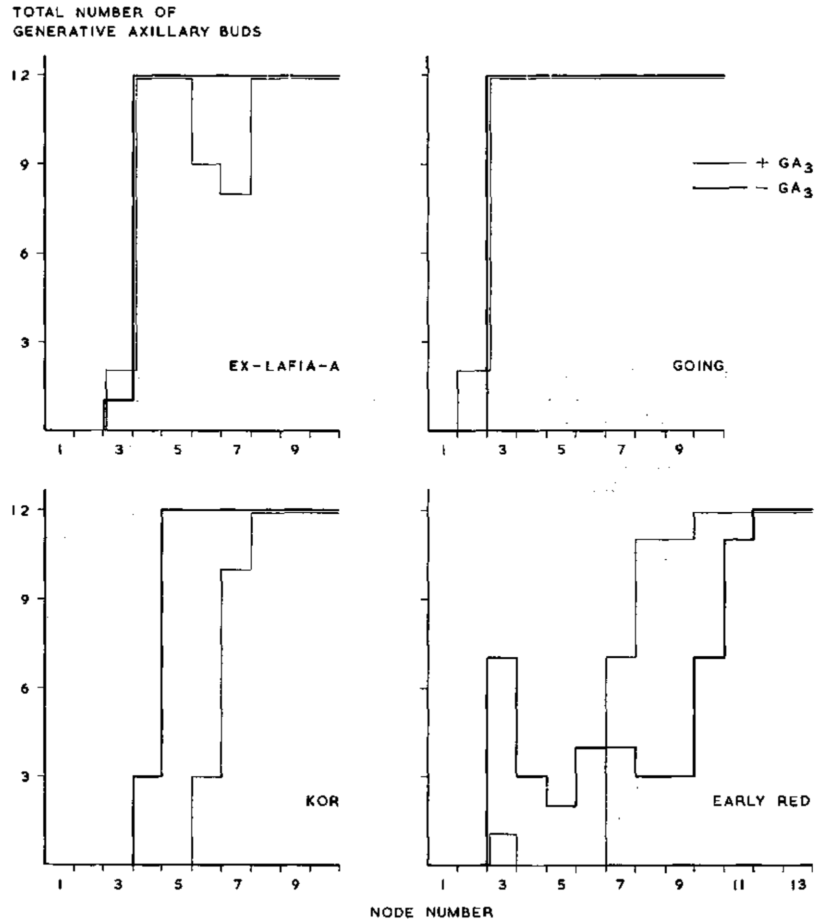
constant high temperature, did not lead to inflorescence initiation on the main stem. In the control plants, which were grown continuously at 30° C, no inflorescence primordia could be detected. Under these conditions apparently neither a constant high temperature nor a diurnal temperature range could bring about inflorescence initiation on the main stem.

The results suggest that only those axillary meristems which have reached a certain stage of development, are sensitive to temperature. It may well be that at this stage some parts of the meristems are more inhibited than other parts, thus favouring a more symmetrical development of the axillary bud which is the characteristic of the onset of inflorescence initiation (*cf.* Chapter V, § 4.2). This has not been further investigated. The only definite fact shown by the experimental results is that under certain conditions a sudden lowering of the temperature may lead to the initiation of a few inflorescence primordia.

The experiment was repeated with night temperatures of 18° and 15° C but no inflorescence initiation took place at these temperatures.

Gibberellic acid. – In Chapter IV, § 1, an experiment was discussed in which the effect of gibberellic acid on the main stem elongation was studied. It was shown that stem elongation was markedly affected by gibberellic acid. Moreover, vegetative development was accelerated since the rate of node production increased as well.

The results of the experiments discussed in the foregoing have repeatedly indicated that a high rate of vegetative development may bring about an inhibition of inflorescence initiation. The results on inflorescence initiation in the experiment with gibberellic acid (Graph 11) confirmed this. Inflorescence initiation in the variety Ex-Lafia-A was interrupted, whereas in the variety Kor a delay of at least two nodes was found. The variety Going appeared not to be affected, although in two plants an inflorescence was borne in the axil of the second trifoliate leaf, a phenomenon which had never been observed earlier



GRAPH 11. Inflorescence initiation on the main stem of plants which were treated with gibberellic acid. Varieties Ex-Lafia-A, Going, Kor and Early Red. Photoperiod 11 h. Data based on 12 plants per treatment.

in this variety. Early Red showed a completely different type of reaction. Inflorescence initiation was inhibited at the first six nodes. At the seventh and higher located nodes inflorescence primordia were found in practically all plants. As compared with the control generative buds were found much more frequently at the 7th, 8th and 9th nodes. No explanation was found for this phenomenon.

It has been discussed earlier that gibberellic acid-treated plants had smaller leaves than untreated ones (Table 23). The variety Early Red formed an exception here. Although the first trifoliate leaf was smaller, the fourth was larger than in the untreated plants. Differences in location on the main stem of generative buds between treated and control plants may therefore be presumed to arise from differences in leaf area. This supposition, however, does not seem very likely since the differences in leaf size which were observed in the preliminary experiment (*cf.* Table 5, p. 14) in photoperiods shorter than 11 h, had practically

TABLE 23. Effect of gibberellic acid on the size of the top leaflet of the first and fourth trifoliate leaf (in cm²). Averages of 12 plants

Variety	First trifoliate leaf		Fourth trifoliate leaf	
	$-GA_3$	$+GA_3$	$-GA_3$	$+GA_3$
Ex-Lafia-A . . .	22.5	20.4	36.2	29.3
Going	19.7	18.1	51.7	48.8
Kor	34.4	25.3	79.9	71.4
Early Red . . .	42.5	37.7	70.9	78.7

no effect on inflorescence initiation. Moreover, the differences in short days are more likely to be caused by a reduced photosynthesis than by differences in leaf area.

A third possible explanation may be found in a direct effect of gibberellic acid on photoperiodic induction. According to the literature it is known that in short-day plants the effectiveness of an inductive photoperiod may be reduced by gibberellin (9, 12, 36). However, gibberellin may also substitute for additional induction periods in promoting the reproductive development of induced plants (31, 98), but this does not seem to be a direct effect on induction (98).

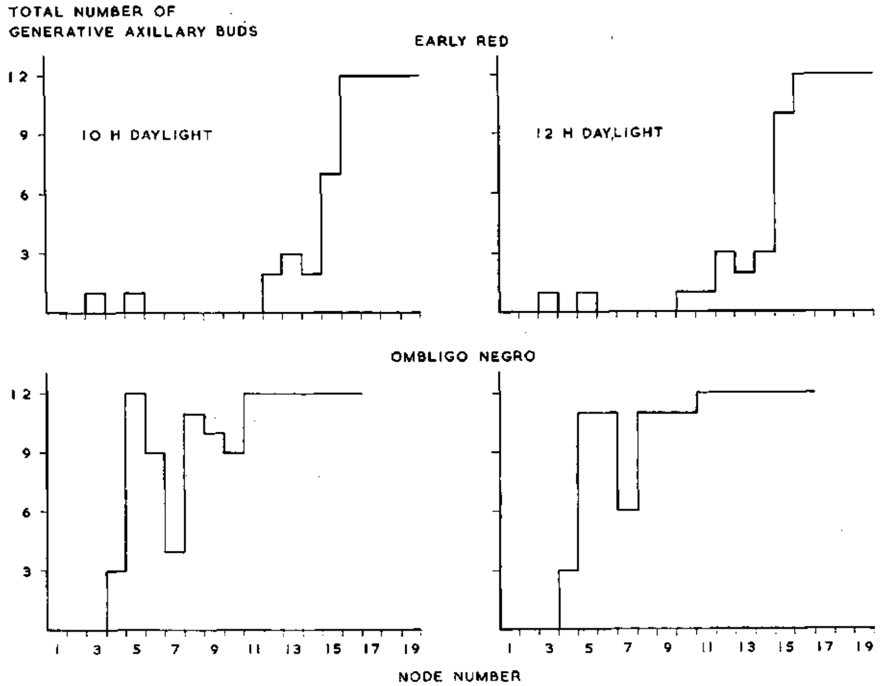
3. LIGHT INTENSITY

In § 1 it was suggested that the high rate of growth during the early growth stages of the cowpea plant could cause temporary lack of carbohydrates with, as a result, a temporary failure of inflorescence initiation. It is possible that under greenhouse conditions a daylight period of 10 h (as used in our experiments) is too short for optimal growth of some cowpea varieties, which in its turn, would affect inflorescence initiation. To investigate this two groups of plants of the varieties Ombligo Negro and Early Red were grown in a photoperiod of 16 h. One group received 10 h the other 12 h daylight. Each group consisted of 12 plants. Ten weeks after sowing the number of inflorescences was recorded.

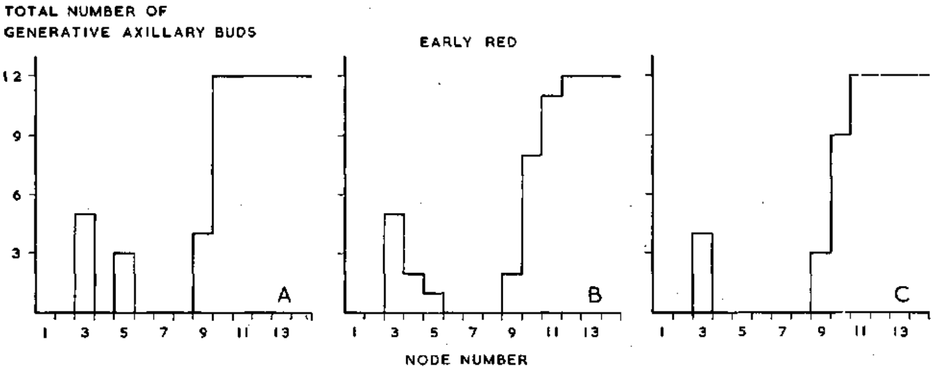
The results (Graph 12) show that there was no marked effect of an increased daylight period on inflorescence initiation. Some slight differences, however, are in favour of the 12 h daylight period, but it is clear that these differences are too small as to be of any appreciable effect. In addition, it is shown that a 12 h daylight period could not prevent failure of inflorescence initiation. From these results it seems justified to conclude that in a 10 h daylight period the temporary failure of inflorescence initiation is not likely to have been caused by a lack of products of photosynthesis.

In a second experiment, in which the influence of light intensity on inflorescence initiation was investigated, two varieties, Ex-Lafia-A and Early Red, were grown in a photoperiod of 12 h 30 min. The plants were subjected to three different treatments, (1) diffuse daylight during 10 h, (2) diffuse daylight during 5 h and (3) control. For details see p. 22.

The results on inflorescence initiation in Early Red obtained in this experiment (Graph 13) clearly demonstrate that reduction of light intensity had no marked effect on inflorescence initiation and did not prevent the initiation of inflorescences at lower nodes. Inflorescence initiation in Ex-Lafia-A was not affected



GRAPH 12. Effect of an extension of the daylight period from 10 to 12 h on inflorescence initiation on the main stem; varieties Early Red and Ombligo Negro. Photoperiod 16 h. Data based on 12 plants per treatment.

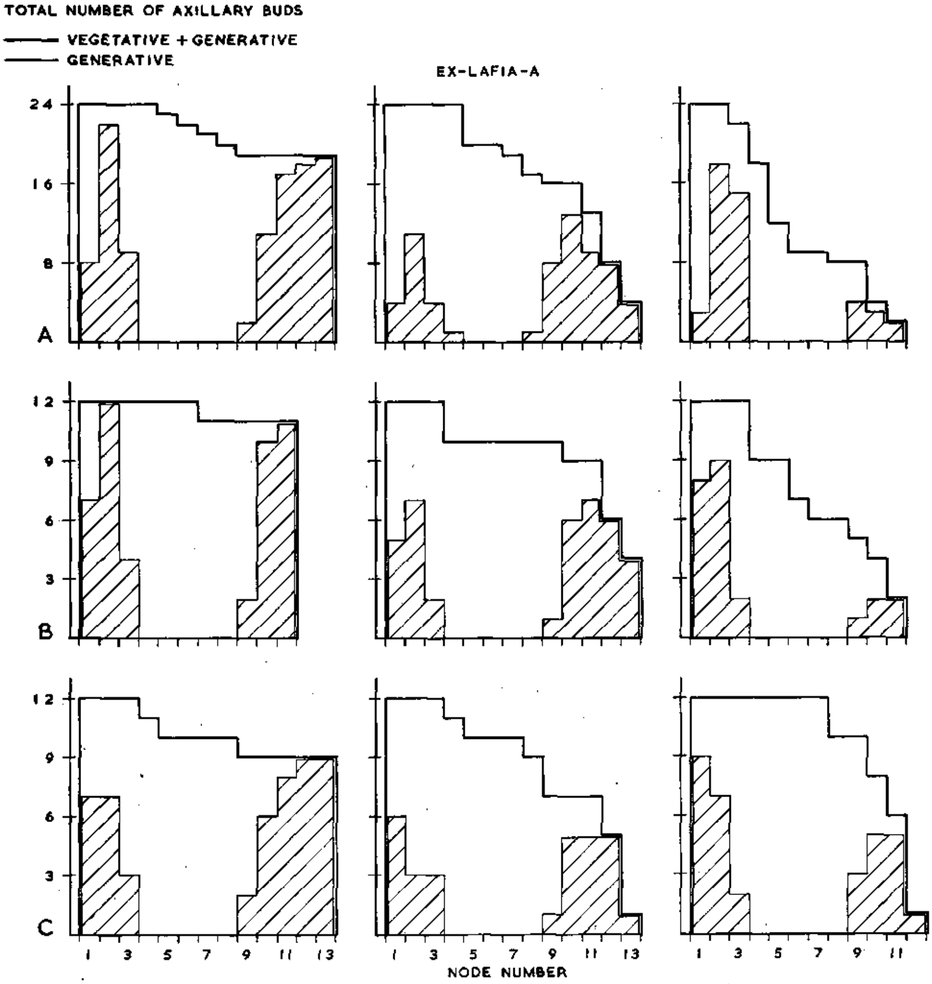


GRAPH 13. Effect of a reduced light intensity (shade) during 0 % (A), 50 % (B) and 100 % (C) of the daylight period on inflorescence initiation on the main stem; variety Earlv Red. Photoperiod 12 h 30 min. Data based on 12 plants per treatment.

either. In all three treatments inflorescences only had been initiated at the higher nodes, but initiation was fairly irregular within the treatments.

In Ex-Lafia-A data on inflorescences were also recorded for the laterals. Usually not more than four laterals were formed per plant, *viz.* two in the axils of the primary leaves, one in the axil of the first and one in the axil of the second trifoliate leaf. The data on inflorescence initiation have been added individually for these three types of laterals. Since not all laterals had formed the same number of nodes, the total number of axillary buds and the number of inflorescence primordia are both given (Graph 14).

Inflorescence primordia were confined to the base and to the top part of the laterals and in practically all laterals no inflorescences were found between the third and the eighth node. On the main stem, however, inflorescence initiation



GRAPH 14. Site of inflorescence initiation on the laterals arising from the axils of the primary leaves (A), the first trifoliate (B) and the second trifoliate leaf (C) of the main stem. Plants were grown in the shade during 0 % (left), 50 % (middle) and 100 % (right) of the daylight period. Variety Ex-Lafia-A. Photoperiod 12 h 30 min. Data based on 12 plants per treatment.

was inhibited until about the sixteenth node. When the growth of the laterals is considered, it is conspicuous that inflorescence intiation took place only in those periods in which the growth of the lateral was slowest, *i.e.* at the beginning and at the end of the elongation of the lateral.

The above indicates that a decrease in photosynthesis as a result of a reduced light intensity cannot account for the interruptions in inflorescence initiation. Therefore, it does not seem likely that under our conditions the carbohydrate status of the plant may have played a role in the observed sequence of inflorescence initiation. However, the possibility that the effect of a reduced light intensity was compensated by an increase in leaf area (*cf.* Table 24) cannot be excluded.

TABLE 24. Effect of reduced intensity of daylight on the size of the top leaflet of the fourth trifoliate leaf (in cm^2). Daylight intensity reduced during the entire daylight period (100), during 50% of the daylight period (50), or not at all (full daylight (0)). Photoperiod 12 h 30 min. Averages of 12 plants

Variety	0	50	100
Ex-Lafia-A. . . .	28.8	41.8	49.2
Early Red	75.7	100.3	113.8

In spite of the negative results from these two experiments, a correlation was found between the inhibition of inflorescence initiation and the vegetative growth. Although no conclusive evidence was obtained as to a causal relation between these two phenomena, the conclusion seems justified that at suboptimal concentrations of the floral stimulus a high rate of vegetative growth may counteract inflorescence initiation.

4. EFFECT OF COTYLEDONS

The interruption of inflorescence initiation which was found in some of our experiments, has been explained in terms of possible temperature and growth rate effects. It might also be, however, that flower-promoting substances present in the cotyledons of the young seedlings bring about inflorescence initiation in a few buds located at low nodes, and that only at later stages, after the plant has resumed vegetative growth for some time (after some vegetative buds have been formed), the leaves become sufficiently induced by the photoperiod to evoke floral initiation in all subsequently formed buds.

As far as the author is aware, an indication for the presence of flower-promoting substances in the cotyledons of young seedlings has been reported only once in literature. HAUPT (37), who studied the flowering of *Pisum sativum* cv. Kleine Rheinländerin, came to the conclusion that in this variety the cotyledons contained flower-promoting substances. This variety, which was known as an early flowering, day-neutral one, appeared to become a long-day plant when the cotyledons were removed. When a late flowering variety was induced to flower early by grafting it onto Kleine Rheinländerin, it was often noticed that the scions bore flowers at a few nodes only, all following nodes became vegetative again, and finally in the same plants flowering started anew at the same node as in the ungrafted controls (38). No explanation was given for this phenomenon, but it seems to us that the early flowering period was brought about by the flower-promoting substances of the cotyledons. Since the total amount of these substances must be limited they can be active for a relatively short time only and, provided the plant itself does not produce an adequate amount of floral stimulus, the following axillary buds become vegetative again. But these results could also be explained in terms of a sub-optimal concentration of the floral stimulus which can be effective only if vegetative growth is reduced.

Our results closely resembled the findings of HAUPT (38). Therefore, in a separate experiment the possible extent of the effect of the cotyledons on inflorescence initiation in the cowpea has been investigated. Embryos were excised from the dry seeds and grown on a culture medium under controlled conditions. The nutrient medium for the embryos consisted of a salt solution as used by RIJVEN (84) with 0.6 % agar and 2 % sucrose. When the primary leaves had unfolded, *i.e.* after about 5 days, the young plants were transferred to small soil-filled pots because root growth in the agar medium was markedly hampered. The growth of plants raised without cotyledons was very poor and it lasted at least eight weeks before plants had formed four trifoliate leaves. This makes a comparison with control plants very difficult, if not impossible.

Plants without cotyledons were raised of both varieties Early Red and Ex-Lafia-A. Those of Early Red were grown in two photoperiods, 10 and 16 h, whereas Ex-Lafia-A was grown in a photoperiod of 12 h 15 min. No fundamental changes in inflorescence initiation were observed, however. Inflorescence primordia were initiated at the nodes 4, 5 and 6 after which axillary buds became vegetative again. This even occurred in Early Red in a photoperiod of 16 h, which is very unusual for this variety in this daylength. Normally, inflorescence initiation in this case does not take place before the fifteenth or sixteenth node and only an occasional inflorescence is initiated at lower nodes. It seems therefore justified to conclude that inflorescence initiation was enhanced by the retarded vegetative growth and not by flower-promoting substances in the cotyledons. The possibility remains that the flower-promoting substances are present in the embryo itself, but the ratio of dry weights of embryos and seeds, being ca. 1 : 50 in the case of Early Red, does not make this very likely.

CHAPTER VII

SPECIFIC VARIETAL RESPONSE

It has been mentioned earlier (Chapter III, § 1.1) that the growth habit of the variety PI 221731 deviates from the normal growth pattern of the cowpea owing to the formation of terminal inflorescences. In addition, it was observed that the number of trifoliate leaves preceding the terminal inflorescence of the main stem was not affected by any photoperiod in this variety.

Soon after the emergence of the seedling, the first axillary inflorescence is initiated at the second or third node and growth proceeds in a similar way as in all the other cowpea varieties. However, after some time growth of the main stem and the laterals stops since terminal inflorescences are formed. To explain this phenomenon one may assume some or all of the following points:

1. The induction level reached in the leaves becomes so high that the apical meristem changes from the vegetative to the reproductive stage.

2. The rate of vegetative growth is low so that the amount of floral stimulus may reach an adequate level to evoke floral initiation in the top meristem before a following leaf is initiated. In other words, inflorescence initiation is promoted either by a decrease in the level of the growth promotors or by the formation of growth inhibitors.

3. The induction level required for inflorescence initiation in this variety is lower than for the other cowpea varieties investigated.

To examine the first possibility it is necessary to use a series of increasing induction levels; in this variety which is practically insensitive to the photoperiod, this can only be achieved by reducing the total leaf area. Therefore, an experiment was carried out in which plants were defoliated above (1) the primary leaves, (2) the first, (3) the second, (4) the third, and (5) the fourth trifoliate leaf. The plants were grown in a photoperiod of 11 h. The defoliation treatment consisted in removing the leaves as soon as they appeared. The node number of the first axillary inflorescence, the number of trifoliate leaves prior to the initiation of the terminal inflorescence and also the number of days from sowing until the terminal inflorescence became visible, have been recorded.

TABLE 25. Effect of defoliation on initiation of axillary and terminal inflorescences in the variety PI 221731. p = plants defoliated above the primary leaves; p + 1 = plants defoliated above the first trifoliate leaf, etc. Averages of 12 plants

Recorded data	p	p+1	p+2	p+3	p+4	control
Number of the first node with an axillary inflorescence	2.9	2.7	2.7	2.8	2.8	2.9
Number of trifoliate leaves on the main stem prior to the initiation of the terminal inflorescence	–	10.7*	10.6	10.3	9.8	10.0
Number of days from sowing until the appearance of the terminal inflorescence	–	34.5*	34.4	34.7	34.6	36.0

* Average of 10 plants.

The results (Table 25) show that there was no effect on inflorescence initiation as far as the axillary inflorescences were concerned. However, when plants were defoliated above the primary leaves, no terminal inflorescence was initiated in the course of the experiment (100 days). The same holds for two plants which were defoliated above the first trifoliate leaf. In the remaining ten plants initiation of the terminal inflorescence did not differ markedly from the other treatments, although there was a slight increase in the number of leaves formed prior to the inflorescence. This may be explained by an increased leaf production stimulated by the defoliation, which can also be seen from the number of days from sowing until the appearance of the terminal inflorescence. The results clearly indicate that the induction level required for initiation of the terminal inflorescence is higher than that required for initiation of axillary inflorescences, but the results do not suggest that this level would be extremely high (p. 61, assumption 1). In addition, when seedlings of different varieties were grafted onto stocks of PI 221731 under short days, a terminal inflorescence was never formed.

No investigations have been carried out on the second assumption (p. 62), but a few remarks may be made on this subject. When seedlings of PI 221731 were grafted onto stocks of Ex-Lafia-A in short days, vegetative growth of the scion was markedly retarded and the internodes did not elongate. In this treatment seven leaves were formed prior to the terminal inflorescence. When it is considered that the stocks had retained three trifoliate leaves and when the graft combination is regarded as one plant, it becomes clear that also in this case 10 trifoliate leaves preceded the terminal inflorescence. The same results were obtained when seedlings were grafted onto stocks of PI 221731. The lowest number of trifoliate leaves ever obtained in these grafting experiments was five, which agrees with the number of leaf initials present in a vegetative terminal bud.

Apparently the induction level required for inflorescence initiation was rather low, since no difference was observed in the location (node number) of the first axillary inflorescence in the various treatments. To this it may be added that PI 221731 is the only variety in which, by means of grafting, the first axillary inflorescence could be obtained at the first node (*cf.* Chapter V, § 2.4).

Summarizing it may be concluded that the most likely explanation for the formation of terminal inflorescences is that a relatively low induction level is required for floral initiation.

The growth of the laterals is also limited by the formation of terminal inflorescences, which are usually preceded by the differentiation of 3 or 4 leaves. In the axils of these leaves inflorescences are borne. Further branching is therefore only possible from buds in the axils of the prophylls at the base of primary laterals and peduncles (*cf.* Chapter V, § 4.2). Usually these buds hardly form any laterals but they may be forced to develop by preventing the plants from forming pods. When flowers are continuously removed, all these buds grow out and very short laterals are formed which all bear terminal inflorescences. Normally these laterals consist of one leaf and two inflorescences only, but sometimes this leaf is completely absent. At the base of these inflorescences buds are found again which may also develop, but these "laterals" consisted of an inflorescence only. Leaves were never observed.

These observations indicate that the vegetative growth in this variety is completely limited and that terminal inflorescences are initiated in all axillary buds of the plant.

DISCUSSION OF REPRODUCTIVE DEVELOPMENT

Using the node number corresponding with the first inflorescence on the main stem as the criterion for photoperiodic response, a preliminary experiment was conducted in which cowpea plants were exposed to a range of photoperiods between 6 and 24 h. Photoperiods ranging from 8 to 11 h appeared to be optimal for inflorescence initiation. Four types of reactions were found, *viz.* (1) varieties which do not flower in long days, (2) varieties in which flowering is only delayed by long days, (3) varieties which show a slight response to the photoperiod, and (4) an ambi-photoperiodic response.

It was investigated whether a juvenile phase could be distinguished in the development of the cowpea plant. The results indicate that a completely insensitive period does not exist or is very short. In the latter case plants are only insensitive until the first trifoliate leaf has unfolded. It was shown that the sensitivity of the plant to inductive conditions increases during the early growth stages until the second trifoliate leaf appears. The fact that in some varieties interruptions in inflorescence initiation occur in short days may suggest, that in these cases the sensitivity of the plant is still less than the maximum sensitivity, which is not reached before the fifth or sixth trifoliate leaf unfolds. In these varieties no investigations on leaf sensitivity have been carried out, however. Results obtained in grafting experiments indicate that the absence of inflorescence primordia at the first two or three nodes is mainly due to initiation of these axillary buds before an adequate level of induction has been reached.

From some results it was deduced that the induction period in short days does not exceed 5 or 6 days. The data on inflorescence initiation in the preliminary experiment showed that more cycles are required when the photoperiodic treatment deviates from the optimum daylength. In a few varieties more cycles are also required when a short-day treatment is preceded by long days. It has been suggested that a long-day treatment either affects the sensitivity of the leaves or the production apparatus of the floral stimulus.

Three stages of reproductive development have been studied, *viz.* inflorescence initiation, inflorescence development and anthesis. It was shown that the difference between a generative and a vegetative axillary bud can be detected only at a rather far advanced stage of bud development, which hinders an accurate determination of the time of inflorescence initiation. Inflorescence development has been found to be affected by long days provided vegetative growth continued. In such treatments flower buds, and sometimes the entire inflorescence abscises. However, there appears to be a certain stage after which further development cannot be inhibited by long days. In some cases inflorescences could be forced to further development by pruning, which leads to abnormal inflorescences, however. Failure of inflorescence development in long days has been explained by high auxin levels and by a quantitative effect of the floral stimulus. Results indicate that anthesis was light-controlled. Normally, provided the period of darkness and/or low-intensity light lasted 12 h or more, flowers open about 12 h after either a change from high-intensity to low-intensity light or after a change from light to darkness. It was also found that in a sensitive variety the opening of the flowers is more abrupt than in an almost insensitive one.

Some results have been reported on interruptions in the sequence of inflorescence primordia along the main stem. The experimental data showed that such temporary failures of inflorescence initiation occur only at a sub-optimal induction level. The fact that in some varieties such failures are brought about in all photoperiods suggests that in those varieties the maximum sensitivity to the photoperiod was not reached before the fifth or sixth trifoliate leaf had unfolded, which appeared to correspond with inflorescence initiation at about the tenth or eleventh node. Inflorescence initiation at lower nodes seemed not impossible, but was only successful when the rate of vegetative growth was low. The fact that a constant low temperature cannot prevent interruptions in inflorescence initiation, and the fact that the varieties show differences in vegetative development during the early growth stages, suggest that differences in growth rhythm also come into play.

Non-photoperiodic effects have received special attention in respect of these interruptions, but neither temperature nor photosynthesis appears to be responsible for this phenomenon. It has been assumed that at sub-optimal induction levels a discrepancy was brought about between the rate of vegetative development and the concentration of the floral stimulus. Results obtained with growth retardants (30, 93, 104) seem to be in accordance with our view.

To study inflorescence initiation quantitatively diagrams have been made by plotting the node number on the abscissa against the total number of inflorescence primordia on the ordinate. This way of representing may be criticized since it implies that there are no differences within the treatments. That this could indeed be assumed may be demonstrated by the results obtained with the variety Kor in a photoperiod of 15 h (*cf.* Graph 4, p. 47). However, this method of representing does not take into account the differences between treatments. In long photoperiods plants grow quicker owing to the larger leaves, whereas in photoperiods shorter than 10 h growth is presumably affected by a limited photosynthesis.

The formation of terminal inflorescences in the variety PI 221731 has been discussed. Some experimental data showed that in this variety the induction level required for inflorescence initiation is very low. It has been concluded that this is the main cause of the formation of terminal inflorescences in this variety.

PART III. RELATION BETWEEN VEGETATIVE AND REPRODUCTIVE DEVELOPMENT

CHAPTER VIII

VEGETATIVE AND REPRODUCTIVE DEVELOPMENT

1. Flowering as affected by vegetative growth

Inflorescence initiation. – In Chapter V, § 2.3, it was pointed out that inflorescence initiation in the variety Ex-Lafia-A was affected by defoliation under short-day conditions. When the plants were grown with only the primary leaves or with the primary leaves plus one trifoliate leaf left intact and all other leaves removed, it was observed that inflorescence initiation was very irregular and absent in some parts of the plant.

The same phenomena were observed when this variety was grown in photoperiods which were super-optimal for inflorescence initiation, but it may occur in any cowpea variety sensitive to the photoperiod. In some varieties, at least under greenhouse conditions, this appeared to be very normal and occurred in all photoperiods used (see Chapter VI). The experiments carried out to investigate the causes for these interruptions in inflorescence initiation did not provide convincing evidence. However, in all treatments a negative correlation was found between a high rate of vegetative growth and inflorescence initiation. For more detailed results the reader is referred to Chapter VI.

Inflorescence development. – This stage of reproductive development has been discussed in more detail in Chapter V, § 4.3. A negative correlation was observed between vegetative growth and inflorescence development. Two possible causes for the inhibition of inflorescence development were assumed, *viz.* a high auxin level and/or a sub-optimal level of the floral stimulus. In addition, inflorescence development may also fail due to a deficiency of assimilates. For instance, when plants of the varieties Ex-Lafia-A and PI 221731 were grown under inductive conditions and when only a few leaves were left on the plant, many inflorescence primordia never developed but abscised although flowering proper was not inhibited. The same has been found for the developed inflorescences. Usually only a few flowers opened and further development of the inflorescence took place only when the flowers were removed continuously.

Flowering proper. – Provided environmental conditions are favourable for anthesis, the production of flowers depends to a great extent on the vegetative development of the plant. Generally it may be stated that the bigger the plants the more leaves are formed. More leaves mean a greater photosynthetic capacity. As a consequence, more flowers may be produced when the plants are bigger.

In our experiments the flower production has been studied in two ways, *viz.* by defoliation and by extending the vegetative period prior to floral initiation. In the varieties Ex-Lafia-A and PI 221731, both grown in short days of 11 h, the following degrees of defoliation were applied:

1. Leaves removed as they appeared, after the development of the primary leaves.
2. As in (1), but after the first trifoliate leaf.
3. As in (1), but after the second trifoliate leaf.
4. As in (1), but after the fourth trifoliate leaf.

The number of plants per treatment was 20 for the variety Ex-Lafia-A and 12 for the variety PI 221731. The number of days from sowing until flowering and the number of flowers per plant were recorded.

TABLE 26. Effect of different degrees of defoliation on the number of days from sowing until flowering and on the number of flowers; p = plants defoliated above the primary leaves; p + 1 = plants defoliated above the first trifoliate leaf; etc.

Recorded data	Variety Ex-Lafia-A				
	p	p + 1	p + 2	p + 4	control
Number of days from sowing until flowering	57.2	46.3	46.0	46.9	47.4
Number of flowers	6.8	14.0	17.6	20.1	47.4
	Variety PI 221731				
	p	p + 1	p + 2	p + 4	control
Number of days from sowing until flowering	50.6	40.9	40.6	41.2	42.2
Number of flowers	5.9	26.7	29.6	37.7	40.1

The results (Table 26) show that in group (1) flowering was markedly retarded in both varieties. Flowers appeared very irregularly and most inflorescence primordia abscised. In the other groups the plants flowered almost simultaneously with the non-defoliated control. However, there was a slight retardation with a higher number of leaves.

In both varieties the number of flowers was markedly affected, but in Ex-Lafia-A the effect was considerably greater than in PI 221731. In the latter there was only a small difference between group (4) and the control, whereas in Ex-Lafia-A the number of flowers in this group was reduced by more than 50 per cent. The difference between groups (1) and (2) was smaller in Ex-Lafia-A than in PI 221731. This may be caused by the inhibition of inflorescence development in Ex-Lafia-A, but it may also be that the differences in leaf area between groups (1) and (2) are greater in PI 221731 than in Ex-Lafia-A with, as a result, a more marked difference in total net assimilation.

For both varieties the results clearly indicate that the number of flowers decreased with a decrease in total leaf surface. Summarizing it may be concluded that all degrees of defoliation were detrimental to flower production. Obviously the amount of photosynthetic products required for flowering is rather high since all degrees of defoliation were associated with a decrease in number of flowers. Apparently this does not hold for all plant species as defoliation, within certain limits, may also stimulate flower production (see *e.g.* 92, 106).

In the experiment in which the vegetative period prior to floral initiation was prolonged, plants of the varieties Ex-Lafia-A and Ex-Bukuru-A were grown in 28 and 14 long days preceding inductive conditions. The groups consisted of 40 plants, which were divided into two lots when the plants were transferred to short days. Twenty plants were grown in a photoperiod of 8 h daylight and 3 h supplementary light (8 + 3), the other group was raised in 10 h daylight and 1 h supplementary light (10 + 1). The number of flowers and the total number of leaves produced were recorded.

TABLE 27. Vegetative period prolonged by treatments with long (16 h) prior to short (11 h) days. Effects expressed in the total number of flowers and leaves formed per plant. Short days based on 8 hours of daylight (8 + 3) or 10 hours of daylight (10 + 1). Averages of 20 plants

	Variety Ex-Lafia-A					
	0 long days		14 long days		28 long days	
	8 + 3	10 + 1	8 + 3	10 + 1	8 + 3	10 + 1
Number of leaves . . .	14.0	12.0	27.9	26.2	35.8	34.3
Number of flowers . .	16.0	20.7	34.4	38.3	41.9	58.6
	Variety Ex-Bukuru-A					
	0 long days		14 long days		28 long days	
	8 + 3	10 + 1	8 + 3	10 + 1	8 + 3	10 + 1
Number of leaves . . .	11.0	11.2	18.5	23.9	24.5	29.2
Number of flowers . .	13.4	19.0	24.2	34.8	33.0	47.9

As this experiment was carried out later in the season than the preceding one, the results in respect of flowering (Table 27) are not comparable. Unfortunately flowering was very poor: the mean number of flowers produced in the control of Ex-Lafia-A at (10 + 1) h was only 20.7 as compared with 47.4 in the same variety in the preceding experiment (Table 26). The results indicate, however, that there is a positive correlation between the number of flowers and the number of leaves in the different treatments. In both varieties a non-inductive period of 28 days, causing an extension of the vegetative period, resulted in about 2.5 times as many flowers as produced by the control. The effect of a reduced daylight period is more marked than would be expected from the difference in number of leaves. In Ex-Lafia-A there was even a very small increase in the number of leaves but flowering was reduced in the 8 h daylight period.

In this experiment environmental conditions other than the photoperiod were not very favourable for flowering. This was also manifested in a second experiment in which plants of the variety Ex-Lafia-A were grown in 14, 28 or 42 long days prior to short-day conditions. The average numbers of flowers produced in this case were 70.4, 93.4 and 108.8 respectively, which is considerably more than in the previous experiment. Leaf production, however, did not differ markedly. In fact even fewer leaves were produced, *viz.* 23.4, 33.6 and 41.8 in the 14, 28 and 42 long-day treatments respectively.

Summarizing it can be said that bigger plants may flower more abundantly than smaller ones. This must be attributed to the greater leaf area which enhances the amount of carbohydrates produced with, as a result, a higher number of flowers. On the other hand, the increased flower production in these experiments may also have been a direct result of the size of the plants when transferred to inductive conditions. Bigger plants mean more leaves and more axillary meristems where the floral stimulus can exert its influence. The fact, however, that even under inductive conditions some inflorescences never developed would indicate that the amount of available carbohydrates is always a limiting factor for flowering proper. This view is supported by the observation that flowering proceeds when the flowers are removed continuously or when pods have matured and the plants are still green, although it cannot be completely ruled out that in the last stage of reproductive development inhibitors may be produced by the maturing pods.

2. VEGETATIVE GROWTH AS AFFECTED BY FLOWERING AND FRUCTIFICATION

When the effect of flowering and fructification on vegetative growth is studied in the cowpea two types of behaviour can be distinguished, *viz.* (1) varieties in which vegetative growth is limited by factors other than maturing, *e.g.* Ex-Lafia-A in which vegetative growth may be photoperiodically inhibited, and PI 221731 which forms terminal inflorescences in all axillary buds (*cf.* Chapter VII); and (2) varieties which continue vegetative growth until the plants mature.

It will be clear that as far as varieties like Ex-Lafia-A are concerned, such studies can only be performed in photoperiods in which vegetative growth and flowering proceed until the plants mature. The varieties of the second group lend themselves to such studies in all photoperiods provided the daylight period is not too short.

However, systematic experiments on this matter have not been carried out.

The size of the plants, the heights which the plants could reach where observations became impossible, as well as the limited space greatly hampered such investigations. In spite of this some observations have been made on individual plants from which the flowers were removed continuously. Therefore, a few remarks seem to be justified. In all cases in which fructification was prevented by continuous removal of flowers, the plants continued growth and flowering as long as environmental conditions remained favourable for vegetative growth (*i.e.* for one season of 6 to 7 months). Neither of these phenomena is surprising when it is kept in mind that both vegetative growth and flowering are indeterminate in the cowpea. In varieties in which the vegetative growth is inhibited the removal of flowers also induces further flowering, which may indicate that flowering is inhibited by the presence of developing pods. There is some evidence which supports this view. When the pods are ripe and the plants have not died, or when mature pods are removed, flowering may be resumed in the same inflorescences. This inhibition of further flowering may be explained by a depletion of food reserves but it may also be that inhibitors are produced by the developing pods (see 41).

The question may arise which factors cause the termination of the life cycle of the cowpea. The few observations do not elucidate this point nor does the literature. Plant senescence has received little attention since the early work of MOLISCH (65) some 35 years ago. From his experiments with various annual plants he concluded that plant senescence was a matter of emptying and utilizing the organic reserves of the plant by the ripening seeds and fruits. LEOPOLD *et al.* (54), who worked with spinach and soybean, came to the conclusion that food depletion is only a partial explanation of the onset of senescence. Their experiments suggested an accumulation of influences which induce senescence with each of the developmental stages of reproduction. The nature of these influences is still unknown, however. From his experiments with peanut DE BEER (5) came to the conclusion that a shortage of photosynthetic products which are utilized by the developing fruits, restricts further vegetative growth. When in this crop the fructification was prevented by high temperature, vegetative growth and flowering were highly stimulated. Under such conditions it remains to be seen whether this continued vegetative growth lasts only for a limited time or whether senescence will not occur at all as long as no fruits are formed. In the Alaska pea, for instance, it was found that removal of flowers as they appeared resulted only in a postponement of senescence (61). In this case it was suggested that the stem apex may lose the capacity to synthesize some factor essential for continued cell division and elongation. When a young stem apex was grafted onto the tip in place of the old apex, growth of the young stem tip continued normally and the rest of the plant was fully capable of perpetuating growth for a much longer time. These results may suggest that even when environmental conditions are favourable and flowers are removed continuously, also the cowpea will continue vegetative growth for a limited time only. The comparatively short time of 6 to 7 months during which plants could be observed do not justify any conclusion, however.

CHAPTER IX

AGRICULTURAL IMPLICATIONS

In both tropics and sub-tropics the effect of the natural daylength on the time of flowering in the cowpea or on the time of appearance of the first ripe pod has long been recognized. The early observations of MOOERS (66) already pointed to the existence of date-fixed varieties, in other words, varieties in which the length of the life span varied only slightly with the season but very markedly with the sowing date. Undoubtedly, one of the most important questions for the practical grower is when to sow cowpeas. In order to answer this question a distinction must be made between the purposes for which the crop is grown, *i.e.* whether it is grown for its vegetative parts (hay, fodder, green manure) or for the seeds. In both cases, however, the grower is interested in optimum yields.

In this chapter we will confine ourselves to the effect of the natural daylength in determining the vegetative and reproductive development of the cowpea, whereas factors such as temperature, mineral nutrition and water supply will not be considered.

The results obtained in our experiments clearly demonstrate that the varieties of tropical origin, such as Ex-Lafia-A, Ex-Bukuru-A and Going, when grown as a seed crop, cannot be used in regions too far from the equator. The same holds for the varieties Banta-B, Kananan Wake-A and CPM 1 which were only observed in the preliminary experiment. Therefore, when tropical cowpea varieties are imported in the sub-tropics one should bear in mind that in most cases these varieties will never produce any pods. Contrary to the tropics, where the cowpea can be planted all the year round, the growing season in the sub-tropics is limited to the summer when night temperatures do not drop too low, since cowpeas are immediately killed by night frosts. During the summer the daylength in the sub-tropics is too long for inflorescence initiation, and when the plants would eventually come into flower the season has advanced too much and plants will be killed by the first night frosts before any pod could have matured. Such varieties are not even suitable for hay production in the sub-tropics since the seed supply would become very difficult if not impossible. In the tropics the growing season is not limited by temperature and the cowpea may be grown the year round. This aspect offers wide possibilities for the grower, since it enables him to choose the right sowing date for his crop in order to obtain optimum yields. This holds particularly for varieties with a high sensitivity to the photoperiod. The type of experiment which is generally used to investigate the influence of the natural daylength is the date-of-sowing experiment. These experiments are undoubtedly of great importance for the practical grower, but they are not very suitable for research on photoperiodism since so many specific and non-specific factors affect the normal photoperiodic response. In such date-of-sowing experiments the photoperiod is often derived from the figures for sunrise and sunset. The photoperiodic effect of the natural daylength is determined by many other factors than this astronomical daylength. This daylength does not allow for exposure to light before sunrise and after sunset which may even exceed the period of twilight. Also cloudiness and fog during twilight may influence the photoperiodic effect of the natural daylength.

An attempt to analyse the photoperiodic effect of the natural daylength has been made by BEST (7). In his experiments with rice he found that the lowest light intensity at which plants still reacted depended on the sensitivity of the variety, on the length of the photoperiod and on the preceding period being one of darkness or of high-intensity light. Low light intensities were much more effective when given at the beginning than at the end of the photoperiod, and also more effective with long photoperiods than with short photoperiods. It is likely that this lowest light intensity also varies with the plant species. Consequently for an interpretation of the results obtained in date-of-sowing experiments light intensities during twilight should be measured in order to get accurate data on the photoperiods to which the plants are exposed.

The most fundamental process which affects yield when cowpea is grown in different daylengths is photosynthesis. An increase in photosynthesis which to a certain extent may be produced by a longer vegetative period, by lengthening the assimilation period per day or by increasing the assimilation rate due to brighter weather, potentially increases the yielding capacity of the plant. This may be achieved when cowpea varieties which are sensitive to the photoperiod are sown in long days which tend to get shorter, provided the sensitivity is such that the plants remain vegetative until the days are short enough for floral initiation. This second aspect of photoperiodism, *i.e.* the control to some extent of the vegetative period of sensitive varieties by the photoperiod, is probably of major importance. It is known, for instance, that normally the best late-maturing varieties of a crop produce higher yields than the best early-maturing varieties. The net assimilation is highest when the plants are still in the vegetative stage. GAASTRA (26), for instance, established that during the vegetative stage of sugar beets between 80 and 90 % of the total organic matter was produced during 44.5 % of the growing season. When plants come into the reproductive stage the net assimilation is reduced due to an increased respiration during flowering and fruit set (see 8).

This might suggest that the longer the vegetative stage the higher the total dry matter production will be and the more pods the cowpea plants are able to produce. However, for maximum seed production there seem to be certain optimal vegetation periods which are not correlated with the maximum dry matter production. BEST (8), who studied the fruit yield and dry matter production of rice and soybean as a function of the vegetation period, demonstrated that the optimum life period for the yield of a rice and a soybean variety was about five and a half months. Although there was still an increase in dry matter production in longer vegetation periods seed production decreased. This was thought to be brought about by factors which were indicated as senility of the plant.

CHANDRARATNA (16) reports an almost complete loss of yield for rice when very sensitive varieties were planted in the wrong season so that the vegetation period was extended to more than a year.

Unless more data become available on the optimum vegetation period for maximum seed yields, it does not seem advisable to sow very sensitive cowpea varieties before the longest summer day. This view is supported by the observations of FAULKNER and MACKIE (22) and NJOKU (75) that, when in Nigeria cowpeas were sown before this day, plants hardly flowered and fruited although they grew very well. Such variaties may be grown successfully as a fodder crop or for hay production.

When cowpea is sown in long days another morphogenetic effect will be of importance for total dry matter production and for highest seed yields. In our experiments it was found that in long days leaves are generally larger than in short days. As a result, an increase in photosynthesis by a longer vegetative period due to sowing in long days may be enhanced by the greater leaf area as long as there is no closed green crop surface. In addition, long days normally cause a relatively more vigorous root development than short days. Plants with an extensive root system normally have a better water supply than plants with a smaller root system which may affect transport of carbohydrates and mineral nutrition in the plant.

When the Nigerian varieties studied in our experiments were grown in short days of 11 to 11 h 30 min and, depending upon the temperature, sometimes also in days of 12 h, the vegetative period was very short, leaves were small, vegetative growth was inhibited and yields were reduced. Although no experiments have been carried out on pod production it was observed that such plants never produced more than 5 or 6 pods and that only the first 2 or 3 were fully filled with seeds. Under these conditions practically all flowers set fruit, but the young pods were soon shed probably due to a lack of carbohydrates. When planting during short days is inevitable, such varieties as mentioned above are completely unsuitable for seed production and should be replaced by others, the growth of which is not photoperiodically controlled. Another possibility is that the lower seed yield of individual plants is compensated by closer spacing. On the other hand, as was shown in our experiments, flowering in these varieties may already be inhibited in photoperiods of 12 h 30 min. This means that for optimum seed yields such varieties can only be grown successfully at certain times of the year and not too far from the equator.

Varieties with an upright growth habit in which vegetative growth is limited by the formation of terminal inflorescences, such as PI 221731 used in our experiments, may offer further possibilities for mechanical harvesting. However, for these varieties it holds that both the yield of hay and seeds are lower as compared with that of varieties with an indeterminate growth habit the growth of which is not photoperiodically controlled. As in the case of the Nigerian varieties the lower yields of individual plants can be compensated by closer spacing.

Varieties like Kor and Early Red do not cause specific difficulties since they flower in any daylength. The vegetative period may be lengthened to some extent by a correct choice of the sowing date, but this can only be achieved in the sub-tropics since flowering in these varieties is only markedly retarded in photoperiods of 15 h and 16 h. Therefore, to obtain optimum seed and hay yields, it seems advisable to sow such varieties shortly before the longest day. As vegetative growth and flowering may be opposing tendencies in the early growth stages of some varieties, a lengthening of the vegetative period also might be achieved by choosing such a sowing date that vegetative growth is favoured by conditions other than the daylength. Especially warm and moist seasons are favourable for vegetative growth and thus may retard flowering until conditions become more favourable for flowering. This may also apply to almost insensitive varieties such as Ombligo Negro.

A completely different picture is found for the variety FC 31705 (FC stands for forage crop). In this variety no effect of vegetative growth on flowering was observed and all inflorescences developed normally. From a photo-physiological point of view no explanation could be given for the practical use of this variety as a forage crop. In this case, however, it may well be that the plant shows a marked thermoperiodical reaction as far as vegetative growth is concerned, but this has not been investigated.

In the foregoing it was stated that in view of the temperature cowpea may be grown all the year round, which enables the grower to choose the right sowing date. However, other factors than the daylength may interfere with this choice. For instance, when cowpeas are grown for seeds, they are usually sown in such a season that pods mature in a dry period. Sowing in dry periods will be impossible when there is no irrigation. A second point is the importance of the crop, used either as a second crop or as the main crop itself, which determines the time available for its cultivation. This holds particularly when the cowpea is grown as a second crop and when the sowing date of the main crop is committed to a certain time of the year.

When cowpea is grown for the green pods and seeds, in other words when pods are removed before they have matured, the sowing date is of minor importance provided vegetative growth is not inhibited in short days. For this purpose it may be advisable to use varieties which are not sensitive to the photoperiod. When sown during the longer days of the year, flowering will not be retarded whereas early flowering does not imply a reduction in the yield since both growth and flowering may continue owing to the constant removal of immature pods.

Summarizing it may be said that the photoperiodic response of the varieties and the purpose for which the crop is grown determine to a great extent the sowing date. In practice also factors other than the daylength come into play and may restrict the cultivation to a certain time of the year which in fact may be unfavourable for optimum yields.

SUMMARY

1. The influence of the photoperiod on vegetative growth and flowering of some cowpea [*Vigna unguiculata* (L.) WALP.] varieties was studied. Most experiments were carried out in the greenhouse where the temperature was controlled within certain limits. The influence of temperature was investigated in controlled-environment rooms or in cabinets where temperature and photoperiod could be regulated.

2. In a preliminary experiment 14 varieties were grown in 15 photoperiods ranging from 6 to 24 h. In all varieties investigated it was observed that lengthening of the daylight period with fluorescent light (intensity 6000 erg/sec/cm^2) caused an increase in stem length, internode length, number of leaves and leaf size (Chapter III, § 1).

3. In respect of growth habit four types of varieties were distinguished (Chapter III, § 1.1). Experiments on the vegetative growth were mainly conducted with varieties in which growth was inhibited in short days, *viz.* Ex-Lafia-A and Ex-Bukuru-A. In short days growth in these varieties was arrested before the onset of flowering, whereas in long days growth continued for at least 6 to 7 months. Once growth was arrested in short days, a long-day treatment could not overcome this inhibition any more (Chapter III, § 2.2).

4. It was demonstrated that the leaves perceived the short-day stimulus and that the sensitivity of the plant to a short-day treatment increased with an increasing number of leaves (Chapter III, § 2.3). The older the plants the sooner short days arrested growth (Chapter III, § 2.1).

5. When plants were grown in long prior to short days (Chapter III, § 2.4), the sensitivity of the leaves to the short days appeared to have decreased considerably or to have vanished completely; in other words, there was an after-effect of the long-day treatment on the sensitivity of the leaves to short days.

6. In general, leaves exposed to short days exerted an inhibitive, leaves exposed to long days a promotive effect on stem elongation. The inhibitive effect of a short-day treatment could partly be overcome by gibberellic acid applications (Chapter IV, § 1). The effect of gibberellic acid on stem elongation was much more marked in the variety Ex-Lafia-A than in other varieties. A comparable effect occurred when the light intensity was reduced (Chapter III, § 2.5).

7. Under controlled temperature conditions it was found that in short days a diurnal change of temperature favoured stem elongation when the day temperature was kept at 30°C; a night temperature of 20°C being more favourable than one of 15°C (Chapter IV, § 2).

8. The results obtained in our experiments may be explained by assuming that the photoperiodically controlled growth of some cowpea varieties was caused by a balance between growth inhibitors and growth promotors. It was thought that in short days growth inhibitors and in long days growth promotors were produced.

9. With the node number of the first inflorescence on the main stem as a criterion for floral response to the photoperiod, experiments were conducted in which cowpea plants were exposed to a range of photoperiods between 6 and 24 h (Chapter V, § 1). The results showed that the cowpea may be regarded as a short-day plant. However, the variety Early Red clearly showed an ambiphotoperiodic reaction, a reaction type which has hitherto been reported for two other plant species only.

10. In the varieties investigated photoperiods ranging from 8 to 11 h appeared to be optimal for inflorescence initiation.

11. In most varieties the first inflorescence was never found below the third node. In grafting experiments it was demonstrated that inflorescence initiation could take place at the first and second node (Chapter V, § 2.4).

12. In some varieties the primary leaves already reacted to a short-day treatment, but it was shown that these leaves were less sensitive to the photoperiod than the higher located ones (Chapter V, § 2.2 and 2.3). The site of floral initiation in the varieties Early Red and Ombligo Negro suggested that the maximum sensitivity of the plant was reached when the fourth or fifth leaf had unfolded.

13. In the varieties Ex-Lafia-A and Ex-Bukuru-A, long days affected photoperiodic induction in subsequent short days (Chapter V, § 2.2 and 3.2).

14. Three stages in reproductive development, *viz.* inflorescence initiation (Chapter V, § 4.2), inflorescence development and anthesis, have been studied in some detail. It was shown that inflorescence development could be inhibited under non-inductive conditions. Notably a stimulation of vegetative growth appeared to affect inflorescence development adversely (Chapter V, § 4.3). In

the greenhouse flowering proper or anthesis was controlled by the change from daylight to either low-intensity lamp light or darkness. Under completely controlled conditions anthesis appeared to be regulated exclusively by the onset of darkness and, provided the nycto-period was long enough, occurred always about 12 hours after the plants had entered the dark period (Chapter V, § 4.4).

15. When inductive conditions became sub-optimal, interruptions in the sequence of inflorescence primordia readily occurred. In the varieties Early Red and Ombligo Negro, however, such interruptions were observed in almost all photoperiods used. In short photoperiods this phenomenon was restricted to the first 8 or 9 nodes (Chapter VI, § 1). Various factors have been studied to find an explanation for these temporary failures of inflorescence initiation. The results obtained in the experiments are explained by suggesting that such interruptions were due to discrepancies between the available floral stimulus and the rate of vegetative development (Chapter VI, § 2, 3 and 4).

16. The formation of a terminal inflorescence was investigated in one variety, PI 221731. Results in a defoliation experiment indicated that in this variety the level of photoperiodic induction required for inflorescence initiation was apparently low (Chapter VII).

17. Continuous removal of leaves above either the primary leaves, or the first, second or fourth trifoliate leaf on the main stem, influenced the production of flowers. Inhibition of fructification greatly stimulated the vegetative growth and the production of flowers, while flowering occurred for a much longer period. The production of flowers was also stimulated when the vegetative period was extended (Chapter VIII).

18. The agricultural implications of the foregoing findings are discussed from a photo-physiological point of view. In order to obtain an optimum seed yield it is suggested to sow plants at such a time of the year that a fairly long vegetation period can be obtained, *i.e.* during relatively long days. This would mean an increase of dry matter production and subsequently higher seed yield owing to the effect of long days on leaf area and the time of flowering. However, when the vegetative period becomes too long, seed yield may decrease in spite of increased total dry matter production (Chapter IX).

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SAMENVATTING

1. De invloed van de fotoperiode op groei en bloei van enkele cowpea [*Vigna unguiculata* (L.) WALP.] rassen werd bestudeerd. De meeste proeven werden uitgevoerd in een kas, waarin de temperatuur binnen bepaalde grenzen regelbaar was. De invloed van de temperatuur werd onderzocht in klimaatka-

mers of in klimaatkasten, waarin de temperatuur en de fotoperiode geregeld konden worden.

2. In een inleidende proef werd het fotoperiodieke gedrag van 14 rassen onderzocht. De planten werden opgekweekt bij 15 fotoperioden variërend van 6 tot 24 uur. In alle onderzochte rassen werd waargenomen dat verlenging van de daglicht periode met TL-licht (intensiteit 6000 erg/sec/cm^2) een toename van de stengellengte, de internodiënlengte, het aantal bladeren en het bladoppervlak teweeg bracht (Hoofdstuk III, § 1.1).

3. Op grond van verschillen in vegetatieve groei werden vier typen van rassen onderscheiden (Hoofdstuk III, § 1.1). Proeven over de vegetatieve groei werden hoofdzakelijk uitgevoerd met rassen waarvan de groei door korte fotoperioden geremd werd, nl. de rassen Ex-Lafia-A en Ex-Bukuru-A. Bij korte fotoperioden stond de groei in deze rassen stil vóórdat bloei optrad, terwijl bij lange fotoperioden de groei gedurende minstens 6 tot 7 maanden doorging zonder dat bloei optrad. Indien de groei eenmaal in korte fotoperioden geremd was, bleek het onmogelijk te zijn deze remming nog ongedaan te maken door een behandeling met lange fotoperioden (Hoofdstuk III, § 2.2).

4. Aangetoond kon worden dat de bladeren de korte-dag stimulus percipieerden en dat de gevoeligheid van de plant voor een korte-dag behandeling toenam met een toenemend aantal bladeren (Hoofdstuk III, § 2.3). Naarmate de planten ouder werden had een behandeling met korte fotoperioden sneller een groeiremming ten gevolge (Hoofdstuk III, § 2.1).

5. Wanneer de planten opgroeiden in lange dagen die vooraf gingen aan korte dagen, dan bleek de gevoeligheid van de bladeren voor de korte dag aanmerkelijk te zijn afgenomen of geheel te zijn verdwenen; met andere woorden, de lange-dag behandeling bleek een nawerking te hebben op de gevoeligheid van de bladeren voor korte dagen (Hoofdstuk III, § 2.4).

6. In het algemeen oefenden bladeren die aan korte fotoperioden werden blootgesteld een remmende, bladeren die aan lange fotoperioden werden blootgesteld een stimulerende invloed uit op de stengelstrekking. De remmende invloed van een korte-dag behandeling kon gedeeltelijk worden opgeheven door het toedienen van gibberella-zuur (Hoofdstuk IV, § 1). De invloed van gibberella-zuur op de stengelstrekking in het ras Ex-Lafia-A was sterker dan in de andere rassen. Een overeenkomstig effect deed zich voor indien de lichtintensiteit gereduceerd werd (Hoofdstuk III, § 2.5).

7. Bij proeven in klimaatkasten, waarbij de temperatuur werd geregeld, bleek dat in korte fotoperioden een dagelijkse wisseling van de temperatuur de stengelstrekking bevorderde. De dag-temperatuur werd op 30° C gehouden. Een nacht-temperatuur van 20° C was gunstiger dan een van 15° C (Hoofdstuk IV, § 2).

8. De resultaten die in onze proeven werden verkregen, kunnen mogelijk verklaard worden door aan te nemen dat het effect van de fotoperiode op de groei van enkele cowpea rassen veroorzaakt werd door een evenwicht tussen groeistoffen en remstoffen. Verondersteld werd dat in korte fotoperioden remstoffen en in lange fotoperioden groeistoffen werden geproduceerd.

9. Het effect van de fotoperiode op de bloei werd nagegaan in enige proeven waarbij het rangnummer van de knoop waarop de eerste bloeiwijze aan de hoofdas verscheen werd aangenomen als het criterium voor de bloeireactie; de fotoperioden die gebruikt werden varieerden van 6 tot 24 uur (Hoofdstuk V, § 1). De resultaten toonden aan dat de cowpea beschouwd kan worden als

een korte-dag plant. Dit met uitzondering van het ras Early Red, dat duidelijk een ambi-fotoperiodieke reactie liet zien, een reactie-type dat in de literatuur tot nu toe slechts voor twee andere plantesoorten werd vermeld.

10. Bij de onderzochte rassen bleken fotoperioden variërend van 8 tot 11 uur optimaal te zijn voor de aanleg van bloeiwijzen.

11. Het eerste bloemgestel werd bij de meeste rassen nooit lager gevonden dan de derde knoop van de hoofdstengel. In entproeven werd echter aangetoond dat de aanleg van bloeiwijzen eveneens plaats kon vinden op de eerste en tweede knoop (Hoofdstuk V, § 2.4).

12. Van sommige rassen reageerden de primaire bladeren reeds op een korte-dag behandeling doch er kon aangetoond worden dat deze bladeren minder gevoelig waren voor de fotoperiode dan de hoger geplaatste bladeren (Hoofdstuk V, § 2.2 en 2.3). Het ontstaan van bloeiwijzen op bepaalde knopen aan de hoofdstengel van de rassen Early Red en Obligo Negro duidde er op dat de maximale gevoeligheid van de planten voor de fotoperiode bereikt werd wanneer het vierde of vijfde blad was ontvouwd.

13. Lange fotoperioden beïnvloedden de inductie in daarop volgende korte fotoperioden in de rassen Ex-Lafia-A en Ex-Bukuru-A (Hoofdstuk V, § 2.2 en 3.2).

14. Van de generatieve ontwikkeling van de cowpea werden drie stadia onderzocht, nl. de aanleg van de bloeiwijze (Hoofdstuk V, § 4.2), de ontwikkeling van de bloeiwijze en de eigenlijke bloei. De ontwikkeling van de bloeiwijze bleek geremd te worden door niet-inductieve daglengten. Dit kwam vooral in sterke mate tot uiting wanneer de vegetatieve groei werd gestimuleerd (Hoofdstuk V, § 4.3). In de kas bleek het openen der bloemen bepaald te worden door de overgang van daglicht naar hetzij lamplicht van lage intensiteit, hetzij duisternis. In de klimaatkasten bleek dat onder gecontroleerde omstandigheden van licht en temperatuur de eigenlijke bloei uitsluitend bepaald werd door de overgang van licht naar donker; indien de donker-periode lang genoeg was openden de bloemen zich altijd ongeveer 12 uur nadat de planten de donkerperiode waren ingegaan (Hoofdstuk V, § 4.4).

15. Indien de inductieve omstandigheden voor bloemaanleg sub-optimaal waren, traden er veelvuldig onderbrekingen op in de volgorde waarin de bloeiwijze-primordia werden aangelegd op opeenvolgende stengelknopen. Bij de rassen Early Red en Ombligo Negro werden dergelijke onderbrekingen echter in practisch alle gebruikte fotoperioden waargenomen, doch in korte fotoperioden bleef dit verschijnsel beperkt tot de eerste 8 of 9 knopen (Hoofdstuk VI, § 1). Verschillende factoren zijn onderzocht om een verklaring te vinden voor deze tijdelijke onderbrekingen van de bloem-aanleg. Er werd aangenomen dat dergelijke onderbrekingen het gevolg waren van een ongunstige verhouding tussen de beschikbare bloeistimulus en de snelheid van de vegetatieve groei (Hoofdstuk VI, § 2, 3 en 4).

16. De vorming van een eindelingse bloeiwijze bij het ras PI 221731 werd onderzocht. De resultaten van een ontbladeringsproef duidden erop dat bij dit ras de mate van fotoperiodieke inductie die nodig is voor de aanleg van bloeiwijzen kennelijk gering is (Hoofdstuk VII).

17. Het voortdurend verwijderen van bladeren, hetzij boven de primaire bladeren, hetzij boven het eerste, tweede of vierde drietallige blad, beïnvloedde het aantal bloemen. Het voorkomen van de vruchtzetting bevorderde de vegetatieve groei en het aantal bloemen, terwijl de bloeiperiode aanzienlijk werd verlengd (Hoofdstuk VIII).

18. Er is nagegaan in hoeverre de resultaten van het bovenstaande onderzoek van betekenis zijn voor de verbouw van de cowpea. Indien het gewas geteeld wordt voor het zaad, dan is er van uitgegaan dat de zaaidatum zó gekozen dient te worden dat een tamelijk lange vegetatieperiode wordt verkregen. Dit houdt in dat de zaaidatum valt in een seizoen met "lange" dagen, hetgeen van invloed is op het bladoppervlak en de bloeidatum. De late bloei heeft een hoge drogestof produktie en hoge zaadopbrengsten ten gevolge. Bij een tè lange vegetatieperiode kan de zaad opbrengst echter weer dalen, zelfs wanneer de verdere drogestof produktie verder zou toenemen (Hoofdstuk IX).

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PHOTO 1. The development of an axillary inflorescence is inhibited in a photoperiodically sensitive variety as a result of the transfer from inductive (short) days to non-inductive (long) days. Note very short peduncle and shrivelled flower bud (a).

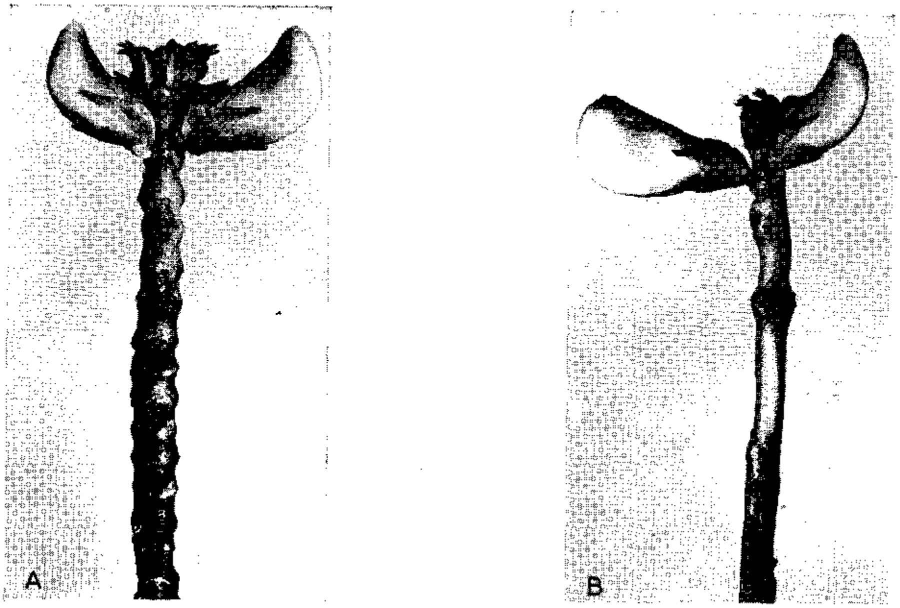

PHOTO 2. The development of an axillary inflorescence in the variety Going as affected by the continuous removal of flowers. Growth of main stem and laterals was reduced by pruning. The pictures show the main axis of the inflorescence. Between the "nodes" where flowers are produced, the "internodes" are either very short as a result of a continuous short-day treatment (A), or elongated as a result of a transfer of the plant to long-day conditions (B).