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THE SPECTRAL DEPENDENCE OF FLOWERING AND ELONGATION [1])

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CONTENTS

ABSTRACT

Experiments with *Salvia occidentalis* (SDP) and *Hyoscyamus niger* (LDP) demonstrated that at least two photoperiodic reactions are involved in the process leading to a long-day effect. The main-light-period reaction is more sensitive to near infra-red and blue light than to red or green light. The effect of near infra-red and blue light can be antagonized by red light. The nightbreak reaction, promoted by red light, is nullified by a relatively short exposure to near infra-red or blue light.

Experiments with various plant species on the elongation of internodes have shown that at relatively low intensities red light is more inhibitive than blue light. At relatively high intensities blue light is the most inhibiting spectral region. The inhibiting effect of red light on the elongation of hypocotyls of light-grown gherkin seedlings is antagonized by a subsequent exposure to near infra-red or blue light. The inhibiting effect of red light on the hypocotyl of dark-grown gherkin seedlings is much more pronounced when the seedlings are pre-irradiated with white or blue light.

[1]) Thesis of the State University Utrecht.

1. INTRODUCTION

1.1 General

The subject of this investigation concerns two aspects of the influence of light of different spectral regions on plant development, 1° the response of the internode elongation and 2° the flowering response of photoperiodically sensitive plants.

Although the ultimate results are different, both processes have in common the same photoreaction, as the effect of an exposure to red light can be reversibly antagonized by an exposure to near infra-red radiation. The result of a treatment with red and near infra-red radiation, alternately given, is determined by the last radiation.

This antagonism between red and near infra-red was first of all reported to control seed germination (Borthwick *et al.* 1952*a*, 1954; Toole *et al.* 1955; Jones *et al.* 1956). Subsequently it was reported to regulate various other processes too, such as the flowering of photoperiodically sensitive plants (Borthwick *et al.* 1952*b*; Downs 1956), auxin induced growth of *Avena*-coleoptile sections (Liverman *et al.* 1953), pigment formation in the cuticle of tomato fruits (Piringer *et al.* 1954), internode elongation of both dark-grown seedlings (Downs 1955) and light-grown plants (Hendricks *et al.* 1956; Downs *et al.* 1957), leaf expansion of dark-grown seedlings (Downs 1955; Livermann *et al.* 1953, 1955), germination of fern spores (Mohr 1956), opening of the plumular hook of dark-grown bean seedlings (Klein *et al.* 1956), formation of protochlorophyll (Withrow *et al.* 1956), anthocyanin formation (Siegelman *et al.* 1957; Mohr 1957), frond multiplication of dark-grown Lemna (Hillman 1957), indole-acetic-acid oxidase activity (Hillman *et al.* 1957), the endogenous diurnal rhythm (Loercher 1958) and the tactic movement of chloroplasts (Haupt 1958). Thus it is obvious that this photochemical reaction is involved in different processes of plant development.

1.2 Photoperiodism

In many plants the initiation of flower buds depends on daylength (photoperiodism). In short days (i.e. long dark periods) flower buds are initiated in short-day plants (SDP); long-day plants (LDP), however, remain vegetative. When the plants are exposed to long days (i.e. short dark periods), flower initiation is prevented in short-day plants but induced in long-day plants. Not in all photoperiodically sensitive plants is the photoperiodic response an absolutely qualitative one. In some species a quantitative response is obtained: flowering is only accelerated by a special daylength.

A long-day effect can also be obtained either by extending a short day (main light period) with several hours of light at a relatively low intensity level (supplementary light) or by interrupting the corresponding long dark period with a relatively short irradiation (night-break). This effect of a night interruption makes it obvious that the photoperiodic response depends on a reaction in the long dark period.

As HAMNER (1940) has shown, however, the influence of the main light period may not be neglected.

A. *Influence of light during the dark period*

For a supplemental light treatment red light is especially effective for prolonging a short day (RASUMOV 1933; WITHROW *et al.* 1936*a*, 1936*b*, 1940; WASSINK *et al.* 1950, 1951; STOLWIJK 1952, 1954; KÖNITZ 1958).

The reaction on supplemental light therefore has the same action spectrum as the nightbreak reaction of both short-day and long-day plants (PARKER *et al.* 1946, 1950; BORTHWICK *et al.* 1948). It has been shown that radiation of the whole visible spectrum is effective provided that sufficient energy is given. A maximum of activity was found in the red region, a minimum in the green part and a second, less effective, maximum in the blue-violet region of the visible spectrum.

A reversible antagonism between red and near infra-red radiation has been found in photoperiodism. The long-day effect of a nightbreak with red light can be nullified by a following irradiation with near infra-red (BORTHWICK *et al.* 1952*b*). This antagonizing effect of near infra-red decreases or is completely absent if either a period of darkness between the red and the near infra-red is given for too long a time or if the irradiation time of the near infra-red treatment increases (DOWNS *et al.* 1956, CATHEY *et al.* 1957).

B. *Influence of the main light period*

The flowering response of *Xanthium pennsylvanicum* (SDP) does not depend only on the length of the dark period (HAMNER 1940) but also on the light intensity of the photoperiod. One long dark period induces flowering provided that it is preceded by a light period of high intensity.

KÖNITZ (1958) found that the flower-initiating effect of a short-day treatment on *Chenopodium amaranticolor* (SDP) was inhibited when the light period was interrupted with near infra-red radiation. This inhibiting effect of near infra-red radiation could be reversed by a following exposure to red light.

WALLRABE (1944) showed that a short-day treatment of *Kalanchoë blossfeldiana* (SDP) in blue light is more effective than the same treatment in red light; in green light no flower initiation occurred at all. In preliminary experiments with *Kalanchoë* and some other plant species MEIJER *et al.* (1957) were unable to confirm these results. Even in green light a short-day effect was obtained.

In long-day experiments in white light with the short-day plants *Perilla* (DE ZEEUW 1953) and *Salvia occidentalis* (MEIJER 1957*a*), a short-day effect (i.e. flower initiation) was obtained when the light intensity was sufficiently low.

In some cases the influence of the light quality of the photoperiod on the effect of a long-day treatment was studied. When *Hyoscyamus niger* (LDP) was grown in light of different spectral regions no long-day effect was obtained when the long-day treatment was given in

yellow or green light. In red light, flower initiation was very much retarded as compared with the flowering response to a long-day treatment in blue, violet or red + near infra-red radiation (STOLWIJK *et al.* 1955). As in these experiments the violet and blue light were contaminated with near infra-red it might be possible that only the near infra-red region was responsible for this effect. CURREY *et al.* (1956), however, obtained the same effect in a long-day treatment in blue light without a near infra-red contamination.

This long-day activity of the violet-blue and the near infra-red regions appears quite remarkable, the more so as STOLWIJK *et al.* (1955) confirmed the results of PARKER *et al.* (1950) that red light —given as an interruption of a long dark period—is the most effective spectral region for obtaining a long-day effect. Similar results have been obtained in experiments with *Salvia occidentalis* (SDP) and some other plants (MEIJER 1957*a*, 1957*b*).

From the results of these long-day experiments in coloured light one cannot determine whether the photoperiodic response was influenced during the main light period or during the supplemental light period. In nightbreak experiments with *Salvia* (SDP) and *Hyoscyamus* (LDP) it was shown that the long-day effect of an interruption of the long dark period with red light depends on the light quality of the main light period too (MEIJER *et al.* 1957). A night interruption was only effective after a main light period in blue light; after a main light period in red or green light a nightbreak failed to induce a long-day effect.

It therefore seems obvious that in order to obtain a long-day effect at least three different reactions must take place: 1° a minimum rate of photosynthesis, 2° a specific main-light-period reaction and 3° a supplemental-light or nightbreak reaction. In this paper evidence is given in support of the assumption that whether a long-day effect is obtained or not depends on at least two photoperiodic reactions and not on the absolute duration of the photoperiod.

1.3 ELONGATION

In literature two opposite views exist about the influence of light of different spectral regions on the elongation of internodes:

1°. the blue part of the spectrum has the greatest inhibiting effect;
2°. red light is much more active in inhibiting the elongation than blue light.

KONINGSBERGER (1922), studying "light growth reactions", reported that a brief exposure to blue light of an intensity of 2 erg/cm²/sec was sufficient to retard temporarily the growth of Avena coleoptiles. Light of longer wave-length regions induced this effect only at much higher light intensities. Moreover the retardation due to blue light lasted longer than the retardation caused by an exposure to red light. The action spectrum of phototropism (e.g. GALSTON *et al.* 1949) also supports the conclusion of many investigators that blue light is the most active part of the spectrum in inhibiting the elongation of

internodes (e.g. POPP 1926; ROODENBURG 1940; STOLWIJK 1954). FUNKE (1944) even concluded "that the red part of the spectrum acts like darkness" as far as the formative effect of light is concerned.

This conclusion, however, is not in agreement with the results of many other investigators who found that blue light was less effective then red light (e.g. DU BUY *et al.* 1930; WENT 1941; WITHROW 1941; WEINTRAUB *et al.* 1947; PARKER *et al.* 1949). This discrepancy could possibly be due to differences in the experimental methods e.g. to impurities of the spectral regions used, to the pretreatment of the plant material, to the light intensity or to differences between plant species.

A. *Light purity*

In some experiments plants were grown in day-light from which different short wave-length regions were eliminated by filters. POPP (1926) and SHIRLEY (1929) found that a lack of blue light caused an increase in internode elongation.

ROODENBURG (1940) using different gas discharge lamps, came to the same conclusion. ÅBERG (1943), however, found that the internodes of tomato plants in mercury light ("blue") were much more elongated than in neon or sodium light (respectively "red" and "yellow"). VAN DER VEEN (1950) used the light of coloured fluorescent lamps, which were coated with different monophosphors. Although he did not purify this coloured light the same results were obtained as with light obtained from fluorescent lamps and filtered by suitable filters (WASSINK *et al.* 1952; STOLWIJK 1954). Short internodes are formed in light of the blue-violet region, whereas in the longer wave-length regions internodes show a marked elongation. This was confirmed with several plant species by VINCE (1956, — *et al.* 1957) and MEIJER (1957*b*).

Nevertheless it was found that a contamination of a spectral region with light of other wave lengths can have a pronounced influence. MEIJER (1957*a*) compared *Salvia occidentalis* plants grown in blue light and in blue light + near infra-red. This light was obtained from blue fluorescent lamps purified by two different blue filters. One filter transmitted only the short wave-length region, the other one transmitted also the near infra-red ($\lambda > 7000$ Å). As the elongation of internodes was markedly increased in blue light + near infra-red as compared to pure blue light it is obvious that even a contamination with small amounts of near infra-red emitted by the fluorescent lamp should not be neglected. It was also shown that an addition of near infra-red radiation to blue or green light resulted in an increased elongation (MEIJER 1957*b*).

ROODENBURG (1940) was probably the first to ascribe to near infra-red an elongating effect. This effect has been definitely demonstrated by WASSINK *et al.* (1951), STOLWIJK (1954), DOWNS (1955, — *et al.* 1957) and HENDRICKS *et al.* (1956). The elongating effect of near infra-red radiation can be reversed by red light (STOLWIJK 1954; DOWNS 1955; — *et al.* 1957).

It has been found that the elongating effect of blue light, reported

by WASSINK *et al.* (1951) and STOLWIJK (1954) must have been due to a contamination with near infra-red and not to the blue region itself (WASSINK *et al.* 1957; MEIJER 1957*a*). Nevertheless MEIJER (1957*b*, 1958*a*) obtained in some cases a stimulation of the elongation by pure blue-light.

B. *Pretreatment*

The varying results could also be due to the pretreatment of the plant material. Whether dark-grown seedlings have been used in the experiments or green plants previously raised in light might have an influence on the result.

Etiolated or dark-grown plants are characterized by a strong elongation of the internodes, the development of small leaves (as far as Dicotyledons are concerned) and usually a lack of chlorophyll (as far as Angiospermae are concerned). Relatively small amounts of light are enough to prevent etiolation: the elongation of the internodes decreases whereas the leaf size increases.

When dark-grown plants are used the material is not yet influenced by white light before the experiments start. With light-grown plants one will not find a primary effect on the elongation but a secondary one, i.e. on the inhibited elongation.

This difference in reaction has been clearly demonstrated by the effect of an irradiation with near infra-red or blue light. Near infra-red has an inhibiting effect on the elongation of dark-grown seedlings (WITHROW 1941; DE LINT 1957). On plants previously irradiated with white light (DOWNS *et al.* 1957) or light of different spectral regions (DE LINT 1957) near infra-red has an elongating effect. Similar effects have been reported for blue light (MEIJER 1957*b*, 1958*a*).

WASSINK *et al.* (1956) stated in a review that "in etiolated plant material the red spectral region is most effective in this respect (i.e. in the inhibition of elongation), whereas in light-grown plants and at high light intensities the violet-blue region of the spectrum is especially effective".

This statement is not always valid. It was shown that several plant species, previously raised in white fluorescent light, acquired much longer hypocotyls in blue than in red light. (MEIJER 1957*b*, 1958*a*). Again VINCE *et al.* (1956, 1957) obtained longer internodes with *Pisum* and *Calendula* in blue light than in red light. In her experiments with *Pisum* this author used "dark-grown" seedlings as the plants were exposed to light of the different wave-length regions directly after sowing. For *Calendula* it is not reported whether the plants were raised in white light before the treatment or not. We were able, however, to confirm this result with light-grown *Calendula* plants.

C. *Light intensity*

According to ÅBERG (1943) it seems possible that the light intensity might influence the results. He postulated that at low light intensities the red region is the most active, whereas at high light intensities

the blue-violet region is the most effective part of the visible spectrum for inhibiting the elongation. Although several investigators have compared light of different energy levels, this assumption has not been confirmed (WITHROW 1941; VINCE 1956, — *et al.* 1957).

D. *Plant species*

As different plant species did not give a similar reaction when grown under exactly the same conditions it was concluded that the response to light of different spectral regions depends more on differences in plant species than on the experimental method (VINCE 1956, — *et al.* 1957; MEIJER 1957*b*). In this paper it will be shown that this conclusion is rather premature and that plants of the same species react in a different way depending on the light intensities used.

2. MATERIAL AND METHODS

Various plants sensitive to daylength were used in the experiments on photoperiodism. *Sinapis alba*, *Arabidopsis thaliana* (3 strains), *Nasturtium palustre*, *Chrysanthemum parthenium*, *Hyoscyamus niger* and *Petunia hybr.* all long-day plants, were sown and raised in a glasshouse under short-day conditions and afterwards subjected to a treatment which was continued until flower buds were macroscopically visible. *Salvia occidentalis*, *Kalanchoë blossfeldiana*, *Euphorbia pulcherrima* and *Xanthium pennsylvanicum*, all short-day plants, were propagated by means of cuttings, the use of clones giving very homogeneous material. These plants were grown under long-day conditions, which prevented flower initiation. After the treatment had lasted sufficiently long to induce flower initiation when exposed to short days, the plants were transferred to the glasshouse under conditions of non-inductive daylength.

At the beginning of the treatment the plants were selected for uniformity. A control group stayed under conditions of non-flower-inducing daylength and was compared with the treated plants to ascertain that flower initiation had not already been induced before the treatment started. The youngest developed leaf was marked at the beginning of an experiment and after the experiment was discontinued all the newly developed leaves or pairs of leaves were counted. Plants were considered to be vegetative when this number of leaves of the non-generative plants was larger than the number of leaves of the generative plants, developed before flower buds were initiated. Moreover the plants were dissected.

In this paper the influence of the light quality on the photoperiodic response is studied with special reference to the long-day effect on *Salvia occidentalis*. A long-day treatment prevents flower initiation in short-day plants and promotes this process in long-day plants. For this reason the results obtained with long-day plants and short-day plants are compared in terms of short-day effect or long-day effect and not in terms of flowering or non-flowering response.

For the sake of convenience the length of a supplemental-light

period is given in number of hours, the duration of a nightbreak in number of minutes followed by an apostrophe.

The experiments with *Salvia occidentalis* are described in 3.1–3.1.3. The results obtained from experiments with other plants are given in 3.1.4.

The influence of light of different spectral regions on elongation was studied on various plant species: *Solanum lycopersicum* (tomato, "Victory"), *Hyoscyamus niger*, *Sinapis alba*, *Cucumis sativus* (gherkin, "Venlose niet plekkers"), *Phaseolus vulgaris* (bean, "Vroege Wagenaar") and *Mirabilis jalapa*.

Two different methods were used.

1. The seeds were left to germinate and the seedlings raised in white light before the treatment with coloured light started ("light-grown plants").

2. The seedlings were not previously exposed to white light but were raised from seed in the light cabinets. Although these seedlings were exposed to coloured light, they will be referred to as "dark-grown seedlings" in contrast with the "light-grown seedlings" which had received white light prior to the treatment in the light cabinets.

In the experiments with "light-grown plants" 7–10 plants were used per treatment. The seeds were sown in seed pans and the seedlings potted after some time. As soon as the plants resumed growth, they were selected and subjected to the treatment.

"Dark-grown seedlings" were sown in pots about 20–25 seeds per pot, except beans of which 7 seeds were used per pot. Some days after germination the seedlings were selected for uniformity. The most vigorous seedlings, which had germinated early, and the seeds which had just started to germinate or had not germinated yet were discarded. The length of internodes was measured each 2–4 days until the organ showed to have finished elongation. The results of these experiments are given in 3.2.

The light cabinets in which the plants were exposed to light of different spectral regions have been described before (VAN DER VEEN *et al.* 1958). Fluorescent lamps (80 Watt) are mounted to the top and at two sides. In this way high light intensities and an equal light distribution are obtained. In those cases in which low light intensities were wanted, either cages of gauze were used or a number of lamps was switched off. In the experiments with supplementary light (3.1.2) and with "very low intensities" (3.2) only some of the lamps mounted to the top were switched on.

The lamps also provided the heat; the temperature was kept constant by means of a water-cooling system controlled by a thermostat. The day temperature was kept at 22° C. When the lamps were switched off the temperature decreased to that of the surrounding room, viz. 17° C. When only some of the lamps were used (see above) it was necessary to use heating elements also controlled by a thermostat. In this way it was possible to keep the temperature constant between 21.5° and 22.5° C.

The visible radiation was obtained from different types of fluo-

rescent lamps ("TL") with suitable filters of "Plexiglas" (Röhm & Haas). The characteristics of the light conditions have been given extensively in a previous paper (MEIJER 1957*a*). "TL" 33 lamps were used to provide "white" light. Red light was obtained in the wave length region of $\lambda = 6000$–7000 Å, although $\pm$ 2 % radiation was emitted in the infra-red region ($\lambda > 7000$ Å). Green light was more or less restricted to the region of $\lambda = 5000$–6000 Å. Blue light, without a contamination of red or near infra-red, consisted of radiation in the region of $\lambda = 4000$–5300 Å. Less than 1 % was obtained in the ultra-violet region ($\lambda < 4000$ Å). Near infra-red (= far red) radiation of the wavelength region of $\lambda > 7000$ Å was obtained from either incandescent lamps or neon lamps. In both cases the radiation was filtered by a combination of "Plexiglas" filters which transmitted radiation with $\lambda > 7000$ Å. To avoid too much radiation with $\lambda > 10000$ Å—which is known to have only a temperature effect—a water filter of 2 cm thickness was used. The intensity is given for the region of $\lambda = 7000$–8000 Å. As incandescent light shows a continuous spectrum and neon light a line spectrum, the intensities of near infra-red radiation obtained from these two types of lamp cannot be compared. Unless stated otherwise, near infra-red radiation was obtained from the incandescent lamps.

The light intensities are given in $\mu W/cm^2$. Foot candles or lux cannot be used because these units depend on the sensitivity of the human eye. Radiation was measured with a photocell. As the sensitivity of a photocell changes with the wavelength, it was calibrated against a thermopile for each combination of lamps and filter(s). The light intensities were measured as incident on a horizontal surface.

3. EXPERIMENTAL RESULTS AND DISCUSSION

3.1 PHOTOPERIODISM

Preliminary experiments in white light have shown that *Salvia occidentalis* is an obligate short-day plant. Specimens irradiated during 16 hours per day remained completely vegetative. When the irradiation was restricted to 10 hours of light per day, flowering was initiated.

The degree of flower initiation depends on the number of short days (10 hours of light per day) to which plants are exposed. It was found that a short-day treatment during 10 days or less was without effect. When the treatment lasted at least 16 days flowering was initiated and in the following long days a normal inflorescence bud was formed. A short-day treatment of 10 to 16 days resulted in a slight flower induction. In the long days which followed only some bractlike leaves developed and the vegetative growth of the growing points was resumed. In the following experiments the treatment lasted at least 21 days to make sure that flowering was sufficiently induced.

The critical daylength was determined by exposing plants to white

fluorescent light during photoperiods of different lengths. It was found that this critical daylength was between 13 and 15 hours of light per day (Table 1). In this experiment the light intensity during the whole photoperiod was 2900 μW/cm^2. The treatment lasted 26 days after which the plants were transferred to long-day conditions.

TABLE 1

The influence of the length of the photoperiod in white fluorescent light on the flowering response of *Salvia occidentalis*. Light intensity: 2900 μW/cm^2. Duration of the treatment 26 days. Number of plants per treatment 3. + = generative (short-day effect), — = vegetative (long-day effect). Observations 26 and 42 days after the beginning of the treatment.

Length of photoperiod in hrs per day	Condition of the growing point after:						Number of newly formed leaf pairs after 42 days					
	26 days			42 days			+			—		
9	+	+	+	+	+	+	4	4	5			
11	+	+	+	+	+	+	5	5	5			
13	—	—	—	+	+	+	6	6	6			
15	—	—	—	—	—	—				> 9	> 9	> 9
16	—	—	—	—	—	—				> 9	> 9	> 10

The last observations were made 42 days after the beginning of the treatment. In the subsequent long-day experiments the photoperiod was 16 hours of light per day, this being of sufficient length for obtaining a long-day effect, i.e. the prevention of flower initiation.

3.1.1 Long-day treatment

a. *White light*

It appeared that the critical daylength also depends on the light intensity of the photoperiod, irradiation during 16 hours of light per day not always having a long-day effect on the flowering response of *Salvia occidentalis*. In Table 2 the results of two experiments are presented. The plants were grown in 16 hours of white fluorescent light

TABLE 2

The influence of the light intensity of the photoperiod on the flowering response to a long-day treatment in 16 hrs white fluorescent light per day. Experiment I: 3 plants per treatment, observed after a treatment of 39 days. Experiment II: 6 plants per treatment, observed 39 days after the beginning of a treatment of 26 days. + = generative (short-day effect); — = vegetative (long-day effect), (—) = vegetative.

Light intensity in μW/cm^2	85	250	400	660	850	1250	2500
Experiment I		+			—	—	—
Experiment II	(—)		+	+			

per day at different intensities. The last observations in Experiment I were made after the treatment had lasted 39 days; in Experiment II, 39 days after the beginning of the treatment which lasted 25 days. It was found that flowering was initiated if the light intensity was sufficiently low, despite the fact the plants were exposed to long days.

At an intensity of 850 μW/cm^2 or higher a long-day effect was obtained whereas at intensities from 250 to 660 μW/cm^2 flower initiation was not prevented. In light of an intensity of 85 μW/cm^2 no flower initiation occurred, the growth being quite poor, only two leaf pairs developing during the treatment. At higher intensities this number was 4 or 5.

b. *Coloured light*

To investigate which spectral region is the most active in obtaining a long-day effect, the plants were exposed to long days in red, green or blue light.

In a number of experiments 16 hours of red, green blue or white light were used per day. Gauze filters enabled three or four different light intensities to be compared in each experiment. The results are collected in Table 3. The duration of the treatment varied for the various experiments but was never less than 26 days.

TABLE 3

The influence of the light quality on the photoperiodic effect of a long-day treatment of 16 hrs light per day. + = generative (short-day effect); — = vegetative (long-day effect); (—) = vegetative.

Irradiation in hrs per day	Light intensity in μW/cm^2 0 500 1000 1500
16 Red	(—) + + — — — —
16 Green	(—) + + + + —
16 Blue	(—) — — — — —
16 White	(—) + + + — —

It is obvious that in a long-day treatment light from each region of the visible spectrum is active in causing a long-day effect provided that the light intensity is sufficiently high. Blue light (16B), however, showed to be the most active type of light, followed by red light (16R). Green light (16G) is only slightly active in this respect, rather high intensities being necessary for obtaining a long-day effect by means of a long-day treatment of 16 hours of light per day. At very low intensities (85 μW/cm^2) no flower initiation occurred during any light treatment. This prevention of flower initiation may be due to reasons other than a long-day effect of the 16-hour light treatment as it was found that at low light intensities even a short-day treatment fails to initiate flower buds.

Although irradiation with 16 hours of red light per day (16R) at an intensity of 370 μW/cm^2 did not prevent flower initiation (see Table 3), this short-day effect is different from the effect of a short-day treatment (10 hours of light per day) in red light of the same intensity. In consequence of the short-day treatment (10R), flowering was initiated as soon as 5 new leaf pairs had developed. After the long-day

treatment (16R), however, the number of leaf pairs developed before flower buds were initiated was eight and the flower buds became later visible too. So there still was some indication of an inhibition of flower initiation (long-day effect) by the long-day treatment (16R) as compared to the response to a short-day treatment (10R) in red light. At an intensity of 260 μW/cm^2 a long-day treatment in red light showed hardly any long-day effect as the appearance of the flower buds was scarcely delayed; the average number of newly formed leaf pairs being 6.3.

A long-day treatment in green light (16G) at an intensity of 500 μW/cm^2 did not cause any long-day effect. Flower buds were initiated after 5 newly formed pairs of leaves. At 900 μW/cm^2 a slight retardation was found; a small increase could be observed in the number of leaf pairs formed prior to the first flower bud, viz. 6.5.

c. *Near infra-red radiation*

The influence of near infra-red radiation on the photoperiodic effect of a long-day treatment in coloured light was studied in the following experiments.

The plants were exposed to red, green or blue light with and without an addition of near infra-red during 16 hours per day (16R, 16RIR, 16G, 16GIR, 16B, 16BIR). The light intensity of the visible radiation was 300 μW/cm^2. It was found (see Table 3) that under these conditions a long-day treatment in red or green light does not prevent flowering i.e. no long-day effect is obtained. Those plants which were exposed to near infra-red radiation were unilaterally irradiated, this method permitting intensity ranges up to 130 μW/cm^2 to be studied. In all 9 different intensities were used. At each intensity only one plant was used to avoid one plant shading the other. At the lowest intensity, 3 plants were used. The number of control plants was 10. After this treatment which lasted 30 days, the plants were transferred to long-day conditions. The last observations were made after 70 days. The results are shown in table 4 (Plate 1–a).

TABLE 4

The influence of near infra-red radiation on the photoperiodic effect of a long-day treatment (16 hrs per day) in red, green or blue light (300 μW/cm^2). Duration of the treatment 30 days. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 70 days.

Light treatment 16 hrs per day	Intensity of I R in μW/cm^2 0 · 50 100 150		
Red + I R	+	+++ +	— — — — —
Green + I R	+	+++ —	— — — — —
Blue + I R	—	— — — —	— — — — —

Near infra-red radiation used simultaneously did not influence the effect of a long-day treatment in blue light (16B, 16BIR); all plants

remained completely vegetative. After 70 days the average number of newly formed leaf pairs of plants treated with 16B and 16BIR was 10.8 and 9.1 respectively.

Addition of near infra-red to green light (16GIR) was found to be very effective in causing a long-day effect since it prevented flowering, initiated in long-days in green light (16G). In 16G the average number of new leaf pairs developed before flower initiation occurred was 5.9. In 16GIR, with a near infra-red intensity of 45 $\mu W/cm^2$ or higher, plants remained vegetative and the number of newly formed leaf pairs was more than 9. Near infra-red of lower intensities did not prevent flower initiation but at most retarded it a little. With increasing intensities from 0–35 $\mu W/cm^2$ the number of newly formed leaf pairs was 6, 6, 6 and 7, respectively.

In long days in red light (16R) flower initiation occurred; it was, however, retarded as compared with plants grown in green light (16G). The average number of leaf pairs developed before flower initiation occurred was 7.7. Addition of near infra-red (16RIR) of a higher intensity than 50 $\mu W/cm^2$ prevented flowering (long-day effect); after 70 days more than 10 pairs of leaves were developed and still no sign of flower initiation could be observed. At lower intensities of near infra-red, flower initiation was not prevented but more or less retarded as compared with plants grown in red light without any addition of near infra-red (16R). With the near infra-red intensity increasing from 0–45 $\mu W/cm^2$ the number of leaf pairs developed before flower buds were initiated was 7.7, 9, 10, 10 and 10, respectively.

In experiments with 16 hours green + near infra-red per day, in which the number of different intensities of near infra-red investigated was reduced to 3 or 4, it was possible to treat simultaneously 3 or 4 plants at each intensity. Probably the effect of one plant shading the other was even better avoided under these conditions since it was found that in this case even 30 $\mu W/cm^2$ near infra-red radiation were effective in producing a long-day effect.

Similar results were obtained when the intensity of the visible radiation was increased. However, at an intensity of e.g. 510 $\mu W/cm^2$, already an irradiation with red light during 16 hours per day was sufficient for obtaining a long-day effect, flower initiation then being prevented. Addition of near infra-red radiation (16RIR) did not counteract this long-day activity of the red light.

In preliminary experiments the plants were exposed to 16 hours of green light per day (16G) to which near infra-red was added during

a) the last 8 hours (8G 8GIR)
b) the first 8 hours (8GIR 8G) or
c) the total photoperiod (16GIR)

It was found that a long-day treatment with 16 hours of green light already resulted in a long-day effect when only during part of the photoperiod near infra-red was added. The results of one of these experiments are given in Table 5.

The intensity of the green light was 400 μW/cm^2 and of the near infra-red radiation 160 μW/cm^2. The duration of the treatment was 25 days after which the plants were transferred to long-day conditions. The results show that it made no difference whether the near infra-red was added during the first or the second 8 hours of the photoperiod.

TABLE 5

The influence of an addition of near infra-red (200 μW/cm^2) on the photoperiodic effect of a long day treatment (16 hrs per day) in green light (400 μW/cm^2). G = green, IR = near infra-red. Duration of the treatment 25 days. Number of plants per treatment 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 48 days.

Light treatment		Condition of the growing point		
8 hrs	8 hrs			
8G	8G	+	+	+
8G	8GIR	—	—	—
8GIR	8G	—	—	—
8GIR	8GIR	—	—	—

If, however, the duration of the near infra-red irradiation was shortened its effect was clearly influenced by the moment at which this radiation was added. In the following experiment plants were exposed to 2, 4 or 8 hours of green + near infra-red, either followed or preceded by 14, 12 or 8 hours of green light (2GIR 14G, 4GIR 12G . . . 14G 2GIR) respectively. The intensity of the green light was 370 μW/cm^2 and of the near infra-red 130 μW/cm^2. The treatment lasted 25 days, after which the plants were exposed to long days. The results are given in Table 6.

TABLE 6

The influence of near infra-red (130 μW/cm^2) on the photoperiodic effect of a long-day treatment (16 hrs per day) in green light (370 μW/cm^2). Duration of the treatment 25 days. Number of plants per treatment 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 42 days.

Light treatment in hrs per day		Condition of the growing point		
2GIR	14G	+	+	+
4GIR	12G	+	+	—
8GIR	8G	—	—	—
8G	8GIR	—	—	—
12G	4GIR	—	—	—
14G	2GIR	—	—	—

The plants which remained vegetative showed 10 or 11 pairs of leaves, developed in the 42 days after the beginning of the treatment. The generative plants stopped leaf formation after 6 or 7 pairs of leaves and subsequently initiated flower buds.

It is obvious from these results that an addition of near-infra-red during 4 hours per day contributed more towards obtaining a long-day effect when given at the end (12G 4GIR) than at the beginning of the 16-hour green light period, (4GIR 12G). Added at the end of

the daily light period, 2 hours of near infra-red (14G 2GIR) were still effective in preventing flower initiation, but they were completely ineffective when given at the beginning of the light period (2GIR 14G).

In other experiments the near infra-red radiation was alternated with green light. In one of these experiments the intensity of the green light was 1200 μW/cm^2 and of the near infra-red (obtained from a neon lamp) 150 μW/cm^2. The daily irradiation with green light lasted 16 hours (16G). One hour of this green light was replaced by near infra-red which was given 0, 3, 6, 9, 12 or 15 hours after the beginning of the light period (1IR 15G, 3G 1IR 12G . . . 15G 1IR). The plants were subjected to this treatment during 25 days and afterwards transferred to long-day conditions. The last observations were made after 48 days; the results are presented in Table 7 (Plate 1–b).

TABLE 7

The influence of near infra-red (150 μW/cm^2) on the photoperiodic effect of a long-day treatment (16 hrs per day) in green light (1200 μW/cm^2). Duration of the treatment 25 days. Number of plants 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 48 days.

Light treatment in hrs per day			Condition of the growing point		
—	—	16G	+	+	+
—	1IR	15G	+	+	+
3G	1IR	12G	+	—	—
6G	1IR	9G	—	—	—
9G	1IR	6G	+	+	+
12G	1IR	3G	+	+	+
15G	1IR	—	—	—	—

The vegetative plants developed 10 to 11 new pairs of leaves in the 48 days after the beginning of the experiment. In the generative plants flower initiation occurred after about 6 pairs of new leaves had been formed.

It is clear that an irradiation with 1 hour of near infra-red is only effective in causing a long-day effect if it is preceded by a green light period of at least 3 hours (3G1 IR 12G). On the other hand such a preceding irradiation cannot be the only condition for obtaining a long-day effect. 9G 1IR 6G and 12G 1IR 3G did not have any long-day effect at all, although in these groups the near infra-red was preceded by even more than 3 hours of green light. Probably a second condition exists: light is also necessary in a period about 9 hours after the beginning of the irradiation with near infra-red. Those treatments which resulted in a long-day effect fulfilled both conditions viz. 15G 1IR, 6G 1IR 9G and 3G 1IR 12G (partly). When flowering was not prevented, either the first condition was not fulfilled viz. 1IR 15G, or the second condition viz. 9G 1IR 6G and 12G 1IR 3G.

d. *Antagonism*

It has been reported that the long-day effect of an interruption of a long night (= short day) with red light can be antagonized by a subsequent exposure to near infra-red radiation. The following

experiments were carried out to investigate whether, conversely, the long-day effect of near infra-red and possibly also of blue radiation can be counteracted by a subsequent exposure to red light or not.

The plants were exposed to 15 hours of green light followed by

a) 1 hour of green light (16G)
b) 1 hour of green and ½ hour of red light (16G ½R)
c) 1 hour of near infra-red (15G 1IR) and
d) 1 hour of near infra-red and ½ hour of red light (15G 1IR ½R).

The intensity of both the green and the red light was 650 μW/cm^2. The near infra-red was obtained from a neon lamp with an intensity of 120 μW/cm^2. Each group consisted of 5 plants. After a treatment of 28 days the plants were transferred to long days. The results of this experiment are given in Table 8. (Plate 1–c).

TABLE 8

The antagonizing activity of red light (650 μW/cm^2) on the photoperiodic effect of near infra-red (120 μW/cm^2) given after a long day in green light (650 μW/cm^2). Duration of the treatment 28 days. Number of plants per treatment 5. + = generative (short-day effect), — = vegetative (long-day effect). Observations after 60 days.

Light treatment in hrs per day			Condition of the growing point				
15G	1G	—	+	+	+	+	+
15G	1G	½R	+	+	+	+	+
15G	1IR	—	—	—	—	—	—
15G	1IR	½R	+	+	+	+	+

It is obvious from these results that the long-day effect caused by 1 hour of near infra-red irradiation (15G 1IR) was nullified by a subsequent exposure to red light (15G 1IR ½R). This red light itself (16G ½R) did not influence the effect of a long-day treatment in green light (16G).

Similar experiments were carried out with blue light instead of near infra-red. In one of these experiments the intensity of the green light was 640 μW/cm^2 and that of both the blue and the red light 760 μW/cm^2. Each lot consisted of 6 plants. After the treatment which lasted 25 days the plants were kept in long-day conditions. The results presented in Table 9 (Plate 1–c) show that the long-day effect of blue light is completely comparable with the effect of near

TABLE 9

The antagonizing activity of red light (760 μW/cm^2) on the photoperiodic effect of blue light (760 μW/cm^2) given after a long day in green light (640 μW/cm^2). Duration of the treatment 25 days. Number of plants per treatment 6. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 70 days.

Light treatment in hrs per day			Condition of the growing point					
15G	1G	—	+	+	+	+	+	—
15G	—	1R	+	+	+	+	+	+
15G	1B	—	—	—	—	—	—	—
15G	1B	1R	+	+	+	+	+	—

infra-red radiation, since both can be antagonized by a subsequent exposure to red light.

From these experiments carried out in long days it can be concluded that blue and near infra-red radiation are the most active types of light in preventing flowering, i.e. for obtaining a long-day effect. Red light was much less effective whereas in green light only at relatively very high intensities a long-day effect could be obtained. In addition it became apparent that this long-day effect caused by blue or near infra-red radiation can be antagonized by a subsequent irradiation with red light.

3.1.2 Supplemental light treatment

The results presented in the foregoing chapter, showing that blue and near infra-red are more active in causing a long-day effect than red or green light, are not in agreement with the results obtained with numerous plants from supplemental or nightbreak experiments, which have shown that red light is the most active type of light.

In a preliminary experiment with *Salvia occidentalis*, the plants were exposed to short days of 8 hours of white fluorescent light per day (main light period). The intensity was 2100 μW/cm^2. During the 8 hours after this main light period, the plants were

a) kept in darkness (8W) or irradiated with
b) red (8W 8r),
c) green (8W 8g) or
d) blue light (8W 8b) of different intensities.

All plants were kept in darkness for the remaining 8 hours per day. Each lot consisted of 5 plants. After a treatment of 28 days, plants were replaced in long-day conditions. The last observations were made after 52 days, the results are given in Table 10.

TABLE 10

The influence of the light quality on the photoperiodic effect of 8 hrs supplemental light (8r, 8g or 8b) given after a main light period (short day) of 8 hrs white fluorescent light per day (2100 μW/cm^2). Duration of the treatment 28 days. 5 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 52 days.

Light treatment	Intensity of the supplemental light (r, g, b) in μW/cm^2									
in hrs per day	0	50	65	85	250	325	415	500	650	830
8W	+									
8W 8r			+			—			—	
8W 8g				+			+			+
8W 8b		—			—			—		

The generative plants developed 5 or 6 pairs of leaves before initiating flower buds, the vegetative plants showed 7 or 8 newly formed pairs of leaves. As can be seen in Table 10, at lower intensities blue light is more active than red light in prolonging the short main light period, resulting in a long-day effect. At higher intensities, both blue and red light are effective.

According to the available literature, experiments on the influence of supplemental light and nightbreak light have always been carried out with main light periods (short days) in white light. This paper describes a number of experiments carried out to determine the influence of the quality of the light, used during this main light period on the photoperiodic effects of supplemental light and nightbreak light (see also 3.1.3).

First of all it was necessary to find out whether the light quality influences the photoperiodic effect of a short-day treatment, i.e. the initiation of flower buds. To this purpose plants were exposed daily to 10 hours of red, green or blue light with an intensity of about 900 $\mu W/cm^2$. These short-day treatments lasted 2, 4, 6, 8, 10, 12, 14 or 16 days after which the plants were transferred to long-days. A short-day treatment during 10 days or less in red or in blue light and during 8 days or less in green light was ineffective in inducing flower initiation. If the short-day treatment lasted longer, plants exposed to red, green or blue light became generative to the same extent, at the same time and after the formation of about the same number of leaves. Apparently under these experimental conditions, the photoperiodic effect of a short-day treatment did not depend on the light quality of the photoperiod but only on the duration of the short-day treatment.

In the following experiment the influence of the light quality of both the main light period and the supplemental light period on the photoperiodic effect is demonstrated. Plants were irradiated daily with 10 hours of red (10R), green (10G), green + near infra-red (10GIR) or blue light (10B). The intensity of the visible radiation was 450 $\mu W/cm^2$ and of the near infra-red added to green light 115 $\mu W/cm^2$. After this main light period 3 plants of each group were exposed for another 8 hours to supplemental light of low intensity in red (10R 8r etc.) or blue (10R 8b etc.). This supplemental light treatment was given at a low intensity of 160 $\mu W/cm^2$. To obtain this low intensity, the plants were only irradiated from above, using the lamps mounted to the top of the light cabinet. For this reason this low light intensity is not quite comparable with those applied during treatments in which plants were irradiated from three sides. The same procedure was followed in all other experiments with supplemental light. After a treatment of 30 days, the plants were kept in long-day conditions for another 35 days. The results are given in Table 11 (Plate 1–d).

The generative plants developed 4–6 pairs of leaves before initiating flower buds; the vegetative plants showed about 12 newly formed pairs of leaves after 65 days.

Supplemental light, whether 8 hours of red or 8 hours of blue used after a short-day period in green light (10G 8r, 10G 8b) did not cause any long-day effect. If, however, near infra-red radiation was used simultaneously with the green light (10GIR), 8 hours of red as well as 8 hours of blue supplemental light (10GIR 8r, 10GIR 8b) did produce a long-day effect.

TABLE 11

Photoperiodic effect of a supplemental irradiation with 8 hrs red or blue light (160 μW/cm^2) given after a main light period of 10 hrs red, green, green + infra-red or blue light (450 μW/cm^2). Intensity of near infra-red 115 μW/cm^2. Duration of the treatment 39 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 65 days.

Main light period in hrs per day	Supplemental light period		
	8 hrs dark	8 hrs red	8 hrs blue
10R	+ + +	+ + +	+ — —
10G	+ + +	+ + +	+ + +
10GIR	+ + +	— — —	— — —
10B	+ + +	+ + +	— — —

After a main light period in blue light only a supplemental light treatment with blue light (10B 8b) caused a long-day effect; 8 hours of red light (10B 8r) did not prolong the short main light period.

After a short day in red light, 8 hours of supplemental red light (10R 8r) did not prevent flower initiation, supplemental blue light (10R 8b), however, did. The long-day effect obtained with 10R 8b was somewhat less pronounced than that obtained with 10B 8b. All the growing points, terminal or axillary, of the plants treated with 10B 8b remained completely vegetative, but the plants exposed to 10R 8b showed a generative tendency, one plant of this group developing 3 pairs of bractlike leaves after which normal vegetative growth was resumed; moreover, all the laterals of the plants of this group initiated flower buds.

In a similar experiment the main light period lasted only 8 hours and the intensity of the supplemental irradiation was only 95 μW/cm^2 in stead of 160 μW/cm^2 as in the foregoing experiment. The results of this experiment which lasted 30 days are collected in Table 12. The last observations were made 75 days after the beginning of the treatment. All plants which remained vegetative had developed about 15 new pairs of leaves, the generative plants initiated flowering after about 6–8 newly formed leaf pairs.

TABLE 12

Photoperiodic effect of a supplemental irradiation with 8 hrs red or blue light (95 μW/cm^2) given after a main light period of 8 hrs red, green, green + infra-red or blue light per day (470 μW/cm^2). Intensity of near infra-red: 115 μW/cm^2. Duration of the treatment 30 days. Number of plants per treatment 4. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 75 days.

Main light period in hrs per day	Supplemental light period		
	8 hrs dark	8 hrs red	8 hrs blue
8R	+ + + +	+ + + +	+ + + +
8G	+ + + +	+ + + +	+ + + +
8GIR	+ + + +	+ + — —	— — — —
8B	+ + + +	+ + + +	+ + + +

Under these conditions only a treatment with a main light period containing near infra-red radiation was active in producing a long-day

effect and blue supplemental light (8GIR 8b) was found to be more active than red supplemental light (8GIR 8r).

Thus the results of the experiments carried out in long days are in agreement with those of the experiments with supplemental light after a short-day period, all results indicating that blue and near infra-red radiation are more active than red light in preventing flowering (long-day effect).

In a previous paper it has been reported that red nightbreak light is more active than blue light in preventing flowering of *Salvia occidentalis*. (MEIJER *et al.* 1957). To get some information about the difference between nightbreak light and supplemental light treatments, experiments were carried out comparing both types of treatment and the change-over from one into the other.

The plants were grown in 10 hours of red (10R) and 10 hours of blue light (10B) per day; the light intensity was 670 μW/cm^2. After this short main light period, separate groups of 3 plants were treated with

a) 8 hours of red (10R 8r, 10B 8r) or blue light (10R 8b, 10B 8b),
b) 4 hours of darkness followed by 4 hours of red (—4D 4r) or 4 hours of blue light (—4D 4b),
c) 6 hours of darkness followed by 2 hours of red (—6D 2r) or 2 hours of blue light (—6D 2b),
d) 7 hours of darkness followed by 1 hour of red (—7D 1r) or 1 hour of blue light (—7D 1b),
e) 7½ hours of darkness followed by ½ hour of red (—7½D ½r) or ½ hour of blue light (—7½D ½b) and
f) no supplemental light (10R and 10B).

All plants were kept in darkness for the remaining 6 hours per day. The intensity of the supplemental red and blue light was 185 μW/cm^2. After 26 days the treatment was discontinued and the plants were returned to long-day conditions. The last observations were made after 56 days, the results are given in Table 13 (Plate 2–e).

TABLE 13

Photoperiodic effect of blue and red light (185 μW/cm^2) given in an 8-hour period following after a main light period of 10 hrs red or blue light (670 μW/cm^2). Duration of the treatment 26 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 56 days.

Main light period		10 hrs Red						10 hrs Blue					
Supplemental 8-hour period		red			blue			red			blue		
hrs dark	hrs light												
0	8	+	+	+*	—	—	—	+	+	+	—	—	—
4	4	+	+	+	+	+	+	—	—	—	—	—	—
6	2	+	+	+	+	+	+	—	—	—	+	+	+
7	1	+	+	+	+	+	+	—	—	—	+	+	+
7½	½	+	+	+	+	+	+	—	—	—	+	+	+
8	0	+	+	+				+	+	+			

*SEE TEXT.

The plants exposed to 10R or 10R 8r did not remain vegetative, but a treatment with 10R 8b prevented flower initiation. Although 10R 8r did not prevent flower initiation, yet this process was somewhat retarded (8 pairs of leaves formed before flower buds were initiated) when compared to the other groups of generative plants (4–6 pairs of leaves developed prior to flower initiation).

All plants, receiving a few hours of darkness between the main light period in blue light (10B) and the additional red light (—r) remained vegetative (10B 4D 4r . . . 10B 7½D ½r). If the red light, however, immediately followed the main light period (10B 8r) no long-day effect was obtained.

When blue light (—b) was given in the 8-hour period after 10B, a long-day effect was only obtained with 4 or 8 hours of additional blue light (10B 4D 4b, 10B 8b); less than 4 hours of blue light (10B 6D 2b, . . . 10B 7½D ½b) were not effective in preventing flower initiation.

It is obvious that as far as 10B 8r is concerned, the ineffectiveness of red supplemental light in causing a long-day effect cannot be due to an inactivity of the red light itself as 4 hours of red (10B 4D 4r) or less succeeded in preventing flower bud formation. On the contrary it is obvious that red light is even more active than blue light, ½ hour of red light (10B 7½D ½r) being already sufficient where 2 hours of blue light (10B 6D 2b) were ineffective. The ineffectiveness of 8 hours of supplemental red light (10B 8r) in producing a long-day effect might be caused by:

a) the absence of a dark period between the main light period and the supplemental light period, or

b) an antagonizing effect of red light (the first four hours of —8r).

In the following experiment plants were exposed to a short-day treatment of 8 hours of blue light per day (8B) with an intensity of 580 μW/cm^2. In the 8-hour period after this main light period the plants were

a) kept in darkness (8B) or treated with
b) 4 hours of darkness followed by 4 hours of red light (8B 4D 4r),
c) 8 hours of red light (8B 4r 4r)
d) 4 hours of blue followed by 4 hours of red light (8B 4b 4r),
e) 8 hours of blue light (8B 4b 4b) or
f) 4 hours of blue light followed by darkness (8B 4b 4D).

The intensity of both the blue and the red additional light was 200 μW/cm^2. After this 8-hour period all plants were kept in darkness for the remaining 8 hours per day. The treatment lasted 29 days after which the plants were transferred to long days. The last observations were made after 59 days.

The results presented in Table 14 (Plate 2–f) showed that the long-day effect of the last 4 hours of red light (8B 4D 4r) is prevented if it is preceded by 4 hours of red light (8B 4r 4r). 4 Hours of blue light given immediately after the main light period (8B 4b 4D) —which in itself did not cause any long-day effect—did not influence the activity of a following exposure to 4 hours of red light (8B 4b 4r).

TABLE 14

Photoperiodic effect of blue and red light (200 μW/cm^2) given in an 8-hour period after a main light period of 8 hrs blue light (580 μW/cm^2). Duration of the treatment 29 days. Number of plants per treatment 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 59 days.

Light treatment in hrs per day			Condition of the growing point		
Main light period 8 hrs per day	Supplemental 8-hour period				
8B	4D	4D	+	+	+
8B	4D	4r	—	—	—
8B	4r	4r	+	+	+
8B	4b	4r	—	—	—
8B	4b	4b	—	—	—
8B	4b	4D	+	+	+

Obviously, red light is more active than blue light in causing a long-day effect provided it is not given immediately after the main light period.

3.1.3 NIGHTBREAK TREATMENT

The influence of the light quality of the main light period on the photoperiodic effect of a nightbreak treatment was studied in the following experiments with *Salvia occidentalis*. Red light was used to interrupt the long dark period as it had been shown to be the most active in causing a long-day effect.

Six lots of plants were exposed to short days of 8 hours of red, green or blue light per day with and without a simultaneous addition of near infra-red radiation. Some of the plants of each group were irradiated with 15 minutes red light to interrupt the corresponding long dark period from 7.45 hours–8 hours after its beginning. The intensity of the light of the main light period was 450 μW/cm^2, of the near infra-red 200 μW/cm^2 and of the red nightbreak light 630 μW/cm^2. The number of plants per treatment was 3. After the experiment had lasted 25 days, the plants were transferred to long days. After 50 days the last observations were collected. The results are presented in Table 15. (Plate 2–g). The generative plants formed

TABLE 15

The influence of the light quality of an 8-hour main light period on the photoperiodic effect of a night interruption with 15 minutes red light (15'R). Intensity of the visible radiation of the main light period 450 μW/cm^2 and of the near infra-red 200 μW/cm^2. Intensity of the red nightbreak light 630 μW/cm^2. Duration of the treatment: 25 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 50 days.

Main light period in hrs per day	Nightbreak light					
	dark control			15'R		
8R	+	+	+	+	+	+
8RIR	+	+	+	+	—	—
8G	+	+	+	+	+	+
8GIR	+	+	+	—	—	—
8B	+	+	+	—	—	—
8BIR	+	+	+	—	—	—

about 5 leaf pairs before flowering was initiated, the vegetative plants had developed 9 or 10 new pairs of leaves after 50 days.

It is clear that an interruption of the long dark period with red light (—15'R) is only effective in preventing flowering when the preceding main light period contained blue or near infra-red radiation (8B–15'R or 8GIR–15'R).

In experiments with white fluorescent light it was often noted that under certain conditions this light is less active in causing a long-day effect than, e.g. natural day-light.

In the next experiments the plants were kept in short days of
a) 10 hours of blue light (10B) with an intensity of 670 μW/cm^2, or
b) 10 hours of white fluorescent light (10W) with an intensity of 3250 μW/cm^2.

From both groups some plants were kept in darkness for the remaining 14 hours (10B, 10W). Other plants of each group were irradiated with red nightbreak light. This light was given only from above; the intensity was 185 μW/cm^2. This irradiation lasted thirty minutes (—30'R), 60 minutes (—60'R) or one hundred and twenty minutes (—120'R) and was given from respectively 7½, 7 and 6 hours up to 8 hours after the beginning of the long night period of 14 hours. The treatment was finished after 26 days; the last observations were made after 80 days. The results are given in Table 16. The generative plants developed 5 to 7 pairs of leaves before flower buds appeared; the plants which remained vegetative showed 13 or 14 newly formed leaf pairs at the end.

TABLE 16

Photoperiodic effect of red nightbreak light (185 μW/cm^2) as influenced by the preceding short-day period of 10 hrs blue (670 μW/cm^2) or 10 hrs white fluorescent light (3250 μW/cm^2) per day. Duration of the treatment: 26 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 80 days.

Main light period in hrs per day	Nightbreak light (minutes per night)											
	dark			30'R			60'R			120'R		
10B	+	+	+	—	—	—	—	—	—	—	—	—
10W	+	+	+	+	+	+	+	+	—	+	—	—

The plants exposed to short days in blue light, proved that a night interruption with 30 minutes of weak red light (10B–30'R) was enough to cause a long-day effect. If, however, the plants were grown in 10 hours of white light per day, it was found that even a night interruption with 120 minutes of red light (10W–120'R) was not completely effective in preventing flowering; only two plants remained vegetative.

It may be noted here that the intensity of the white light was about five times the blue light intensity. As calculated from the emission spectrum of the lamp ("TL" 80W/33), white fluorescent light contains 25 % blue radiation in the wave-length region of λ = 4000–5000 Å i.e. about 800 μW/cm^2. This was even higher than

the intensity of 10B (670 μW/cm^2) for which a nightbreak with 30 minutes of weak red light was sufficient to cause a long-day effect.

As was shown in experiments mentioned before, both blue and near infra-red radiation are active in the same way: the activity of both can be antagonized by red light. The following experiments were carried out to determine whether the long-day effect of a night interruption with red light can be counteracted by a following exposure to blue in a similar way as by an exposure to near infra-red, the antagonistic effect of the latter having been proved for many plant species.

The plants were grown in 10 hours of blue light per day (10B). Five hours after the beginning of the long dark period groups of 4 plants were exposed to 10 minutes of red nightbreak light (–10'R) after which 0 minutes (10B–10'R), 15 minutes (10B–10'R15'RI) or 30 minutes (10B–10'R30'IR) near infra-red radiation were given. Other groups were not exposed to the red nightbreak light but only to 15 or 30 minutes near infra-red radiation (10B–15'IR and 10B–30'IR). In another experiment the plants were treated with 15, 30 or 60 minutes of blue light instead of near infra-red radiation. (10B–10'R15'B; 10B–15'B etc.). The intensity of the blue light was 580 μW/cm^2, of the red light 700 μW/cm^2 and of the near infra-red, obtained from a neon lamp, 175 μW/cm^2. The treatment lasted 25 days after which the plants were returned to long-day conditions; the last observations were made after 56 days.

The results of the experiment with near infra-red are given in Table 17 (Plate 2–h). The generative plants developed 4 or 5 pairs of leaves before flower buds appeared. After 56 days the vegetative plants showed 10 newly formed pairs of leaves.

TABLE 17

The antagonizing activity of near infra-red (175 μW/cm^2) on the long-day effect of a nightbreak with 10 minutes red light (700 μW/cm^2) after a main light period of 10 hrs blue light (580 μW/cm^2). Duration of the treatment 25 days. Number of plants per treatment 4. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 56 days.

Main light period in hrs per day	Night interruption in minutes per night		Condition of the growing point			
10B	—	—	+	+	+	+
10B	10'R	—	—	—	—	—
10B	—	15'IR	+	+	+	+
10B	10'R	15'IR	+	+	+	+
10B	—	30'IR	+	+	+	+
10B	10'R	30'IR	+	+	+	+

It is obvious that in *Salvia occidentalis*, too, the long-day effect of a night interruption with red light (10B–10'R) is nullified by a following exposure to near infra-red (10B–10'R15'IR) and 10B–10'R30'IR). The near infra-red radiation itself (10B–15'IR and 10B–30'IR) did not show a photoperiodic effect under these conditions as flower initiation was not prevented.

As can be seen in Table 18 (Plate 2–h) blue light too was effective in antagonizing the effect of red nightbreak light. In this experiment the generative, respectively vegetative, plants developed about the

TABLE 18

The antagonizing activity of blue light (580 μW/cm^2) on the long-day effect of a night interruption with 10 minutes red light (700 μW/cm^2) after a main light period of 10 hrs blue light (580 μW/cm^2). Duration of the treatment: 25 days. 4 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 56 days.

Main light period in hrs per day	Night interruption in minutes per night		Condition of the growing point			
10B	—	—	+	+	+	+
10B	10′R	—	—	—	—	—
10B	—	15′B	+	+	+	+
10B	10′R	15′B	+	—	—	—
10B	—	30′B	+	+	+	+
10B	10′R	30′B	+	+	+	+
10B	—	60′B	+	+	+	+
10B	10′R	60′B	—	—	—	—

same number of leaves as the corresponding plants in the foregoing experiment.

A nightbreak with blue light did not cause a long-day effect (10B–15′B ... 10B–60′B). However, 30 minutes of blue light were sufficient to antagonize the long-day effect of a foregoing exposure to 10 minutes of red light (10B–10′R30′B). It is remarkable that a longer exposure to blue light, viz. 60 minutes did not nullify this long-day effect of 10 minutes of red nightbreak light (10B–10′R60′B).

In the following experiments the photoperiodic effect of near infra-red, given as nightbreak light, is demonstrated. Two groups of plants were daily exposed to 8 hours of red light (8R) or to 8 hours of red light, followed immediately by one hour of near infra-red (8R1IR). Seven hours and 20 minutes after the end of the main light period lots of 4 plants, treated daily with 8R1IR, were exposed to

a) 10 minutes of red nightbreak light (8R1IR–10′R),
b) 10 minutes of red followed by 15 minutes of near infra-red (8R1IR–10′R15′IR) or followed by
c) 60 minutes of near infra-red (8R1IR–10′R60′IR) and
d) 60 minutes of near infra-red without preceding red light (8R1IR–60′IR).

The intensity of the red radiation during the main light period was 670 μW/cm^2, of the red nightbreak light 700 μW/cm^2 and of the near infra-red radiation, obtained from neon lamps, 200 μW/cm^2. The treatment lasted 25 days, the last observations were made after 55 days. The results are presented in Table 19A (Plate 2–i).

Separate lots of 4 plants, treated with a short daily light period of 8R, were

a) kept in darkness during the remaining 16 hours per day (8R) or exposed to

b) 10 minutes of red light (8R–10′R) and
c) 10 minutes of red followed by 60 minutes of near infra-red (8R–10′R60′IR), both treatments started 20 minutes past the middle of the dark period;
d) 30 minutes of red (8R–30′R) and
e) 30 minutes of red followed by 60 minutes of near infra-red (8R–30′R60′IR), both treatments started at the middle of the night period;
f) 60 minutes of red (8R–60′R) and
g) 60 minutes of red followed by 60 minutes of near infra-red (8R–60′R60′IR), both treatments started 30 minutes before the middle of the night period;
h) 60 minutes of near infra-red (8R–60′IR) given at the same time as in *c*, *e* and *g*, i.e. 8½ hours after the beginning of the long dark period.

TABLE 19 A AND B

The influence of a nightbreak with red (700 μW/cm²) and/or with near infra-red (200 μW/cm²) after a main light period of A: 8 hrs red light (670 μW/cm²) + 1 hr near infra-red (200 μW/cm²) or B: 8 hrs red light (670 μW/cm²). Duration of the treatment: 25 days. 4 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 55 days.

Main light period in hrs per day	Night interruption in minutes per night		Condition of the growing point			
A						
8R 1IR	—	—	+	+	+	+
8R 1IR	10′R	—	—	—	—	—
8R 1IR	10′R	15′IR	+	+	+	+
8R 1IR	—	60′IR	—	—	—	—
8R 1IR	10′R	60′IR	—	—	—	—
B						
8R	—	—	+	+	+	+
8R	—	60′IR	+	+	+	+
8R	10′R	—	+	+	+	+
8R	10′R	60′IR	+	+	+	+
8R	30′R	—	+	+	+	+
8R	30′R	60′IR	+	+	+	—
8R	60′R	—	+	+	+	+
8R	60′R	60′IR	—	—	—	—

The conditions were just the same as described above; the results of this experiment are given in Table 19B (Plate 2–i). In both experiments the generative plants developed 5 or 6 new pairs of leaves before flower buds were initiated; the plants which remained vegetative showed, 55 days after the beginning of the treatment, about 9 or 10 newly formed leaf pairs.

As can be seen in Table 19, a night interruption with –10′R was only effective in causing a long-day effect when given in co-operation with a main light period of 8R1IR (8R1IR–10′R) but not with 8R (8R–10′R). With 8R, a nightbreak with even 60′R was not effective, flowering being not prevented.

Moreover it was found that a nightbreak with –60'IR was photoperiodically active when given in combination with a main light period of 8R1IR as a long-day effect was obtained (8R1IR–60'IR). In co-operation with a main light period of 8R, a night interruption with 60'IR was not effective in this respect (8R–60'IR). If, however, the –60'IR was preceded by –60'R a long-day effect was obtained (8R–60'R60'IR), in spite of the ineffectiveness of each component (–60'R and –60'IR) when used separately. 60'IR after –30'R caused some prevention of flowering (8R–30'R60'IR).

Obviously the effect of red nightbreak light can be counteracted by a subsequent exposure to near infra-red or blue light. It was also shown that under certain conditions near infra-red radiation can be active as nightbreak light.

3.1.4 Experiments with other plants

Some experiments were carried out with other plants than *Salvia occidentalis*.

Long-day experiments with *Hyoscyamus niger* (LDP) confirmed the results of Stolwijk *et al.* (1955) and Currey *et al.* (1956), blue or near infra-red radiation being necessary for obtaining a long-day effect. In nightbreak experiments it was shown that red nightbreak light was only effective in causing a long-day effect when it was given in combination with a main light period in blue light (10B–10'R), the effect of near infra-red was not investigated (Meijer *et al.* 1957). In experiments with supplemental light, the plants were daily exposed to a short day (main light period) in red, green, blue (490 μW/cm^2) or green + near infra-red (160 μW/cm^2) after which the plants were kept in darkness or exposed to 8 hours of red or blue light (165 μW/cm^2). It was found that blue supplemental light did not cause a long-day effect and that red supplemental light was only effective in this respect when it was preceded by either 10 hours blue (10B 8r) or 10 hours of green + near infra-red (10GIR 8r).

Petunia hybr., a non-obligate long-day plant, exposed to long days (16 hours light per day) in red, green, blue or green + near infra-red (400 μW/cm^2), started bolting almost immediately in 16B or 16GIR and flowering was obtained about 6 weeks after the beginning of the treatment. In 16R or 16G the plants remained in the rosette form; no flowering occurred, even not after 4 months when the treatment was discontinued. The elongation in 16B and 16GIR is not a long-day effect because it also results from a short-day treatment (10 hours of light per day). In this case, however, no flowering was obtained.

With *Chrysanthemum parthenium* (LDP) it was found that a long-day treatment in red, green or blue light (700 μW/cm^2) resulted in a long-day effect. In blue light, however, flowering was accelerated as in 16B flower buds were visible after 19 days, in 16R and 16G after 29 days.

Similar results were obtained with representatives of the *Cruciferae*.

In long-day experiments with *Sinapis alba* (LDP), with a light intensity of 610 μW/cm^2 it was found that blue light accelerated

flowering when compared with red or green light: in 16B plants showed flower buds after 15 days, in 16R or 16G after 32 days. With a light intensity of 250 $\mu W/cm^2$, in 16B the flower buds were visible after 27 days, whereas in 16R or 16G the plants remained vegetative even after two months.

A long-day treatment of *Nasturtium palustre* (LDP) with red, green, blue or green + near infra-red at an intensity of 450 $\mu W/cm^2$ showed that a long-day effect was only obtained when the plants were exposed to blue or near infra-red radiation. At an intensity of 700 $\mu W/cm^2$, however, 16R was also effective in causing a long-day effect.

Of *Arabidopsis thaliana* (LDP) three strains of different origin were compared. At an intensity of 470 $\mu W/cm^2$ only one strain initiated flower buds in 16B and in 16BIR. In the other two varieties flowering was only obtained when near infra-red was given simultaneously with the blue light (16BIR). One of these less sensitive strains initiated flowering in 16B when the intensity was raised to 650 $\mu W/cm^2$. In 16R or 16G (470 or 650 $\mu W/cm^2$) all three varieties remained vegetative.

Some other plant species as *Kalanchoë blossfeldiana*, *Euphorbia pulcherrima* and *Xanthium pennsylvanicum*, all short-day plants, did not show this spectral dependence under our experimental conditions.

Obviously the requirement of blue or near infra-red for obtaining a long-day effect is not restricted to *Salvia occidentalis* and *Hyoscyamus niger*, although there seem to exist plants which do not show this spectral dependence.

3.1.5 Discussion

1. *Dual effect of light on flower formation*

Several authors have observed that the flower formation of various plants does not depend on light but even occurs in darkness (Borgström 1939; Lang *et al.* 1943; Leopold 1949, 1952; Fife *et al.* 1953).

Tashima (1953, — *et al.* 1953) sowed and cultivated *Pharbites Nil* (SDP) and *Raphanus sativus* (LDP) on a culture medium in complete darkness. Under these conditions flower initiation occurred. When the plants were irradiated, however, no flowering was initiated unless the plants were exposed to an inducing daylength, i.e. *Pharbites* to short days, *Raphanus* to long days. No differences were observed between the plants in darkness and those in the inducing daylength as far as the flower initiation was concerned. Similar results were obtained with some other long-day plants. Apparently light inhibits flower formation, which inhibiting effect can be antagonized by a certain light treatment (photoperiodic reactions).

2. *Light intensity and photoperiodic response*

Whether a light treatment is succesful or not in inducing flower formation does not depend on the daylength only (photoperiodic reactions), but also on the light intensity (photosynthesis).

In the case of *Xanthium pennsylvanicum* (SDP), Hamner (1940)

demonstrated that flower formation was only obtained after an inductive long dark period (short-day treatment) if this had been preceded by a light period of a sufficiently high light intensity. This light of high-intensity could be replaced by a supply of carbohydrates. Therefore it was concluded that in this case the photoperiod is only necessary to produce sufficient photosynthates. (BONNER *et al.* 1953). Hence the absence of flower formation in our experiments with *Salvia occidentalis*, exposed to a light intensity of 85 $\mu W/cm^2$ (Tables 3 and 4), may also be due to a lack of photosynthates.

In experiments with *Perilla* (DE ZEEUW, 1953) and *Salvia* (Table 2), both short-day plants, it was found that with a long-day treatment no long-day effect was obtained when the light intensity was too low. From the experiments described in this paper it is obvious that this phenomenon is not caused by the decrease of photosynthesis (Table 3).

3. *Short-day treatment*

Information on the spectral dependence of the effect of a short-day treatment is scanty. WALLRABE (1944), using *Kalanchoe* (SDP) has reported that blue light was more active than red light in causing a short-day effect, green light being not active in this respect. She supposed some relation to exist between the photoperiodic response and photosynthesis. Short-day experiments with *Salvia occidentalis* (SDP) and *Kalanchoe* did not confirm this spectral dependence of the short-day effect (MEIJER *et al.* 1957). It is possible, however, that during these experiments the light intensity was too high for obtaining a possible dependence of the photoperiodic response on wave length.

4. *Long-day treatment*

The spectral dependence of the activity of a long-day treatment which has been demonstrated by STOLWIJK *et al.* (1955) and CURREY *et al.* (1956) in the case of *Hyoscyamus niger* (LDP) was confirmed for *Salvia occidentalis* (SDP) and some long-day plants. Long-day experiments with *Salvia* in coloured light at different intensities (Table 3) show that:

1°. all spectral regions are active in producing a long-day effect;
2°. near infra-red and blue light are, however, the most active types of light in this respect. Red light is less effective whereas green light is only slightly active (Plate 1–a).

Similar results were obtained with the long-day plants *Arabidopsis thaliana*, *Nasturtium palustre* and *Sinapis alba* (3.1.4).

In the case of *Kalanchoe* and *Euphorbia* (both SDP) a long-day treatment was equally effective in red, green or blue light. Judging from the response of the other plant species used it is possible that the light intensity to which these two species were exposed was too high, to find a spectral dependence.

5. *Nightbreak treatment*

It has been shown that red light is more active than blue light when it is used to interrupt the long dark period after a short day

in white light (e.g. PARKER *et al.* 1950). This spectral dependence of nightbreak light was confirmed for both *Hyoscyamus* (STOLWIJK *et al.* 1955) and *Salvia* (MEIJER 1957*a*).

STOLWIJK *et al.* supposed that for obtaining a long-day effect not only the blue, near infra-red reaction was required because a short-day treatment in light of these wave-length regions did not result in causing a long-day effect. They suggested that "an additional photoperiodic stimulus is required . . .".

In the present paper it is clearly demonstrated that for obtaining a long-day effect at least two photoreactions with a different spectral sensitivity are required. In nightbreak experiments with *Salvia* and *Hyoscyamus* it was observed that red nightbreak light was only effective in combination with a main light period (short day) in blue or in green + near infra-red. After a main light period in red or in green light, a night interruption with red light did not cause a long-day effect (Plate 2–g).

Hence it may be concluded that it depends on at least two photoreactions whether a long-day effect will be obtained or not, viz.:

1° a "main-light-period reaction" which is most sensitive to near infra-red and blue radiation;

2° a "nightbreak reaction", in which red light is the most promotive spectral region.

In the case of a long-day treatment with e.g. 16B it seems as if the "main-light-period reaction" is already sufficient to cause a long-day effect. Although red light is the most active wave-length region in inducing the "nightbreak reaction", the other spectral regions too are active, even near infra-red (CATHEY *et al.* 1958), but to a much lesser extent. For this reason both reactions can occur when the plants are exposed to 16B. The first 10 hours of blue light will induce the main-light-period reaction, whereas the last part of the 16-hour photoperiod will be sufficient, even in blue light, to cause the nightbreak reaction.

The long-day effect of 16R and 16G (provided that the light intensity is sufficiently high) can be explained in a similar way: the last 6 hours of red "nightbreak" light may be sufficient for obtaining a long-day effect after a weak main-light-period reaction caused by the first 10 hours of red light.

6. *Relation between the two reactions.*

The quantitative relation between both reactions assumed above is confirmed by the observation that the effect of a certain amount of nightbreak light depends on the intensity of the main-light-period reaction. It was found that 30 minutes of nightbreak light of low intensity was sufficient after a main light period of 10 hours of blue light but insufficient after a main light period of 10 hours of white light. (Table 16). A main-light-period reaction, however, was also induced by white light but for obtaining a long-day effect more nightbreak light was necessary. The data presented in Table 11 and 12 confirm this conclusion. Besides, these data demonstrate that near infra-red

is more active than blue light in inducing the main-light-period reaction, a main light period of 8GIR being more effective than a main light period of 8B.

In addition to the dependence of the nightbreak reaction on the intensity of the main-light-period reaction, yet another correlation between both reactions was observed. It has been reported that nightbreak light is the most active when used near the middle of the long dark period. The closer the moment of nightbreak to the beginning or the end of the dark period, the higher the light intensity necessary for obtaining a long-day effect (e.g. KÖNITZ, 1958). This influence of the time interval is clearly demonstrated in the experiment presented in Table 7 (see also Plate 1–b). One hour near infra-red given alternately with green light only causes a long-day effect if:

1° the near infra-red period is preceded by some hours of light (Plate 1–b, region between dotted lines); the influence of this light period is unknown, but it may be necessary for the production of carbohydrates and

2° light is given in a period, 8 to 10 hours after the beginning of the near infra-red period (region between broken lines).

In preliminary experiments *Salvia* was exposed to a main light period of 8G 1IR. It was observed that 10 minutes of red light was not effective in causing a long-day effect when given 7½ hours after the beginning of the near infra-red irradiation. When used one hour later, however, it was effective in this respect. The dependence of the long-day effect on both conditions mentioned above is also demonstrated in experiments presented in Plate 2–i.

It is supposed that near infra-red or blue light induces the main-light-period reaction, the green or red light being active in causing a nightbreak reaction but only when given a certain number of hours after the main-light-period reaction was induced.

7. *Supplemental light treatment*

A supplemental light treatment with low light intensity may be conceived as a nightbreak treatment, the dark period between the main light period and the nightbreak being filled up with light. This conception is supported by the spectral dependence. It has been reported for almost all plant species that red light is more active in producing a long-day effect than blue light, either as a night interruption or as supplemental light.

An exception, however, has been reported for a number of plants, all belonging to the Cruciferae (FUNKE, 1948). For these plants it was noted that on the contrary blue supplemental light is photoperiodically more active than red supplemental light. WASSINK *et al.* (1950) and STOLWIJK (1954) confirmed this activity of blue light, used as supplemental light, for some other cruciferous plants and observed an activity of near infra-red radiation too, in this respect.

In this paper results obtained from long-day experiments with three *Cruciferae* (3.1.4) show the same blue and near infra-red sensitivity. It may well be that representatives of this plant family

are exceptional in their response to light in that only the "main-light-period reaction" is involved in the process leading to a long-day effect. However, as far as known, no nightbreak experiments with Cruciferae have been carried out in coloured light. Experiments with *Hyoscyamus* showed that this exceptional spectral dependence of supplemental light is not restricted to the Cruciferae, near infra-red being more active in causing a long-day effect than red light (STOLWIJK *et al.* 1955).

For *Salvia occidentalis* the same spectral dependence was observed as found for the *Cruciferae*, blue light being more active in causing a long-day effect than red light (Plate 1–d). In the nightbreak experiments it was found that red light was more active than blue light (Plate 2–g). However, as far as *Salvia occidentalis* is concerned it was demonstrated that the exceptional spectral dependence was only apparent. Experiments in which the supplemental light period was shortened and a dark period was inserted between the main light period and the "supplemental light" demonstrate that the inactivity of a treatment with red supplemental light was not caused by any inactivity of the red light, but was due to an antagonizing effect of the red light on the main-light-period reaction induced by blue light (Plate 2–e, f).

Hence it is obvious that the photoreaction activated by supplemental light is just the same as the photoreaction activated by a nightbreak. It is quite probable that the results of FUNKE, of WASSINK *et al.* and those of STOLWIJK mentioned above are also due to the antagonizing effect of red light on the main-light-period reaction.

8. *Antagonism*

a. Main-light-period reaction

This antagonizing activity of red light on blue light is also demonstrated in long-day experiments (Plate 1–c). Blue light, given supplementarily after green light (15G 1B), caused a long-day effect. This activity of blue light was reversed by subsequent exposure to red light (15G 1B 1R). In similar experiments the antagonizing activity of red light on the effect induced by near infra-red was shown (Plate 1–c). 15G 1IR caused a long-day effect which was nullified by a subsequent exposure to red light (15G 1IR ½R).

The lower activity of white light, as compared to blue light, in causing a long-day effect (Table 16), may be due to the antagonizing effect of red on blue light. WASSINK *et al.* (1957) too, have demonstrated this antagonizing activity in long-day experiments with *Hyoscyamus*. Red light, given simultaneously with blue light prevented the long-day effect caused by blue light.

b. Nightbreak reaction

An antagonism comparable to that described above for the main-light-period reaction has already been shown for the nightbreak reaction, near infra-red antagonizing the effect of red nightbreak light (BORTHWICK *et al.* 1952). This antagonizing activity of near infra-red, demonstrated with various plants, is confirmed in the case

of *Salvia occidentalis* (Plate 2–h) and *Hyoscyamus niger* (STOLWIJK *et al.* 1955).

In experiments described in this paper it was observed that blue light too can nullify the effect of red nightbreak light (Plate 2–h). This antagonizing effect of both blue and near infra-red is in agreement with the results obtained from experiments on the germination of seeds (FLINT *et al.* 1935, WAREING *et al.* 1958) and of fern spores (MOHR 1956).

9. *Dual role of light*

It appears, however, that blue light does not only antagonize the nightbreak reaction induced by a preceding night interruption with red light. It has been demonstrated that light of this wave-length region is also effective in promoting the nightbreak reaction, a much larger amount of energy being necessary than with red light (PARKER *et al.* 1950). This promotive activity of blue light is also shown in this paper (Plate 2–e).

A similar antagonizing activity (BORTHWICK *et al.* 1952) and promoting activity (CATHEY *et al.* 1957) of near infra-red radiation used as nightbreak light was reported and confirmed for *Salvia occidentalis*. In Table 19A (Plate 2–i) both the antagonizing and the promotive activity of near infra-red on the nightbreak reaction are demonstrated.

Concerning the main light period it is obvious that red light not only counteracts the promoting effect of blue or near infra-red (Plate 1–c), but can also induce the main-light-period reaction, although to a much lesser extent than blue or near infra-red. A long-day effect with 16 hours red light per day is only obtained with relatively high light intensities (Table 3).

So it will depend on the amount of light whether an antagonizing or promoting effect is obtained: of blue and near infra-red on the nightbreak reaction and of red light on the main-light-period reaction.

10. *Conditions for obtaining a long-day effect*

From the data discussed above it may be concluded that for obtaining a long-day effect the following conditions must be fulfilled:

a. a main-light-period reaction must be present (Table 20);

b. a nightbreak reaction must take place (Table 20);

TABLE 20

The spectral dependence of the two photoreactions required for obtaining a long-day effect.

1. Main-light-period reaction		2. Nightbreak reaction	
Promoted by	Promotion nullified by	Promoted by	Promotion nullified by
Near infra-red, Blue (Red *)	Red	Red (near infra-red,* Blue *)	Near infra-red, Blue

* Slightly active.

c. a certain number of hours must elapse between the main-light-period reaction and the nightbreak reaction (Plate 1–b, see also page 219).

Besides, it was noted that the amount of nightbreak light necessary for obtaining a long-day effect depends on:

1° the number of hours between the main light period and the night interruption (e.g. KÖNITZ 1958) and

2° the intensity of the main-light-period reaction (Table 16).

11. *Critical daylength*

During experiments with *Chenopodium amaranticolor* (SDP), it was found that flower initiation occurred when the plants were exposed to 13 hours of "white" light per day (KÖNITZ 1958). This light was obtained from fluorescent lamps. Its emission spectrum shows that about the same amount of energy is emitted in the blue and in the red part of the visible spectrum. It may be noted here that the relative amount of near infra-red radiation present in this white light is very much less than in natural daylight or in "white" light obtained from incandescent lamps.

In this daylength, however, flower initiation was prevented when the 13-hour light period was interrupted with near infra-red radiation. Thus a long-day effect was obtained. Moreover it was shown that near infra-red was the most active spectral region when given around the fifth hour after the beginning of the light period and that red light nullified this effect of near infra-red radiation.

This experiment shows a typical resemblance with the experiment in which *Salvia* was exposed to 16G (flower initiation occurring i.e. no long-day effect) and 6G 1IR 9G (flower initiation prevented, i.e. long-day effect, Plate 1–b). It is obvious that in KÖNITZ's experiment the inactivity of 13 hours of white light per day in producing a long-day effect was caused by the "absence" of near infra-red.

It is supposed that in fluorescent light both photoreactions were not sufficiently intensive because of

1° the lack of near infra-red and

2° the antagonizing activity of light of one spectral region on the effect of light of another spectral region.

Therefore no long-day effect could be obtained. After the near infra-red had been supplied the main-light-period reaction may have been induced, the last hours of the photoperiod acting as a nightbreak and in this way a long-day effect was obtained. This assumption is also supported by the observations of ROODENBURG (1954), TAKIMOTO (1957) and WASSINK *et al.* (1951) and Table 16 of this paper. TAKIMOTO found that *Silene armeria* (LDP) did not initiate flower buds in a long-day treatment of 18 hours per day in "white" fluorescent light. With the same daylength a long-day effect was obtained when part of the irradiation with fluorescent light was replaced by incandescent light. As already mentioned, incandescent lamps emit relatively much larger amounts of near infra-red than fluorescent lamps. In the experiments of WASSINK *et al.* with *Brassica* it was demonstrated that

a short-day treatment in white fluorescent light did not cause a long-day effect. If, however, part of the white fluorescent light was replaced by blue + near infra-red, a long-day effect was obtained.

The experiments of WASSINK *et al.* and KÖNITZ mentioned above demonstrate that even a short-day treatment can cause a long-day effect, depending on the light quality of the photoperiod. The relative value of the "critical daylength" was also shown in the experiments of TAKIMOTO (1957) and in our experiments which show that the light quality largely determines whether a long-day effect is obtained or not.

Evidently the long-day effect does not simply depend on the length of the photoperiod or that of the dark period, but on the conditions mentioned in 10.

12. "*Endogenous Diurnal Rhythm*"

As far as the long-day effect is concerned it is obvious that during a certain part of a natural 24-hour cycle the plant will be in a condition in which blue and near infra-red are promoting and red light is inhibiting the process leading to the long-day effect. In a following period the plant is in a condition in which, on the contrary, red light has a promotive effect and blue and near infra-red may inhibit this promotive effect. Both periods with different spectral sensitivities (Table 20) alternate with each other in a 24 hour rhythm. The results in Table 19 (Plate 2–i) show that the alternating periods may even be interchanged: the "main-light-period reaction" is not only induced by the main light period but, under certain conditions, also by the original nightbreak light period. The original main light period will be active in inducing the nightbreak reaction (region between broken lines). 8R 1IR will cause the main-light-period reaction and 10′R or 60′IR the nightbreak reaction. It is obvious, however, that the original main light period is not effective when the near infra-red is omitted (8R), as under this condition 10′R or 60′IR are not active in causing a long-day effect. If, however, the 60′IR of nightbreak light are preceded by 60′R, it is probable that this combination will induce the main-light-period reaction and the original "main light period" will induce the nightbreak reaction. This assumption is supported by the requirement of supplying a certain amount of light prior to the near infra-red, which was already shown on page 219. In this case 10′R are insufficient, whereas 60′R appear to be sufficient, 8R–10′R60′IR not causing, 8R–60′R60′IR causing a long-day effect.

These alternating periods with a different spectral sensitivity show a 24-hour rhythm. The phase of the rhythm appears to be controlled by radiation. This is in agreement with the theory of the "Endogenous Diurnal Rhythm" developed by BÜNNING (1958).

13. *Photoreactions and Pigments*

From the two photoreactions mentioned above, the one which is involved in the nightbreak reaction is governed by the red-absorbing pigment controlling so many phenomena (see 1.1). According to BORTHWICK *et al.* (1954), the effect of an irradiation with red light is

antagonized as soon as near infra-red is supplied and this antagonism appeared to be reversible. For this reason these authors suggested that only one pigment be involved, which would be converted into a near infra-red absorbing form (P') after having absorbed red light. The near infra-red absorbing form would be converted into the red absorbing form (P) after irradiation with near infra-red.

From the data presented in this paper it is obvious that the red absorbing form (P) of the pigment is not only regenerated by irradiation with near infra-red but also with blue light:

$$P \underset{IR,\ B}{\overset{R}{\rightleftharpoons}} P'$$

The main-light-period reaction will be governed by a pigment absorbing blue and near infra-red. The antagonizing effect of red light on the effect of blue and near infra-red might also be caused by a pigment conversion, similar to that suggested for the nightbreak reaction.

No decisive answer can be given to the question whether two different pigment systems are involved, one in the main-light-period reaction, the other in the nightbreak reaction, or two different forms of one pigment. In the latter case a long-day effect can only be explained by assuming that both forms of the pigment alternately replace each other in a 24-hour rhythm. The reported data do not indicate, which of either possibility has the best chance of being correct, nor do they yield any indications about the character of the pigment(s).

3.2 Elongation

3.2.1 Introduction

In the beginning of the study of the influence of light quality on elongation, various plant species, plants previously raised in white light, have been used. The plants were exposed to 16 hours per day of red, green or blue light with and without a simultaneous addition of near infra-red radiation. After the treatment had lasted for some time the length of the internodes was measured. The results obtained from experiments with several plant species are given in Table 21. The intensity of the visible radiation was 475 $\mu W/cm^2$ and of the near infra-red 120 $\mu W/cm^2$.

It was found that the effect of light of different spectral regions varied with the plant species. In the case of gherkin and *Salvia occidentalis* elongation was much less inhibited in blue light than in red or green light. Near infra-red stimulated elongation, especially when it was added to green (gherkin) or to green or blue light (*Salvia*). Other plant species which reacted in a similar way are *Petunia*, *Calendula*, *Perilla*, *Helianthus* and bean.

Mirabilis jalapa on the other hand showed a marked elongation in

red and in green light, while in blue light the internodes were much shorter. Near infra-red was slightly active in promoting the elongation only when it was added to blue light. *Rivina humilis* and *Mentha longifolia* reacted in a similar way.

TABLE 21

The influence of an irradiation (16 hours per day) with red (16R), green (16G) and blue light (16B), with or without near infra-red (IR), on the elongation of light-grown plants. Intensity of visible radiation 475 $\mu W/cm^2$ and of near infra-red 120 $\mu W/cm^2$. Length in mm, N days after the beginning of the treatment (second column).

Plant species	N	Light treatment in hrs per day					
		16R	16RIR	16G	16GIR	16B	16BIR
Gherkin (hypocotyl) 5 days *	8 days	23	36	26	101	79	81
Mirabilis jalapa (1st internode) 14 days *	30 days	182	179	174	188	128	153
Salvia occidentalis (internode) 20 days *	30 days	42	60	43	82	64	90
Tomato (hypocotyl) 14 days *	11 days	27	29	24	54	28	42
Tomato (1st internode) 14 days *	15 days	69	74	62	63	38	38

* Age of the plants at the beginning of the treatment.

The hypocotyls of tomato plants reached about the same length in red, green or blue light. The assumption that this hypocotyl was already fully developed cannot be valid, an addition of near infra-red to green or blue light causing an increase in length. The first internodes of the same tomato plants, however, reacted in about the same way as in the case of *Mirabilis;* near infra-red given simultaneously did not have any effect. At the beginning of the treatment with coloured light this first internode was in a younger stage of development than the hypocotyl. For this reason it was possibly less affected by the pretreatment with white light than the hypocotyl.

Experiments with gherkin seedlings demonstrated that, after sowing in coloured light, the difference in length between plants grown in red and plants grown in blue light was much smaller than after sowing in white light. The higher the light intensity the smaller the difference in length.

Bean plants sown in coloured light became somewhat longer in red than in blue light; with light-grown bean plants, however, the

reversal result was obtained: the internodes were longer in blue than in red light.

So the question arose whether a pretreatment with white light influences the effect of a subsequent exposure to light of different spectral regions and whether this effect depends on the intensity of the coloured light.

3.2.2 Different light intensities

In the following experiments various plant species, either previously raised in white light ("light-grown plants") or immediately sown in coloured light ("dark-grown plants") were exposed to coloured light at different light intensities. When a relatively low light intensity was wanted, only the lamps mounted to the top of the light cabinet were used. The light intensity of such an irradiation is not quite comparable with the intensities obtained by irradiation from three sides.

The temperature during the experiments at higher intensities was 22° C during the photoperiod and 17° C during the dark period. In the experiments with low intensities the temperature was kept constant at 22° C.

Hyoscyamus niger

The results of experiments with light-grown plants have been given in the foregoing section (3.1.4) and showed that in red and in green light the plants remained in the rosette form. In blue light elongation occurred only in long days (16 hours of light per day), not in short days. The elongating effect of blue light is a long-day effect as it always was correlated with flower initiation.

The results of an experiment with dark-grown plants are given in Fig. 1. Immediately after sowing, pots with 25 seeds each were placed in 16R, 16G, or 16B. The intensity was 500 μW/cm^2. After 16 days the seedlings were selected for uniformity and 10 plants were left

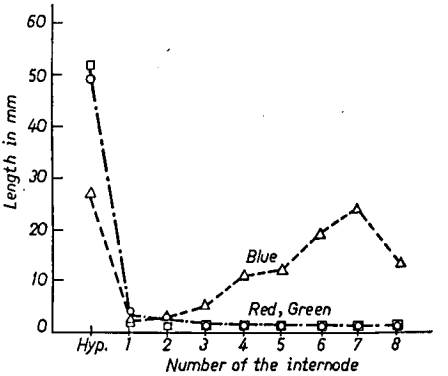

Fig. 1. The length of the hypocotyl and internodes of *Hyoscyamus niger*, sown in red, green or blue light. Irradiation 16 hrs per day. Light intensity 500 μW/cm^2. Day temperature 22° C. Night temperature 17° C. Length in mm, 60 days after sowing.

in each pot. At this time the hypocotyls were already completely developed. The length of the internodes was measured after 60 days. As can be seen the hypocotyls reached the same length in red and in green light but are much longer than those developed in blue light. The next internodes were very short in red and in green light, rosettes being formed. In blue light, however, after 2 or 3 short internodes elongation occurred. This elongation may have been caused by the long-day effect of 16B as all plants showed flower buds at this time. When germination had taken place in short days in blue light (10B) the internodes remained short and a rosette was formed.

Similar experiments with dark-grown seedlings were carried out at low light intensities, the plants being irradiated only from above. Three different light intensities were obtained by using gauze filters: 25, 120 and 210 μW/cm^2. A control was kept in darkness at the same temperature, 22° C. As can be seen in table 22 the hypocotyls of

TABLE 22

The influence of the light quality at low intensities on the elongation of the hypocotyl of *Hyoscyamus niger* sown in coloured light. Temperature 22° C. Length in mm, 38 days after sowing.

Light treatment in hrs per day	Light intensity in μW/cm^2			
	0	25	120	210
16 red		38	31	28
16 green		40	34	32
16 blue		39	33	31
16 white		34	25	22
dark control	54			

the plants grown in red, green or blue light of low intensity reached about the same length. In white light the seedlings were somewhat shorter than in coloured light.

Bean, "Vroege Wagenaar"

In preliminary experiments with bean plants it was found that light-grown seedlings reacted like gherkin seedlings in that in blue light the hypocotyl and the internodes were longer than in red or in green light. When the plants were sown in coloured light, however, the hypocotyls of plants grown in red or in green light were longer than of those grown in blue light.

In the following experiment the difference between light-grown and dark-grown seedlings is clearly shown. Seeds were sown in pots and left to germinate in continuous white fluorescent light (3200 μW/cm^2). After 11, 9, 7 and 5 days, pots were transferred to the light cabinets. The plants were irradiated daily during 16 hours with red, green or blue light (475 μW/cm^2). Each 3 or 4 days the length was determined; about 20 days after sowing the treatment was discontinued. At that moment the development of the hypocotyls and the first two internodes was completed. It was found that the hypocotyls and internodes which had first been exposed to white

light became longer in blue than in red or green light, as far as they had not already finished development when the treatment with coloured light started. Those internodes which developed later, and for that reason had never been exposed to white light, were longer in red and green than in blue light.

In Fig. 2 the data are given of the development of the second internodes of plants sown 9 days (group II) and 5 days (group IV) and grown in white light before being transferred to the light cabinets.

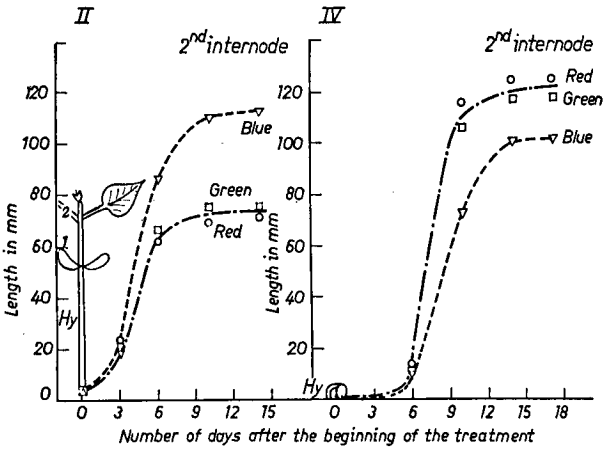

Fig. 2. The elongation of the second internode of bean plants grown in 16 hrs per day red, green or blue light (475 μW/cm^2) as influenced by a previous irradiation with white light. II: irradiation with coloured light started 9 days after sowing; IV: idem 5 days after sowing. The initial lengths of the plants are given at 0. Day temperature 22° C, night temperature 17° C.

The second internode of seedlings of group II started to develop at the beginning of the treatment (0 days). In this case longer internodes were obtained in blue than in red or green light. Although the seedlings of group IV just came above the soil surface, the influence of the white light was notable, the hypocotyls being more elongated in blue light (128 mm) than in red light (105 mm). The second internode had not been affected by the white light so that they became longer in red than in blue light.

At very low light intensities, however, it was found that the elongation of the hypocotyls of seedlings sown in coloured light was much more inhibited in red than in blue light. The seeds were sown in red, blue or white (fluorescent) light and irradiated 16 hours per day. The light came only from above and by means of gauze filters three different light intensities were obtained. The temperature was kept constant at 22° C. After 11 days the treatment was discontinued as it was found that the hypocotyls did not develop any further. The results are given in Table 23.

The influence of the light intensity on the elongation was demonstrated in similar experiments but with higher intensities. The seeds were sown in red, blue or white light and irradiated 16 hours per day.

By means of gauze filters three light intensities were obtained. The day temperature was 22° C, the night temperature 17° C. 15 days after sowing, the elongation of the hypocotyls was completed. The results are given in Fig. 3.

TABLE 23

The influence of the light quality at low intensities on the elongation of the hypocotyl of bean seedlings sown in red, blue and white light. Temperature 22° C. Length in mm, 11 days after sowing.

Light treatment in hrs per day	Light intensity in $\mu W/cm^2$			
	0	25	120	210
16 red		143	127	126
16 blue		179	173	157
16 white		161	136	127
dark control	253			

It is obvious that the inhibiting effect of red and blue light on the elongation of the hypocotyl depends on the light intensity. At higher intensities (about 750 $\mu W/cm^2$) blue light is more active in this respect than red light. With decreasing light intensity the differences in length between plants grown in red or in blue light also decrease

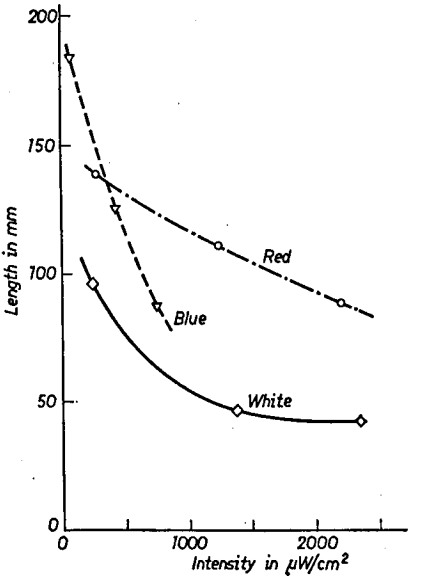

Fig. 3. The length of the hypocotyl of bean seedlings sown in red, blue and white light. Irradiation 16 hrs per day. Day temperature 22° C, night temperature 17° C. Length in mm, 15 days after sowing.

and at a certain intensity there is no difference at all. From the slope of the curves it may be expected that at lower intensities red light will be more inhibitive to elongation than blue light. This expectation is confirmed by the results obtained with experiments carried out with very low light intensities (see Table 23). In a certain intensity range

(200–700 μW/cm^2) the effect of white light is stronger than that of red or green light and at higher intensities it resembles that of blue light. At lower intensities it is between the effects of red and blue light.

Sinapis alba

Experiments with this plant species were carried out at high intensity and at low intensities (irradiated only from above). The plants were sown in pots immediately placed in the light cabinets. After 11 days the development of the hypocotyl was finished. The data are given in Table 24.

TABLE 24

The influence of the light intensity on the inhibiting effect of light on the elongation of the hypocotyl of *Sinapis alba* sown in light of different spectral regions; at high intensity (Experiment I), day temperature 22° C, night temperature 17° C; idem at low intensities (Experiment II), temperature 22° C. Length in mm, 11 days after sowing.

	Light intensity μW/cm^2	Light treatment (16 hrs per day)			
		red	green	blue	white
Exp. I	580	61	78	55	—
Exp. II	210	72	94	104	79
	120	70	98	109	86
	25	89	126	137	109
	0	180			

At 580 μW/cm^2 the hypocotyl of seedlings grown in blue light was shorter than that of seedlings in green and slightly shorter than that of the plants in red light (Experiment I). At the lower intensities it is obvious that even blue light is less active in inhibiting the elongation than red light. The activities of green and white light are between those of red and blue light.

Mirabilis jalapa

The effect of light of different wave-length regions on light-grown Mirabilis has already been given in Table 21. Younger internodes, which had not yet received white light before the treatment with coloured light started, reacted in the same way, the internodes of plants grown in blue light being shorter than in red and green light.

Also when the plants were sown in red or blue light (695 μW/cm^2) it was found that blue light was more active than red light in inhibiting elongation. However, at very low intensities (irradiation only from above) it was found that the difference in activity between blue and red light was much less pronounced, while at the lowest light intensity used (25 μW/cm^2) blue light was even less inhibitive than red light.

The results of two experiments with dark-grown seedlings are given in Table 25.

Tomato, "Victory"

In Table 21 it was shown that the hypocotyl of tomato plants, previously grown in white light, reached the same length in red,

green or blue light and that the first internode of the same plants became longer in red or green light than in blue light.

TABLE 25

The influence of red and blue light on the elongation of *Mirabilis jalapa* sown in coloured light. Irradiated 16 hrs per day. Experiment I: at high intensity (695 μW/cm^2). Day temperature 22° C, night temperature 17° C. Length of hypocotyl and 1st internode in mm, 20 days after sowing. Experiment II: at low intensities, irradiated only from above. Temperature 22° C. Length of hypocotyl in mm, 18 days after sowing.

	Light intensity in μW/cm^2	Light treatment 16 hrs per day		
		red	blue	white
Experiment I				
hypocotyl	695	101	21	—
1st internode	695	133	47	—
Experiment II				
hypocotyl	210	97	88	80
	120	107	94	97
	25	102	122	104
	0	139		

In the following experiment the reactions of light-grown plants were compared to those of dark-grown seedlings. The light-grown plants were raised in white fluorescent light. After the hypocotyl had reached a length of about 30 mm, the seedlings were potted

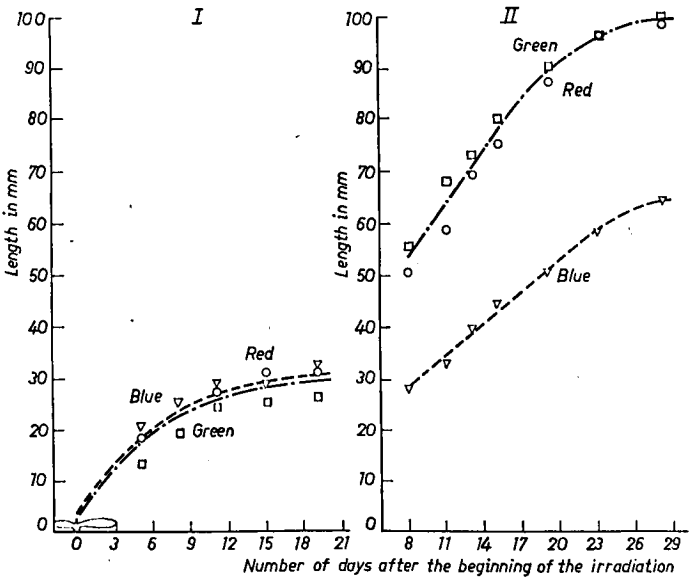

Fig. 4. The increase in length of the hypocotyls of tomato seedlings in red, green or blue light (475 μW/cm^2). Irradiation 16 hrs per day. Experiment I: seedlings germinated in white light and transferred to the light cabinets 13 days after sowing. Initial length of the hypocotyl about 30 mm. Experiment II: seedlings sown in the light cabinets. Day temperature 22° C, night temperature 17° C.

with the cotyledons on the soil surface. The next day, the plants were transferred to the light cabinets (Experiment I) .The dark-grown seedlings were sown immediately in the light cabinets (Experiment II). The plants were irradiated with red, green or blue light, 16 hours per day. The light intensity was 475 μW/cm^2. The day temperature was 22° C, the night temperature 17° C. The length of the hypocotyls was measured each 3 or 4 days. The increase in length of the hypocotyls of the light-grown plants, 30 mm being under the soil surface, and of the seedlings sown in coloured light is given in Fig. 4. The hypocotyls of plants germinated in white light reached the same length whether grown in red, green or blue light. The elongation of the hypocotyls of the seedlings sown in coloured light was much more inhibited in blue than in red or green light.

When different light intensities were compared it was found that only at very low light intensities (irradiation only from above) the difference in activity between blue and red light decreased with decreasing light intensity. In these experiments the plants were sown in red, blue or white light and irradiated 16 hours per day. The temperature was kept at 22° C. The results of one of these experiments are given in Fig. 5. At the lowest intensity, blue light was even less effective than red light in inhibiting the elongation of the hypocotyl.

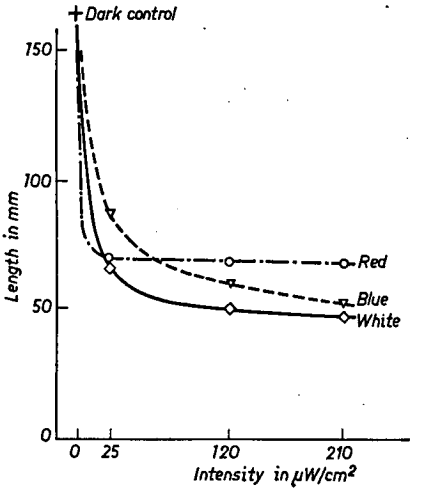

Fig. 5. The elongation of the hypocotyl of tomato seedlings sown in 16 hrs per day red, blue or white light of low intensities (irradiation only from above). Temperature 22° C. Length in mm, 16 days after sowing.

At the highest intensity the effect of white light resembled that of blue light, at the lowest intensity it was similar to that of red light. Evidently there is an intensity range in which white light is more active in inhibiting the elongation than red or blue light.

Gherkin, "Venlose niet-plekkers"

Gherkin seedlings, germinated in white light, later on developed longer hypocotyls and longer internodes in blue light than in red or

green light (Table 21). When these seedlings were transferred to a dark room the hypocotyls developed until the same length was reached as occurred in red or green light.

Fig. 6 gives the results obtained from an experiment (I) with light-grown seedlings exposed to light of different qualities and low intensities. The lengths were measured 12 days after the beginning

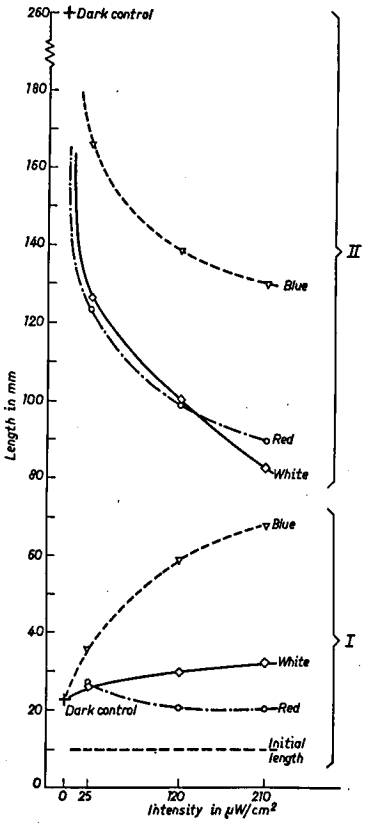

Fig. 6. The influence of red, blue or white light on the elongation of the hypocotyl of gherkin seedlings germinated in white light (I) and seedlings germinated in red, blue or white light (II). Irradiation 16 hrs per day with low light intensities (irradiation only from above). Temperature 22° C. Length in mm, 12 days (I) and 11 days (II) after the beginning of the exposure to coloured light. The length of the dark control in I is given after 7 days as the seedlings wilted and died quite soon afterwards.

of the irradiation with 16 hours per day of red, blue or white light. The low light intensities were obtained by irradiating the plants only from above. The temperature was maintained at 22° C. It can be seen that with increasing light intensity the length of the hypocotyl of light-grown seedlings in blue light increases much more than in white or red light, in which elongation was about the same as in darkness. The initial length of the hypocotyls was 10 mm.

If gherkin seedlings were sown, however, in the different light cabinets under the same conditions as in the foregoing experiment the elongation of the hypocotyl decreased with increasing light intensity. Blue light was the least active type of light in inhibiting the elongation, red and white light showed to be active to the same extent when the light intensity was low (Fig. 6, Experiment II).

In experiments with seedlings sown in darknesss and in red, blue or white light of higher intensities than used in the foregoing experiment, it was found that the difference between the activity of red and blue light in inhibiting the elongation decreases with increasing light intensity (Fig. 7). At a certain light intensity both red and blue

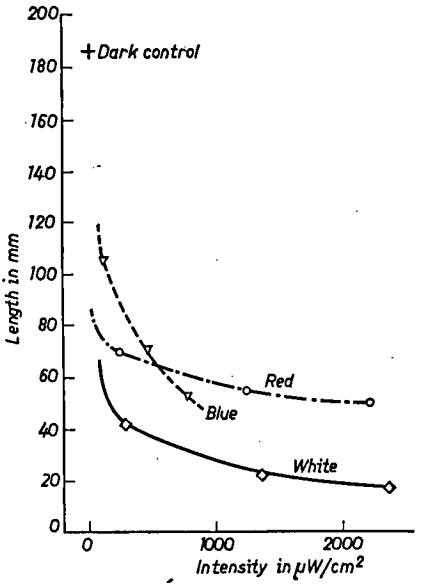

Fig. 7. The influence of the light intensity on the elongation of the hypocotyl of gherkin seedlings sown in darkness, red, blue or white light. Irradiation 16 hrs per day. Day temperature 22° C, night temperature 17° C. Length in mm, 11 days after sowing.

light will inhibit the elongation to the same extent. From the slope of the curves it may even be expected that with intensities higher than were used, blue light will be more active than red light. Besides it is obvious that in a certain intensity range white light is more active than red or blue light of the same intensity.

Thus the experiments described above clearly demonstrate that the difference between the inhibiting effects caused by light of different spectral regions does not depend on the plant species but on the light intensity used. The difference between the plant species is that they are not equally sensitive to light of a certain intensity.

3.2.3 Light-grown plants in continuous darkness

Plants completely grown in darkness show an excessive elongation which can be inhibited by very small amounts of light. When seedlings germinated in white light were transferred to darkness, however, it was often noted that hardly any additional elongation occurred. In the case of gherkin seedlings this difference between dark-grown and light-grown seedlings is clearly shown in Fig. 6 (+). The same difference was obtained with tomato plants.

Using light-grown gherkin seedlings it appeared that in blue light the elongation was stimulated (Fig. 6, I). The elongation of seedlings not exposed to white light before was inhibited by blue light. The

light-grown seedlings died some time after being exposed to darkness or to 25 $\mu W/cm^2$ of blue light while seedlings sown in darkness or in blue light (25 $\mu W/cm^2$) still continued growth. To study this effect the following experiment was carried out.

The light-grown gherkin seedlings were transferred to continuous darkness. The temperature was maintained at 22° C. Of one group of seedlings, one cotyledon was continuously soaked in a vessel containing water or a 5 % sucrose solution. The results of three experiments are given in Table 26. The length was measured 8 days after the beginning of the treatment. From these data it is obvious that the slight elongation in darkness—the initial length was 10 mm—

TABLE 26

The elongation of the hypocotyl of light-grown gherkin seedlings in continuous darkness without or with one cotyledon continuously soaked in water or a 5 % sucrose solution. Temperature 22° C. Length in mm, 8 days after the beginning of the dark treatment.

Treatment	Experiment		
	I	II	III
Control	32	35	20
Water	29	—	20
5 % sucrose	107	103	110

was not caused by any after-effect of the previous irradiation with white light, but probably to a lack of photosynthates as a supply of sucrose caused a marked elongation. Similar results were obtained with light-grown tomato plants exposed to continuous darkness with or without a sucrose supply.

Light-grown gherkin seedlings transferred to darkness or to red light elongate to about the same extent. As photosynthesis takes place in red light, it is obvious that the slight elongation in red light is not caused by a lack of photosynthates but may be due to an inhibiting effect of red light on the elongation. In blue light the hypocotyls elongate to a much larger extent, photosynthates are also formed, the higher the intensity the more photosynthesis. Besides, blue light in this intensity range is much less effective in inhibiting the elongation than red light. All this accounts for the fact that elongation in blue light increased with increasing light intensity (Fig. 6, I). The results of the following experiment support this assumption.

Light-grown gherkin seedlings were exposed to continuous darkness or irradiated with red or blue light, 16 hours per day. One part of each group was treated with sucrose by immersing one cotyledon in a vessel containing a 5 % solution of this carbohydrate. The light intensity was 640 $\mu W/cm^2$. The temperature was maintained at 22° C. The length of the hypocotyls was measured 7 days after the beginning of the treatment. From the data, presented in Table 27 it can be seen that a sugar supply to plants grown in red or in blue light did hardly influence the elongation.

TABLE 27

The elongation of the hypocotyl of light-grown gherkin seedlings in darkness, red or blue light (640 μW/cm^2) without or with one cotyledon continuously soaked in a 5 % sucrose solution. Irradiation 16 hrs per day. Temperature 22° C. Length in mm, 8 days after the beginning of the treatment.

Spectral region	Control	5 % sucrose
Red	37	46
Blue	88	93
Dark control	25	101

3.2.4 ANTAGONISM BETWEEN LIGHT OF DIFFERENT SPECTRAL REGIONS

In a previous paper (MEIJER 1958*a*) it has already been reported that blue light has not only an inhibiting effect but can also promote the elongation of already inhibited internodes. This was concluded from experiments in which light-grown gherkin seedlings were exposed to 8 hours of red light per day (600 μW/cm^2). Some of the plants were kept in darkness during the remaining 16 hours (8R), other groups were exposed to 8 hours of supplemental blue light of three different intensities and afterwards kept in darkness for the remaining 8 hours (8R 8B). The results are listed in Table 28. Plants

TABLE 28

The influence of 8 hrs blue light (I) and of 10 minutes near infra-red radiation (II) supplementarily given after 8 hrs red light (600 μW/cm^2), on the elongation of the hypocotyl of light-grown gherkin seedlings. Length in mm, 7 (I) and 8 (II) days after the beginning of the treatment.

Light treatment	I		II	
	Blue light μW/cm^2	Length in mm	Near infra-red μW/cm^2	Length in mm
8R	0	23	0	39
8R8B	60	52		
8R8B	300	75		
8R8B	600	79		
8R10'IR			200	104

exposed to 16 hours of red light are even somewhat shorter than those exposed to 8 hours of red light. The elongating effect of blue light cannot be due to a larger production of photosynthates than in the case of plants which did not receive supplemental light, a sugar supply being virtually ineffective in the latter case (Table 27).

With near infra-red radiation the same effect was obtained as with blue light. Light-grown gherkin seedlings were exposed to 8 hours of red light per day (670 μW/cm^2). Some of the plants were irradiated immediately afterwards with 10 minutes of near infra-red (obtained from a neon lamp). The intensity of this radiation was 200 μW/cm^2. The temperature during the day and the first 8 hours of the dark period was 22° C, during the second 8 hours 17° C. After 8 days the treatment was discontinued and the length measured in mm (Table 28).

From these results it is obvious that both near infra-red and blue radiation are active in antagonizing the inhibiting effect of red light.

3.2.5 Discussion

1. *Plant species*

In a previous paper (Meijer 1957*b*) it was suggested that the spectral region which is most active in inhibiting the elongation of internodes, may vary with the plant species. In Table 21 (p. 225) the results were given of experiments with several plant species exposed to light of different spectral regions. In all these experiments the plants had grown before in white light and the other conditions were the same. These results show that, as far as the activity of red and blue light on the elongation is concerned, there are two extreme types of plants:

1° the "Mirabilis type": inhibition by blue light more pronounced than by red light;

2° the "Gherkin type": red light more inhibitive than blue light.

This distinction between the two types can only be indicative because the differences between the inhibiting effects of red and blue light are quantitatively not always the same; there also exist plants which stand between these two types. Vince (1956) also concluded from her experiments with Pisum and tomato that the difference in response may be due to the plant species.

2. *Light intensities*

The experiments carried out with different light intensities demonstrate, however, that it depends on the light intensity and not on the

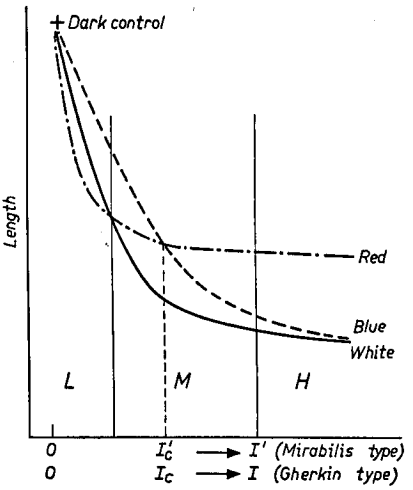

Fig. 8. The elongation of an internode in red, blue or white light as a function of the light intensity. The intensity scale of the "Mirabilis type" (I') is different from that of the "Gherkin type" (I): I > I'. I_c and I'_c are the "critical intensities". L, M and H are the relatively low, the medium and the high intensity zones. (A schematical representation of the results of the experiments described in 3.2.2).

plant species whether blue light or red light is most effective in inhibiting the elongation of internodes. It was found with plants of the two types that at relatively high light intensities blue light is more active than red light, whereas at relatively low light intensities the situation is reversed.

Evidently there must exist a certain "critical intensity" at which the elongation of the internodes of plants exposed to red and of those exposed to blue light will be inhibited to the same extent, i.e. at which the internodes will reach the same length. This is clearly demonstrated in Figs. 3 ,5 and 7 and also in Table 22. Now the value of this "critical intensity" depends on the plant species: with plants of the "Mirabilis type" e.g. tomato, *Mirabilis* and *Hyoscyamus* it is reached at low light intensities, but in the case of plants of the "Gherkin type", e.g. gherkin, bean and *Petunia*, it is found at much higher light intensities.

The elongation of an internode as a function of the light intensity is schematically given in Fig. 8 for red, blue and white light. In this figure I_c and I'_c represent the "critical intensity". The intensity scale for the Mirabilis type, I', is more extended than that for the "Gherkin type", I.

3. *Two photoreactions*

a. Difference in activity

Possibly at low intensities (Fig. 8, zone L) only one photoreaction is involved in inhibiting the elongation of internodes, which is more sensitive to red than to blue light. This photoreaction will be saturated with red light at a lower intensity than with blue light.

It was found, however, that the blue light curve does not only appraoch the red light curve but even crosses it (I_c). When the blue light reaction approaches saturation (zone H), blue light is even more effective than red light. This can only be explained by assuming that two different photoreactions are involved in the process inhibitive to the elongation, one photoreaction being sensitive to red light, the other to blue light. The blue light reaction increases less with increasing intensity and is saturated at a higher intensity than the red light reaction, but the inhibition caused by the blue light reaction at saturation intensity is stronger than that caused by the red light reaction.

b. Interaction

It has been reported that a combination of red and blue light is more inhibitive than an addition of the effects of each type of light (MEIJER 1958*a*). Gherkin seedlings were left to germinate in darkness. When a certain length was reached two groups of plants were exposed to blue (B) and two groups to red light (R). The light intensity was 310 μW/cm^2. After two days one group of plants irradiated with blue light was transferred to red light (B $\rightarrow$ R) and one group previously exposed to red light was transferred to blue light (R $\rightarrow$ B). The increase in length of plants exposed to blue light only was about 80 mm and

of those exposed to red light only 60 mm. The plants which received two days of blue light before the exposure to red light (B → R), however, were much more inhibited than the other groups, the increase in length being only 30 mm. On the other hand, blue light after red light (R → B) had almost the same effect as red light alone. These results too give an indication that blue and red light are involved in two different photoreactions, the red sensitive reaction being much more pronounced after blue or white light than without such a pretreatment.

This interaction between red and blue light may also be the cause of light-grown gherkin seedlings being much more inhibited in red light than seedlings sown in red light of the same intensity. In blue light, dark-grown and light-grown gherkin seedlings reached about the same height.

4. *White light*

It was calculated from its emission spectrum that white fluorescent light contains about 25 % blue radiation ($\lambda = 4000$–5000 Å) and 75 % green and red radiation ($\lambda = 5000$–7000 Å). Although the results with green light are not discussed in this paper it may be mentioned here that this light quality is active in a similar way as, but to a lesser extent than red light.

In case both the blue light reaction and the red light reaction become stronger with increasing light intensity, it is obvious that the activity of white light will be intermediary between the activity of red and of blue light (Fig. 8, zone L).

When the red light reaction is more or less saturated, the blue light reaction still becomes stronger with increasing light intensity. For that reason, at moderate intensities white light is even more active than red or blue light in inhibiting the elongation (zone M).

At still higher intensities (zone H) the blue photoreaction, too, approaches saturation and with it the reaction to white light.

5. *Antagonism*

Experiments with light-grown gherkin seedlings showed that, in addition to this inhibiting effect blue light also has an antagonizing effect on the inhibition by red light (Table 28). The inhibition caused by a previous red irradiation will be antagonized only to a certain extent. This elongating effect of blue light was not found with some other plants species; possibly the light intensities were sufficiently high for the inhibiting activity to dominate the antagonizing activity. So the ultimate result will depend on an equilibrium between both activities.

A similar dual rôle as mentioned for blue light, has been reported for near infra-red radiation (De Lint 1957). Near infra-red was found to inhibit the elongation of dark-grown seedlings (Withrow 1941; De Lint 1957). On the other hand the inhibition of the elongation by light can be reversed partly by subsequently exposing the plants to near infra-red immediately after the irradiation which caused the

inhibition (HENDRICKS *et al.* 1956; DOWNS *et al.* 1957; DE LINT 1957). The extent to which near infra-red reverses the inhibition caused by a previous irradiation depends on its own inhibiting action.

This antagonizing effect of near infra-red is also shown in the present paper (Table 21). In these experiments exposure to near infra-red was simultaneous with exposure to the visible, inhibitive, radiation. Exposure together with red light had hardly any or no effect. This may be explained by the reversibly antagonizing effects of both spectral regions (BORTHWICK *et al.* 1952*b*). Simultaneously given with green light, near infra-red caused elongation (i.e. reversed the inhibiting effect of the visible radiation) only at those intensities in which blue light was less effective than red light (zone L), e.g. gherkin, *Salvia* and tomato (hypocotyl). When red light was less effective than blue light (zone H) no influence was found e.g. *Mirabilis* and tomato (first internode). The same is valid for near infra-red given simultaneously with blue light (Table 21).

6. *Photosynthesis*

The method used in our experiments of growing plants in coloured light has the advantage that the plants can be exposed to a large amount of light. The disadvantage is the difference between the photosynthetic rates of plants grown in red light and of those grown in blue light. It was found that the dry weight of plants grown in red light is higher than that of plants grown in blue light. This was valid for all the light intensities investigated (zones L, M and H). Therefore a difference in photosynthesis cannot be of primary importance. It was reported (Table 27) that sucrose supplied to plants grown in red and blue light did not markedly change the difference in activity between these two light qualities. Similar results have been reported by VINCE (1956).

BATALIN (1871) and TRUMPF (1924) have concluded that the excessive elongation in darkness is not caused by the absence of photosynthesis because it was possible to obtain plants without chlorophyll by a brief exposure to light of a high intensity. These plants had a shape similar to that of normal light-grown plants. It was also shown that albino and potentially green barley seedlings have the same action spectrum for elongation (BORTHWICK *et al.* 1951). Another indication that the inhibition of elongation is not correlated with photosyntheses or even with the chlorophyll content was given by WITHROW (1941) and KLEIN *et al.* (1957).

7. *Light-grown plants*

WASSINK *et al.* (1956) concluded that light-grown plants and dark-grown seedlings react in a different way. In the case of the former red light would be the most active type of light but with the latter blue light would be most active in inhibiting the elongation. In this paper, however, it has been shown that, depending on the intensity, blue light can be the most active light in inhibiting the elongation of

dark-grown seedlings. With light-grown plants it was shown that blue light is sometimes less effective than red light.

It is possible that the "critical intensity" of light-grown plants has a higher value than that of dark-grown plants. It was found that at the same light intensity blue light was more active than red light when dark-grown seedlings were used. If, on the other hand, light-grown seedlings were exposed to blue and red light of the same intensity, it was shown that red light was the most effective in inhibiting the elongation (Fig. 2). Apparently this difference between light-grown plants and dark-grown seedlings is only a quantitative difference instead of a qualitative one.

Another difference was found in the reaction to continuous darkness. It was noted that light-grown plants (gherkin, tomato) hardly elongate while exposed to darkness. When, however, sucrose was supplied, a remarkable elongation was obtained. Similar results have been acquired with pea stem sections of light-grown seedlings, kept in darkness (GALSTON *et al.* 1951).

8. *Auxin*

It has been assumed that both the blue light reaction and the red light reaction are involved into different processes, leading to the same ultimate result e.g. a decrease of the auxin content (MEIJER 1958*b*). Although this assumption is quite tentative several indications where obtained that the auxin metabolism is influenced by light.

a. First of all GALSTON *et al.* (1949) demonstrated that indole-acetic acid, which is a natural auxin, can be photo-oxidized by blue light in the presence of riboflavine. The inhibiting effect of blue light on elongation may be caused by this IAA-inactivation.

b. It is possible that near infra-red and blue light, too, increase the auxin content (MEIJER 1958*b*). When young tomato plants, raised in white light, were exposed to green + near infra-red, a strong epinastic curvature of the leaves occurred within about four hours and disappeared after about 48 hours. Almost immediately the internodes started elongation. The epinastic curvature was exactly the same as was obtained in white light with plants sprayed with an IAA-solution. In blue light this epinasty was also found although to a lesser extent, however, no elongation of the internodes occurred. In red or green light this phenomenon was not noted at all. When the plants in green + near infra-red were pretreated with an anti-auxin like coumarin or penta-chlorophenoxy-acetic acid, the epinasty as well as the subsequent elongation was prevented.

c. In the same paper it was reported that the elongation of gherkin seedlings in red or green light and even the much stronger elongation in green + near infra-red or in blue light, was stimulated after an application of auxins. It was remarkable that indole-acetic acid was less effective than the other indole compounds used, such as tryptophol or tryptamine.

This auxin-induced elongation of light-grown gherkin seedlings but also the elongation caused by blue light was prevented when an anti-

auxin was supplied. It might be mentioned here that the development of the plants was normal as no injurious effect was obtained.

d. The following phenomenon also gives an indication that near infra-red or blue light may increase the auxin content (MEIJER 1958*b*). When light-grown gherkin seedlings were transferred to continuous darkness after a previous exposure to 16 hours of blue light or near infra-red, almost all plants drooped down on the fifth day in darkness. Just before this occurred, it was found that in a region about 10 mm below the insertion of the cotyledons small droplets appeared on the epidermis, which was followed by a loss of turgor in this zone causing the seedlings to droop. The other parts of the seedlings were still completely turgescent, but wilted quite soon afterwards. This phenomenon was not observed, however, if the plants were pre-illuminated with red light instead of blue or near infra-red radiation. When the seedlings previously exposed to red light were also treated with an auxin, exactly the same drooping effect was obtained as with plants previously exposed to blue or near infra-red.

It is obvious therefore that certain phenomena induced by blue or near infra-red can also be obtained with an auxin treatment.

Evidently the auxin content is influenced by light. Blue light causes a photo-oxidation of the indole-acetic acid in the presence of riboflavine. Red light may also decrease the auxin content, but this process will be different from the blue-light reaction. It may be that either IAA is inactivated in a different way or that the production of IAA is inhibited. This process can be reversed by blue and near infra-red, as far as (in the case of blue light) the photo-oxidizing activity does not dominate. BLAAUW–JANSEN (1959) has shown that the auxin content decreases after an irradiation with red light.

It is to be expected, that the inhibition of the elongation is much more complicated than can be concluded from the results of our experiments. HILLMAN *et al.* (1957) reported that red light decreases the activity of indole-acetic-acid oxidase which will result in a higher auxin content. This process is reversed by an exposure to near infra-red and this reversal will cause a decrease of the auxin content. These results do not agree with our experiments in which indications were found that near infra-red may cause an increase of the auxin content. GOLDACRE *et al.* (1953) found that the indole-acetic-acid oxidase activity of extracts of pea epicotyls was much higher when the plants were grown under continuous red light than in darkness.

The response of the plant to auxin may also be influenced by light, the sensitivity to auxin was reported either to be increased (KENT *et al.* 1951, LIVERMAN *et al.* 1953) or to be reduced (GALSTON *et al.* 1953, KLEIN *et al.* 1956) by red light. Recently BLAAUW–JANSEN (1959), in her experiments on phototropism, found a "red light factor" which enhances the effect of blue light and of IAA at low concentrations on the *Avena* coleoptile. It was found that gibberellic acid had a similar effect as red light in this respect.

9. *Conclusion*

Several authors reported results of experiments concerning the influence of the amount of light on the elongation. ÅBERG (1943) suggested the light intensity to determine which spectral region would be most active in inhibiting the elongation. Our experiments confirm this suggestion.

In those investigations in which it was found that red light was more effective in inhibiting the elongation than blue light, the "critical intensity" might not have been reached yet. In the other investigations in which blue light appeared to be more effective than red light, the intensities used might have been always higher than the "critical intensity". Obviously the conclusion that the difference in response to red and blue light does not depend on the light intensity but on the plant species (VINCE 1956; — *et al.* 1957; MEIJER 1957*b*; VAN DER VEEN 1958) might be explained by assuming that in the experiments of VINCE the differences between the intensities were too small. For *Pisum* the intensities of red and blue light may have been both in zone L, for tomato in zone H.

4. SUMMARY

4.1 *Photoperiodism*

The influence of light of different spectral regions on the long-day effect was studied on several plant species, with special reference to *Salvia occidentalis* (SDP).

I. A long-day effect was obtained by means of:
   1° a long-day treatment in coloured light; near infra-red and blue light appeared to be the most active spectral regions;
   2° a nightbreak treatment in coloured light; the requirement was found that the main light period had to contain blue of near infra-red; red light showed to be the most active nightbreak light;
   3° a supplemental light treatment in coloured light; the same spectral dependence for the main light period was found as in 2°, blue light was more active as supplemental light than red light.

II. It was demonstrated that:
   1° the effect of near infra-red and blue light (main-light-period reaction) could be counteracted by red light;
   2° the effect of red light (nightbreak reaction) could be reversed by near infra-red or blue light;
   3° the inactivity of red supplemental light (low intensity) was only seeming, it was caused by the antagonizing effect of red light on the main-light-period reaction induced by blue light (II, 1°).

III. It was concluded that it depends on the interaction of two photoreactions and not on the daylength whether a long-day effect is obtained or not; under certain conditions these reactions will even take place within short photoperiods (short days).

4.2 *Elongation*

The influence of light of different spectral regions on the elongation of various plant species was studied.

1° It depends on the light intensity whether red light is more active than blue light or, conversely blue light is more active than red light, in inhibiting the elongation of internodes.

2° At relatively low intensities red light is the most active type of light; at relatively high intensities blue light is more active than red light. This implies that at a certain intensity ("critical intensity") red and blue light are equally effective.

3° The value of the critical intensity depends on the plant species used. For plants belonging to the "Mirabilis type" the value of the "critical intensity" is lower than in the case of plants belonging to the "Gherkin type".
4° In addition to an inhibiting activity, blue light also has an antagonizing effect on the inhibition caused by red light ("dual rôle").
5° The results are briefly discussed in connection with a possible influence on the auxin content.
6° Just as in photoperiodism (II, 2°) the effect of red light can be reversed by near infra-red or blue radiation.

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Plate 1 and 2. Photoperiodic response of Salvia occidentalis to light of different spectral regions.

The numbers of the corresponding Tables are given in brackets.

= red light; = green light; = blue light; = near infra-red (broken lines: low intensity light.)

Short-day effect: +; long-day effect: —; long-day effect (partly): (—)

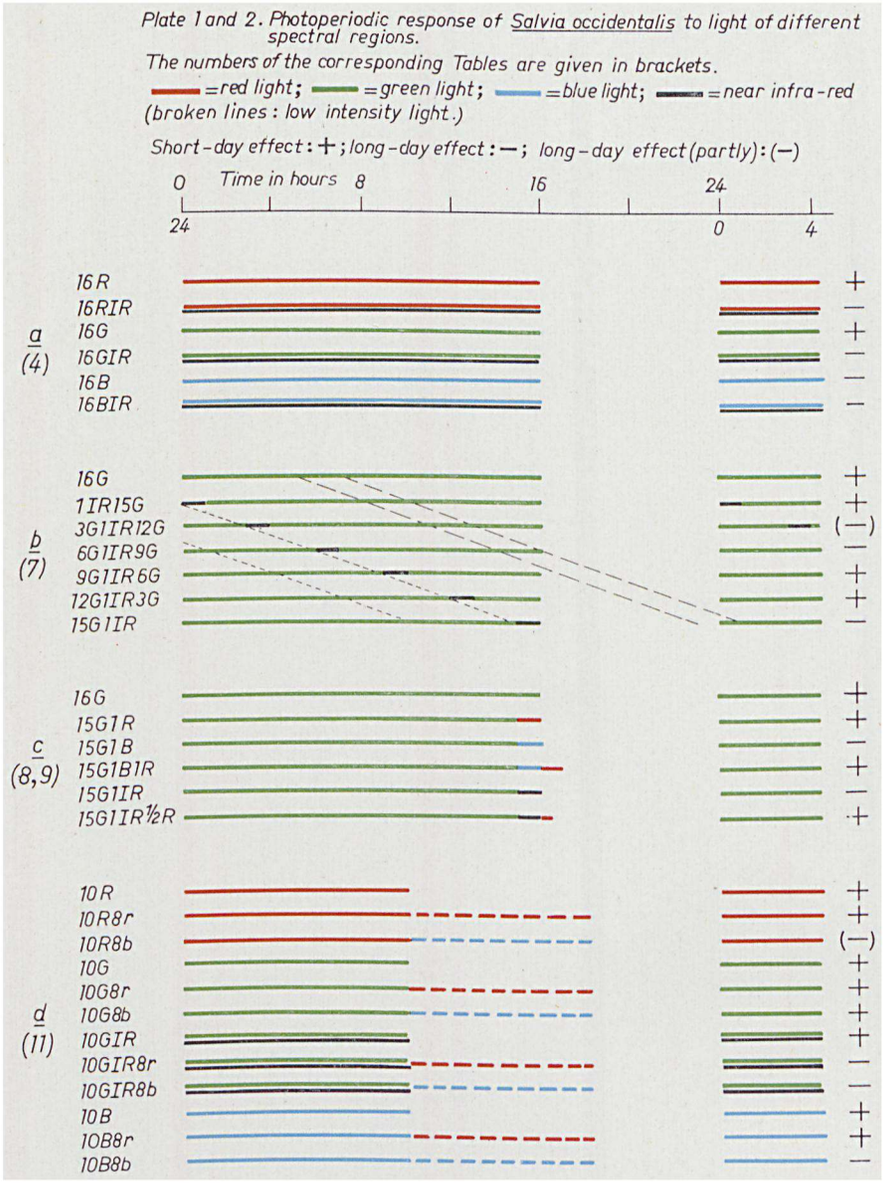

Plate 1

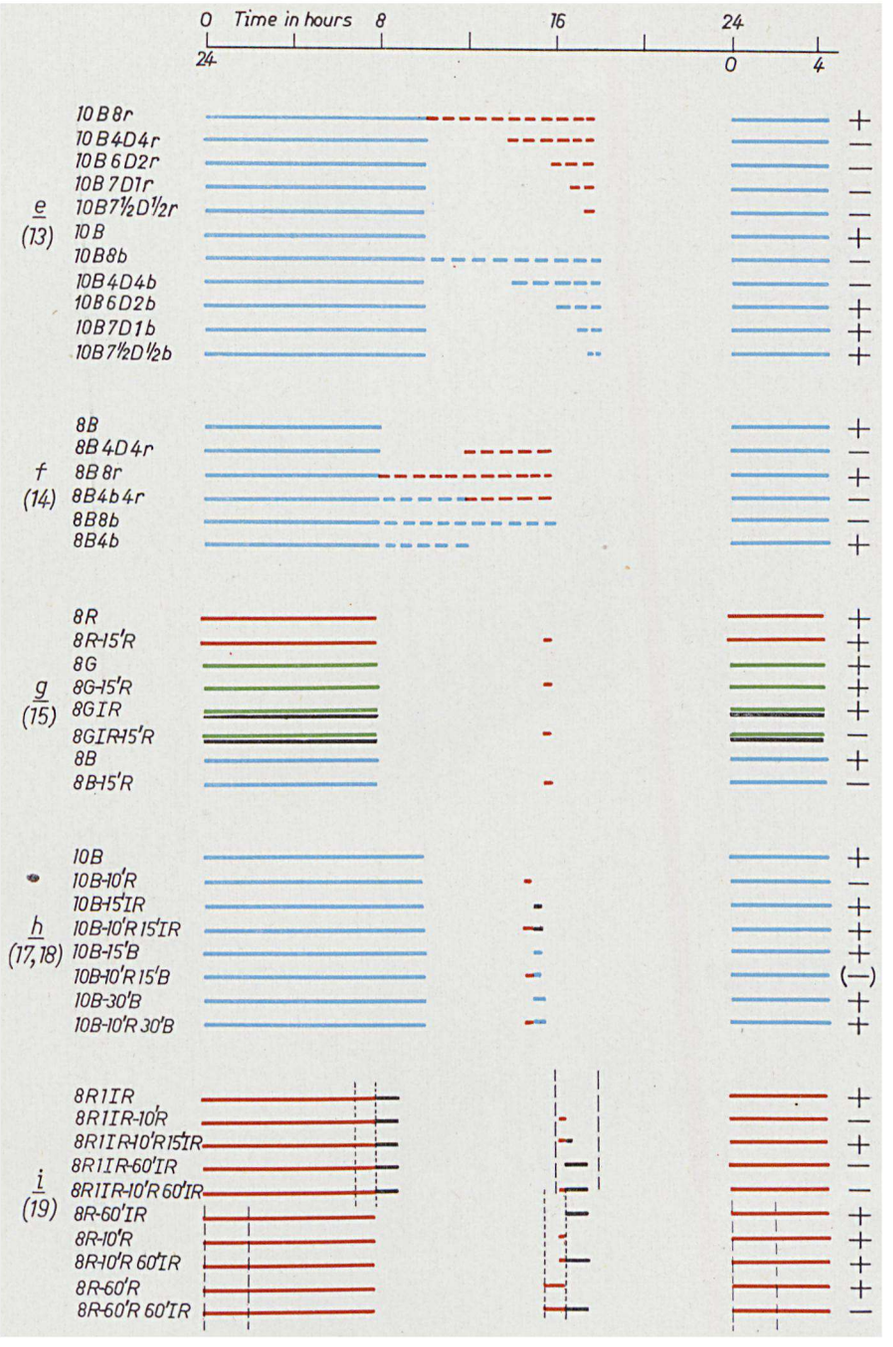

Plate 2