INFLORESCENCE INITIATION IN *LOLIUM TEMULENTUM* L.

II. EVIDENCE FOR INHIBITORY AND PROMOTIVE PHOTOPERIODIC PROCESSES INVOLVING TRANSMISSIBLE PRODUCTS

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Summary

Plants of *Lolium temulentum*, raised in short days, were given an inductive treatment by exposure of one leaf blade to a 32-hr period of continuous illumination. Then either the leaf exposed to this one long light period or varying areas of lower leaves which were simultaneously in short-day conditions were removed at intervals after the long-day exposure. The longer the long-day leaves remained on the plants, the greater was the proportion of plants which initiated inflorescences and the greater the rate of development of their inflorescences. This was so even when short-day leaves were present above the long-day ones. The longer the short-day leaves remained, and the greater their area, the lower was the proportion of plants which initiated inflorescences.

Low temperatures during the long-day exposure, and particularly during the period of low intensity illumination, prevented subsequent inflorescence initiation.

It is concluded (1) that the effect of time of removal of the leaf blades exposed to the long light period indicates the production by them of a transmissible substance which can initiate inflorescence development, provided the temperature during the long light period is above 10°C; (2) that the effect of time of removal of leaves exposed only to short days indicates the production by them of a transmissible inhibitor to inflorescence initiation which competes with the stimulus translocated from the long-day leaves.

I. INTRODUCTION

The exact role of light in controlling the flowering of long-day plants remains an enigma. The requirement for a daily period of high intensity light may be simply to provide photosynthates (Liverman 1955), which play only a preparatory, albeit necessary, role in the photoperiodic reactions. Beyond this the requirement for a daily light period of more than a certain length may be merely a need for the absence of darkness. Thus Lang (1952), in his masterly survey of the physiology of flowering, concludes that the essential element in the photoperiodic response of long-day plants is the inhibitory effect of long dark periods, and that the formation of the floral stimulus is not dependent on light, provided this dark inhibition is absent. He concludes further "that the inhibiting action of darkness is localized entirely within the leaves" since no evidence has been presented for the production of a transmissible inhibitory material. Consequently, he supposes that the process which leads to the appearance of the floral stimulus occurs in the leaves, and that

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the dark inhibition is directed against the formation, rather than against the functioning of this floral stimulus.

In this paper evidence is presented of the occurrence of an inhibitory process in leaves of *Lolium temulentum* L. kept in short days, and of a stimulatory process in leaves exposed to a single long period of light. In the experiments to be described either the leaves exposed only to short days, or those exposed to the long light period, were removed at intervals. The effect on inflorescence initiation of their time of removal provides indirect evidence that both the inhibitory and the stimulatory products are translocated from the short-day and from the long-day leaves respectively. Thus, instead of the dark inhibitor preventing the formation of the transmissible flower-promoting substances in the leaves, as Lang (1952) supposes, it appears to operate against the functioning of the flower-promoting substances produced by the long-day leaves, at some site other than the leaves, and probably at the shoot apex during the production of the ultimate floral stimulus.

II. Experimental Methods

Most of the materials and conditions for the experiments reported here have already been described in the first paper of this series (Evans 1960*a*). All plants were grown for at least 5 weeks in 8-hr days until the sixth leaf was fully expanded. The treated plants were then exposed to one long period of continuous light, by extension of the 8-hr period in daylight with 16 hr of incandescent light of either 2 or 15 f.c. intensity at plant height. They therefore had 32 hr of continuous illumination, which will be referred to below as the long-day exposure. They were then returned to the standard short-day conditions (8-hr photoperiods, at 25°C/20°C) for 3 more weeks before dissection of the apices of the primary shoot. Plants were recorded as having initiated inflorescences when they had at least reached the double ridges stage of differentiation.

In some treatments the whole shoot was exposed to the long day, in others only the blade of the sixth leaf on the main shoot. In the latter treatments the other leaves were either wrapped in aluminium foil or else removed just before the end of the first daylight period, at 4·30 p.m. on the given long day. In this way plants with a single leaf blade exposed to a single long day could have a variable area of leaves simultaneously exposed to short-day conditions. Then, either the short-day or the long-day leaf blades were cut off at various intervals after the beginning of the long-day exposure.

In the larger experiments, the wrapping of the short-day leaves with aluminium foil took about 2 hr, in all cases being completed by 4.30 p.m. Care was taken to distribute the earliest-wrapped plants at random among the various treatments. Unwrapping, the following morning, was always completed within the first half hour of the daylight period. The efficiency of wrapping as a short-day treatment was checked in each experiment by having totally wrapped plants under the long-day conditions, these being compared with control plants maintained in short-day conditions throughout. All handling of plants during the dark periods, for example for the removal of leaves, was carried out in weak green light and trial exposures of plants to this light in no case elicited any flowering response.

III. Results

(*a*) *Evidence for the Movement of a Flower-promoting Stimulus from Long-day Leaves*

The evidence is presumptive, since it is based on the effect on inflorescence initiation of the time of removal of the one leaf blade on each plant which was exposed to a long day. These effects were examined in four experiments. In half of the treatments, leaves other than the long-day leaf were in short days during the long-day exposure, and were left on the plants until dissection. In the other treatments these leaves were removed just before exposure to the long day: thus, when the blades of leaf 6 were subsequently removed, only the sheath of leaf 6, and those parts of the younger leaves enclosed by it, were left on these plants. The results for one experiment are given in Figures 1(*a*) and 1(*b*).

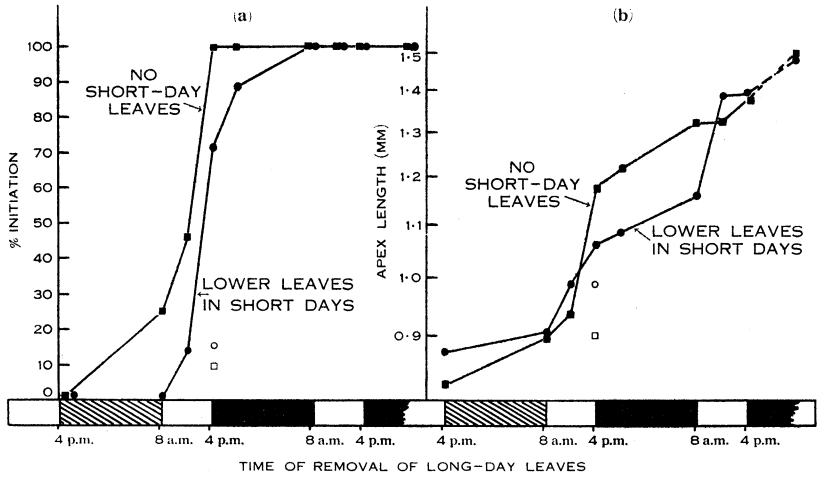

Fig. 1.—Effect of the time of removal of the blade of leaf 6 exposed to a single long day on the percentage of plants initiating inflorescences (*a*) and on the elongation of the shoot apices (*b*). Plants 48 days old at long-day treatment; supplementary illumination of 2 f.c. intensity; 8–12 plants per treatment. Plants, with short-day leaves (○) and without (□), given only low intensity illumination (2 f.c.) during the final 24 hr of the long light period.

Clearly, the longer the long-day leaf blades were left on the plant, the greater was the proportion of plants which initiated inflorescences (Fig. 1(*a*)) and the higher was the rate of apical development (Fig. 1(*b*)). It may be concluded that the curves indicate the translocation of a stimulus to inflorescence initiation out of the leaf blades exposed to the long light period.

For the plants with no short-day leaves it is apparent (from Fig. 1(*a*)) that removal of the long-day leaf blade at the end of the 16-hr period of low intensity light resulted in the subsequent initiation of inflorescences by one-quarter of the plants. Delaying the removal of the long-day leaf blade until the end of the following 8-hr period of daylight resulted in inflorescence initiation subsequently occurring in all plants. The results in Figure 1(*b*) indicate that still further delay in its removal resulted in increased rates of development of the initiated inflorescences.

Where short-day leaves were present on the plants during the long-day treatment, the pattern of results for both percentage flowering and apex length was similar to that where no short-day leaves were present. The longer the leaf blades exposed to the long light period were left on the plant, the greater was the proportion of plants subsequently initiating inflorescences, and the greater their rate of apical development. However, it is evident from Figure 1(*a*) that the presence of short-day

TABLE 1

EFFECT OF TIME OF REMOVAL, AND OF POSITION RELATIVE TO THE SHORT-DAY LEAVES, OF THE LEAF BLADE EXPOSED TO A SINGLE LONG LIGHT PERIOD, ON SUBSEQUENT PROGRESS TO FLOWERING

Plants 43 days old at long-day treatment; supplementary illumination of 15 f.c. intensity; 8–12 plants per treatment; plants dissected 3 weeks after long-day treatment. Mean areas of the blades of leaves 5 and 6 were 16·1 and 18·7 cm^2 respectively

Time of Removal of Long-day Leaf	Leaf 6 in Long Day, Leaf 5 in Short Day		Leaf 6 in Short Day, Leaf 5 in Long Day	
	Initiation (%)	Apex Length (mm)	Initiation (%)	Apex Length (mm)
4.30 p.m. (I) (short-day controls)	0	1·22	0	1·16
8.30 a.m. (II)	90	1·55	88	1·42
12.30 p.m. (II)	100	1·95	100	1·75
4.30 p.m. (II)	100	1·98	100	1·79
8.30 p.m. (II)	100	1·99	100	1·92
Leaf not removed (long-day controls)	100	2·55	100	2·23

leaves reduced the proportion of plants initiating inflorescences when the leaf blades exposed to the long light period were cut off during the second period of high intensity light.

In two treatments the plants, instead of being exposed to 8-hr of daylight of high intensity following the 16-hr period of low intensity illumination, were maintained under incandescent light of 2 f.c. intensity until the removal of the long-day leaves at the end of the long period of illumination. Under these conditions the proportion of plants initiating inflorescences, and the rate of their apical development, was much lower than in those plants defoliated at the same time after 8 hr of daylight (Figs. 1(*a*) and 1(*b*)).

The results of the second experiment were essentially similar to those described above, and differed only in the proportion of plants initiating inflorescences after the various times of leaf removal. There was no inflorescence initiation among plants from which the long-day leaf blades were cut off prior to the end of the long light period and only 70 per cent. and 50 per cent. among the plants without and

with short-day leaves respectively when defoliation occurred at the end of the long light period. Among the plants on which the long-day leaf blade was not removed, all those without short-day leaves, and 80 per cent. of those with short-day leaves subsequently initiated inflorescences.

In the third experiment, only 10 cm^2 of the sixth leaf blade was exposed to one long light period, and although this area is sufficient for inflorescence initiation in the absence of short-day leaves (Evans 1960*a*), it proved to be insufficient when all other leaves were in short days. Nevertheless, the length of the shoot apices increased significantly with the length of time before removal of the leaf blade exposed to a long light period.

In the fourth experiment, the effect of the time of removal of the leaf blade exposed to one long light period was compared in two series of treatments. One series was comparable to those described above in that leaf 6, the upper leaf, was given the long day, while leaf 5 was in short-day conditions. In the other series leaf 5 was given the long day while leaf 6 above it remained in short-day conditions. The results of the experiment are given in Table 1.

The results of both series are comparable to those described above in that the later the time of removal of the leaf blade exposed to the long light period the greater was the proportion of plants which had initiated inflorescences at the time of dissection and the greater the rate of development of their inflorescences. In the series in which the short-day leaf was above the long-day leaf the rate of inflorescence development was, however, slightly but consistently lower.

(*b*) *Evidence for the Movement of an Inhibitory Substance from Short-day Leaves*

From the results given in the preceding section it is evident that progress towards flowering in *L. temulentum* plants depends on the balance between the short-day and the long-day leaf areas. In the first experiment described above, the balance was such that all plants with the long-day leaves remaining on them could initiate inflorescences in spite of the presence of short-day leaves, while in the third, in which the leaf area exposed to the long light period was smaller, none did. In the experiments described below the leaf area exposed to the long light period was between these extremes, to permit expression of the effect of time of removal of the short-day leaves. The actual areas of the long-day leaves, the intensity of their illumination, and the areas of short-day leaves for the three experiments are given in Figure 2.

In all three experiments, the longer the short-day leaves remained on the plant after its exposure to a long light period, the smaller was the proportion of plants subsequently initiating inflorescences, and the slower their rate of apical development. The inhibition of initiation was greatest in the experiment with the highest ratio (6·5) of short-day leaf area to long-day leaf area, least in that with the lowest ratio (4·0). In all three experiments the inhibitory effect of the short-day leaf blades was almost maximal by the end of the succeeding 8-hr period of daylight. In two of the experiments a considerable inhibitory effect was apparent even when the short-day leaves were removed only 6 hr after the beginning of the dark period.

In a further experiment the area of leaf exposed to the long light period was kept constant, but both the area of the short-day leaves and the time at which they were cut off varied, with the results shown in Figures 3(*a*) and 3(*b*).

For all four times of removal of the short-day leaves, the greater their area the smaller was the proportion of plants which initiated inflorescences, and the slower their rate of apical development, with one minor exception. As in the preceding experiments, a marked inhibitory effect due to the presence of the short-day leaves was apparent even when they were removed only 6 hr after the beginning of the dark period.

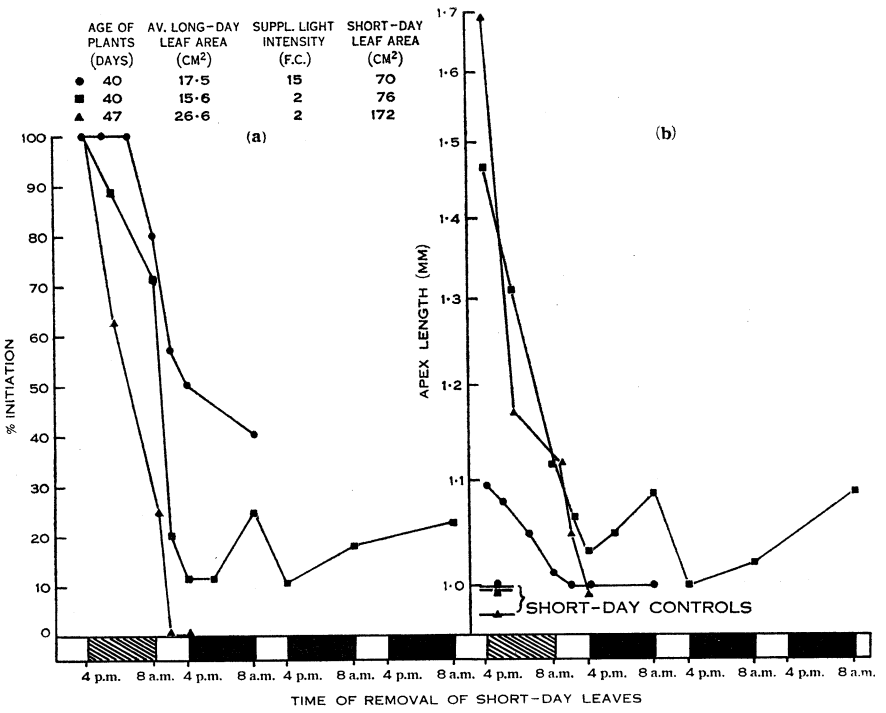

Fig. 2.—Effect of time of removal of the leaf blades kept in short-day conditions, during exposure of the sixth leaf to a single long light period, on the percentage of plants initiating inflorescences (*a*), and on the elongation of the shoot apices (*b*). 8–12 plants per treatment; other data given on figure.

(*c*) *Effect of Temperature during a Single Long-day Exposure*

Four experiments have been carried out in which the temperature during the whole or part of a single long-day exposure, given to undefoliated plants of full photoperiodic sensitivity, has been varied.

In two experiments different temperatures were maintained throughout the first 24 hr of the long light period. The 8-hr periods of high intensity light in one were in daylight at temperatures 5°C above those of the following 16-hr periods, which were in incandescent light of 15 f.c. intensity. In the other, which involved

more extreme temperature treatments, the 8-hr period of high intensity light (1500 f.c.) was provided by fluorescent and incandescent lamps and the temperatures were held constant over the whole 24-hr period. For both these experiments dissections were carried out 5 and 35 days after the long-day exposures, allowing estimation of the relative growth rates of the inflorescences, with the results presented in Figure 4.

The marked influence of temperature on the inductive efficiency of a single long day is evident. Inflorescence initiation occurred in all plants of the treatments whose temperatures during the period of low intensity illumination ranged from 10 to 25°C, but there was a pronounced optimum at 25°C/20°C for the subsequent

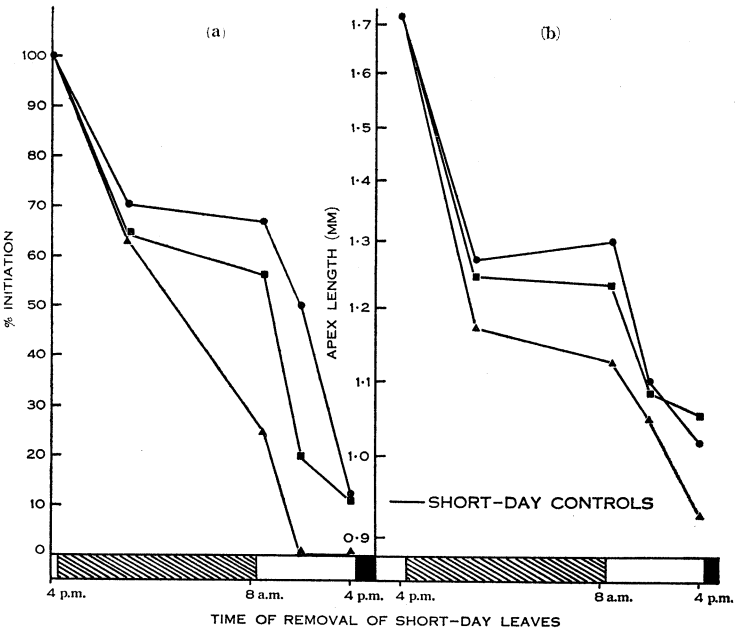

Fig. 3.—Effect of time of removal of the leaf blades kept in short-day conditions, during exposure of the sixth leaf to a single long day, on the percentage of plants initiating inflorescences (*a*) and on the elongation of the shoot apices (*b*). Plants 47 days old at long-day treatment; long-day leaf area 26·6 cm²; short-day leaf areas 21·1 cm² (leaf 5, ●); 45·9 cm² (leaves 3, 4, and 5, ■); or 172·4 cm² (all lower leaves, ▲).

growth rates of the initiated inflorescences and for the rate of their morphological development. Whereas the plants given a long day at 25°C/20°C had differentiated floret primordia at the time of the final dissection, those at 20°C/15°C and 30°C/25°C had only differentiated glume primordia and those at 15°C/10°C were only at the double ridges stage. At the highest temperature regime (30°C) only 75 per cent. of the plants initiated inflorescences, and at the lowest temperatures initiation was limited (12·5 per cent. at 7·5°C) or prevented (none at 3°C) despite the favourable photoperiod.

In the two remaining experiments the temperature during only part of the one long day was varied. In one experiment the temperature during the first 8-hr period of daylight was 25°C in all treatments while the temperature during the following 16-hr period of low intensity (15 f.c.) incandescent illumination varied from 4 to 35°C. In the other, the 16-hr period of low intensity illumination was at 20°C in all treatments, while the temperature during the preceding 8-hr period of daylight varied from 7·5 to 25°C. The results of the dissections made after all plants had spent a further 3 weeks in short days at 25°C/20°C are given in Figure 5.

Inflorescence initiation occurred in all plants whatever the temperature of the high intensity light period, but it is nevertheless evident that this temperature has had a pronounced after-effect on the rate of inflorescence development. The morphological differentiation of the induced apices also reflected this effect in so far

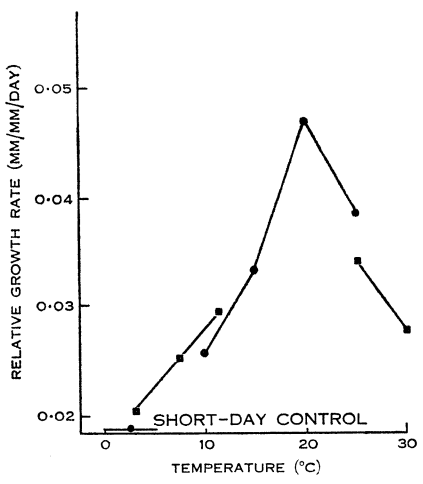

Fig. 4

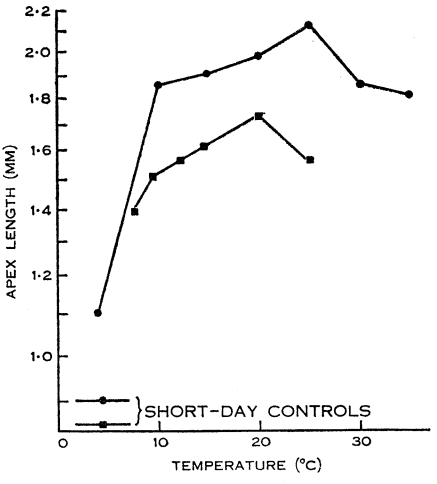

Fig. 5

Fig. 4.—Effect of temperature during a single day of continuous illumination on the subsequent relative growth rates of the shoot apices of plants of *L. temulentum*. ● Plants exposed to 8 hr of natural illumination, followed by 16 hr of incandescant light of 15 f.c. intensity at the temperatures indicated, which were 5°C lower than during the daylight period. ■ Plants exposed to 8 hr of high intensity (1500 f.c.) illumination from fluorescent and incandescent lamps, followed by 16 hr of incandescent light of 15 f.c. intensity at the same temperature.

Fig. 5.—Effect of temperature during part of a single day of continuous illumination on the mean apex length of plants subsequently returned to short days for 3 weeks. ● All treatments given 8 hr of daylight at 25°C, followed by 16 hr of incandescent illumination of 15 f.c. intensity at the temperatures indicated. ■ All treatments given 16 hr of incandescent illumination of 15 f.c. intensity at 20°C, preceded by 8 hr of daylight at the temperatures indicated.

as those in daylight at 7·5°C had only reached the earliest double ridges stage, and those at 9·5°C advanced double ridges, while the remainder had at least differentiated glume primordia. The temperature during the second part of the one long day, the 16-hr period and low intensity illumination, had a decisive after-effect on inflorescence development. No inflorescence initiation occurred when the temperature

during this period was 4°C. All temperatures from 10 to 35°C permitted initiation in all plants, the rate of apical development being highest at 25°C. At this temperature plants had differentiated floret primordia at the time of dissection, whereas only lemma primordia were differentiated at the other temperatures.

IV. Discussion

(a) *Dark Inhibitory Process and the Transmissibility of its Product*

The results of the experiments in which the short-day leaves of plants were removed at intervals provide direct evidence of the net inhibitory effect of short-day leaves on inflorescence initiation in *L. temulentum*. They also provide circumstantial evidence of the transmissibility of this inhibitory effect, and of the time of its translocation from the leaf blade.

It could be argued that the inhibitory effect of the short-day leaves when left on the plants beyond a certain time is due to their acting as sinks for stimulatory substances from the long-day leaves, or because they generate a solute stream opposed to that from those leaves. Two lines of evidence refute these explanations. The first is that the inhibitory leaves were, with one specific exception, those inserted below the long-day leaves and, according to Lang (1952), could not act in this way. Secondly, were the short-day leaves to operate in either of the ways suggested, their inhibitory effect could scarcely precede, as it usually does, the apparent translocation of the stimulatory effect from the leaves exposed to the long light period.

Thus, we may conclude that the dark inhibitor is transmissible and that it acts at a distance from the short-day leaves. Although previously there has been no clear evidence for the transmissibility of the dark inhibitor, so that Lang (1952) was forced to conclude that the inhibiting action of darkness was localized entirely within short-day leaves, three earlier experiments have been suggestive of it. Lang (1941) obtained flower initiation in plants of *Hyoscyamus niger* kept in short days, provided they were defoliated continuously. The inhibitory action of the short-day leaves must therefore have extended over some distance from the leaves. Lang (1952) considered that this was due to the diversion from the axis tissues to the leaves of material necessary for the production of the floral stimulus. With spinach, Withrow, Withrow, and Biebel (1943) found that when plants with only one or three mature upper leaves were given 26 long days they flowered, whereas those also having their lower leaves in short days did not. As these investigators did not remove the leaves developing in short days above the long-day leaves, their results are inconclusive, since the young short-day leaves could have been acting as sinks for the products of the long-day leaves. That this might be so is indicated by the results given in Table 1, and by the results of Chailahjan (1946) with *Sinapis*. He found that when the short-day leaf was situated between the long-day leaf and the apex its inhibitory effect was far greater than when it was situated below the long-day leaf. However, incision of the stem for 5–8 cm below the insertion of the short-day leaf, when this was above the long-day leaf, greatly reduced the inhibitory effect, and Chailahjan concluded that this depended on the distance of the short-day leaf from the apical bud rather than on its disposition with respect to the long-day leaf.

(b) Long-day Promotive Process and the Transmissibility of Its Product

The results of the experiments in which single leaves of *L. temulentum* plants were exposed to a single long period of continuous illumination and were removed at intervals during and after this, indicate the formation and translocation from these leaves of a stimulus capable of initiating inflorescence development both in the presence and in the absence of leaves simultaneously in short-day conditions. Most of the translocation from the leaf blades exposed to the long light period appeared to take place in the second 8-hr period of high intensity light. In plants with no short-day leaves, sufficient stimulus had been translocated from the long-day leaf blades by the end of the period of low intensity illumination to initiate inflorescence development in a proportion of the plants. It may therefore be concluded that the second period of high intensity light is not required to complete the long-day process. Nevertheless, exposure of the plants to low intensity light following the 24 hr of continuous light resulted in far slower translocation of the stimulus from the long-day leaves, a result which is suggestive of passive translocation of the stimulus along with photosynthates. Carr (1957) has obtained comparable results with *Xanthium*, while Guttridge (1959) has presented evidence for the passive translocation with photosynthates of a growth-promoting, flower-inhibiting substance from long-day donor strawberry plants to short-day receptors.

It has been suggested (Barber 1959) that the long-day leaves promote flowering in long-day plants merely by acting as sinks for transmissible inhibitory substances from the short-day leaves. Known patterns for the distribution of assimilates (Belikov 1958; Thaine, Ovenden, and Turner 1959) hardly support this view.

It might also be suggested that the long-day leaves exert an apparently promotive effect by generating a solute stream opposed to that from the short-day leaves. The timing of their promotive effect in relation to the time of movement of the inhibitor from the short-day leaves does not conflict with this suggestion, but other evidence does so. In the first place, results similar to those presented in Figures 1(*a*) and 1(*b*) were also obtained from treatments in which the relative positions of the long- and the short-day leaves were reversed, i.e. in which the long-day leaf was below the short-day leaf and hence unlikely to generate a solute stream opposed to that carrying the inhibitory substance to the site of inflorescence initiation. Also, if the only effect of a long day is the suppression of the dark inhibitory process, it is difficult to account for the pronounced effect of temperature during that one long day on subsequent progress to flowering. In fact, the finding that a long-day exposure cannot initiate inflorescence development when the period of supplementary low intensity illumination was at a low temperature can only be explained by the assumption that a promotive process which is optimal at about 25°C, and severely retarded at 4°C, takes place in leaves during exposure to long-day conditions. Morley and Evans (1959) and Doorenbos and Wellensiek (1959) have also found that low temperatures during the exposure of plants of *Trifolium subterraneum* and *T. pratense* to long days prevented subsequent flower initiation.

Moreover, if a dark inhibitory process only was involved in the flowering of long day plants, as von Denffer (1950) suggests, since that process is known to be

greatly retarded at low temperatures (Lang 1952), flowering could be expected to occur in plants kept in short days with high day and low night temperatures. However, *L. temulentum* plants kept for 2 weeks in 8-hr photoperiods at 25°C/4°C showed no advance towards inflorescence initiation in subsequent short days at 25°C/20°C. It may be concluded then that a positive stimulus to flowering is formed in leaves of *L. temulentum* during exposure to long days, provided the temperature is not too low, and that this stimulus is subsequently translocated from these leaves, probably along with photosynthates.

(c) *Interrelation of the Inhibitory and Promotive Processes*

Leaves in short days have been shown to have a net inhibitory effect on inflorescence initiation in *L. temulentum* which is transmissible, and not merely localized within the short-day leaves. Similarly, leaves in long days have been shown to produce a stimulus to inflorescence initiation which is also transmissible. We may conclude, therefore, that the dark inhibitor does not operate against the formation of the flower-promoting substance within short-day leaves, as Lang (1952) supposed, but against its functioning, after translocation from long-day leaves, presumably at the site of the potential inflorescence and in the process which finally leads to the initiation of inflorescence development. Since *L. temulentum* plants require exposure to progressively fewer long days as they become older (Evans 1960*a*), and in view of the competitiveness of the products transmitted from the short-day and the long-day leaves, it must be presumed that the dark inhibitor does not accumulate at the site of inflorescence initiation. The fact that interpolation of short days among a number of long days did not reduce the inductive effect of the long days (Evans 1960*b*) supports this conclusion. This absence of any accumulation of the dark inhibitor at the site of inflorescence initiation could account for Wellensiek's (1960) failure to find an inhibitory action of darkness in his experiments with several long-day plants.

The results given in this paper raise the possibility that light may play a direct and positive role in the initiation of flowering in *L. temulentum*. Since the net inhibitory effect of leaves exposed to long dark periods is not confined to those leaves, but acts at a distance from them in opposition to products from leaves not so exposed, light may not only operate to suppress the inhibitory dark process but may also accelerate the promotive processes occurring in long-day leaves. Two distinct photochemical processes, with different action spectra, may therefore be involved in the initiation of flowering in long-day plants. If so, much of the apparent diversity among long-day plants in their spectral requirements for flower initiation could be explained, since the balance between the inhibitory and promotive processes is likely to vary from species to species.

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