

INFLORESCENCE INITIATION IN *LOLIUM TEMULENTUM* L.

I. EFFECT OF PLANT AGE AND LEAF AREA ON SENSITIVITY TO PHOTOPERIODIC INDUCTION

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Summary

As they increase in age, plants of *L. temulentum* require exposure to progressively fewer long days before they can initiate inflorescences, until, after being grown for 5 weeks at 25°C for 8 hr and at 20°C for the remainder of each day, they require only one long day. This increase in sensitivity to photoperiodic induction with age varies to a slight degree with seasonal light conditions. In young plants, exposure to long days for less than the period required for inflorescence initiation increases the rates of leaf initiation and apex elongation.

When the leaf areas of mature plants are reduced by removal of all the lower leaves, exposure of only a few square centimetres of leaf blade to one day of continuous light is sufficient for inflorescence initiation. On the other hand, when only the lower leaves are left the plants require exposure to the same number of long days as do younger plants with the same leaves present.

It is concluded that the expansion of leaves of higher ontogenetic rank contributes more to the increase in sensitivity to photoperiodic induction than do increase in total leaf area, leaf age, or apex age of the plants.

I. INTRODUCTION

Mature plants of *Lolium temulentum* L. have been shown (Evans 1958) to require exposure to only one long day for the initiation of inflorescence differentiation. It has also been found that only a few square centimetres of one leaf need be exposed to this long day, and that the intensity of light during the supplementary period of illumination need be only 1-2 f.c. for inflorescence initiation to occur. This pre-eminent sensitivity of the species to induction by long days, which renders it quite comparable to *Xanthium pensylvanicum* among short-day plants, is not present in young plants, however, and is only attained after about 5 weeks of growth.

Seedlings and young plants of many short-day species are known to require more short days for photoperiodic induction than are mature plants (Borthwick and Parker 1938, 1940; Moshkov 1939; Harder and von Witsch 1942; Lona 1949). Among long-day plants, Chouard (1950) has shown that *Scabiosa ukranica* needs exposure to 3 weeks of continuous light at 3 months of age, but to only 1 week at 9 months of age. Juvenile insensitivity to photoperiodic induction thus appears to be a fairly widespread phenomenon, although there are exceptions such as *Arachis hypogaea* (Rossem and Bolhuis 1954). It is the purpose of the present paper to analyse the factors responsible for the increase in sensitivity to photoperiodic induction with age in *L. temulentum*.

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II. METHODS

All plants were grown singly in small plastic pots containing either vermiculite or perlite, and were given Hoagland's nutrient solution and water daily. The pots were held in boxes providing automatic control of the photoperiod to a length of 8 hr. The boxes were kept in a glass-house whose temperature was maintained at approximately 25°C for 8 hr and at 20°C for the remainder of each day (designated 25°C/20°C). Departures from the set temperature conditions were not great, and the main variation between experiments was probably in seasonal light intensity and spectral composition. Leaves on the main stem of all plants were notched for identification as they appeared. At various times groups of plants were removed and exposed to one or more days of continuous light, each consisting of daylight

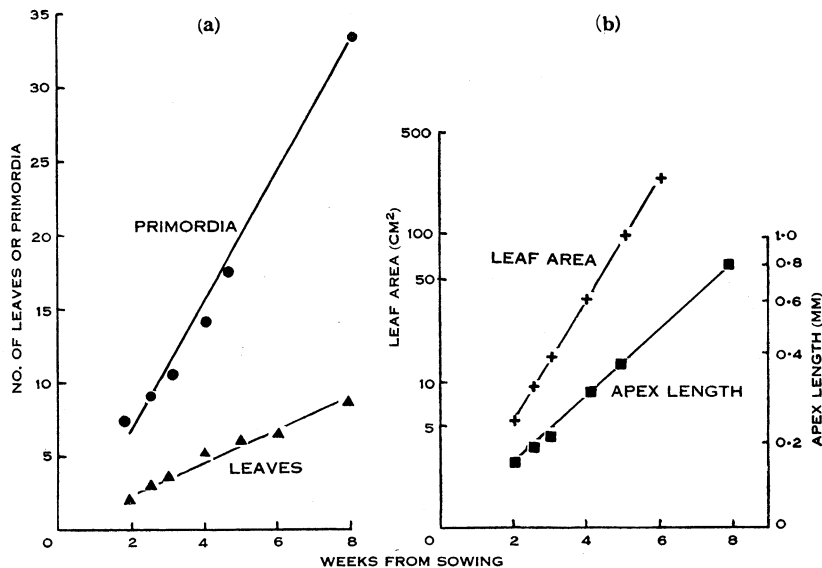


Fig. 1.—Course of growth in *L. temulentum* plants at 25°C/20°C in 8-hr photoperiods of summer daylight.

for 8 hr (at 25°C) followed by illumination of 10–15 f.c. intensity at plant height from incandescent sources (at 20°C). They were then returned to the short-day boxes for 2 or 3 weeks before dissection. At dissection the state of differentiation of the main shoot apex and its length were recorded, together with the number of leaves and of nodes to flowering, and the total number of primordia present.

III. RESULTS

(a) *Change in Photoperiodic Sensitivity with Chronological Age*

In all, five age-sensitivity series have been examined. These were grown at different seasons, and the results of the most complete series will be described first. This series was sown in January, with eight plants in each treatment group. The course of growth in 8-hr photoperiods at 25°C/20°C may be seen from Figure 1, from

which it is evident that leaf area increased exponentially throughout the experimental period, while leaf appearance and leaf initiation increased approximately linearly at rates of one per 6.4 and 1.7 days respectively. Thus, about three-quarters of the initiated leaf primordia accumulated at the shoot apex under these conditions, with consequent increase in its length.

TABLE 1
EFFECT OF PLANT AGE AND OF NUMBER OF LONG DAYS ON THE PERCENTAGE OF *L. TEMULENTUM* PLANTS WHICH INITIATED INFLORESCENCES, AND ON THE NUMBER OF NODES TO FIRST FLOWERING
Plants dissected 2 weeks after exposure to the first long day

	Age of Plant (days)	Days of Continuous Light:						
		0	1	2	3	4	6	8
Plants (%)	14	0	0	0	0	75	100	100
Nodes						7.5	7.0	6.6
Plants (%)	18	0	0	0	25	100	100	100
Nodes						7.8	7.4	7.0
Plants (%)	21	0	0	62.5	87.5	100	—	100
Nodes				9.3	8.8	8.0		8.0
Plants (%)	28	0	0	100	100	100		
Nodes				9.3	9.0	8.9		
Plants (%)	34	0	100	100	100			
Nodes			10.6	10.3	9.5			
Plants (%)	42	0	100	100				
Nodes			11.7	11.1				

The results of the dissections made 2 weeks after exposure to the first long day are given in Table 1 and in Figures 2 and 3. Plants which were only 2 weeks old apparently required exposure to more than 4 days of continuous light before they all initiated inflorescences, while plants 18, 21, 28, and 34 days old at their first exposure to long days required only 4, 4, 2, and 1 days respectively (Table 1).

The results in Table 1 also indicate that the number of nodes to flowering tends to be lower the more inductive long days given, and the younger the plants at induction. The lowest values for each age are very similar to those obtained by Cooper (1956) with plants of *L. temulentum* of equivalent leaf-appearance age. Comparison of these numbers with the numbers of primordia that were present at the time of inflorescence induction (Fig. 1) indicates that, in all except the youngest plants, a proportion of the initiated leaf primordia must ultimately subtend spikelet primordia, this proportion increasing markedly with advance in age of the plants and with the number of long days given.

The data given in Figure 2 indicate that apex length increased with the number of long days given in all cases, even when no long day effect was manifest in the proportion of plants which had initiated inflorescences. Similarly it is evident from Figure 3 that the rate of initiation of primordia increased with increase in exposure to long days even when the number of long days given was insufficient to elicit the differentiation of double ridges.

(b) *Variations in Sensitivity not due to Chronological Age*

The results of the other age-sensitivity series were all similar in pattern, but in only one case were they identical to the series already described. In the others, particularly in those grown during the winter months, plants were less sensitive to induction than plants of the same chronological age in the series described. They were also smaller in leaf area, and had initiated fewer primordia, the plastochrone

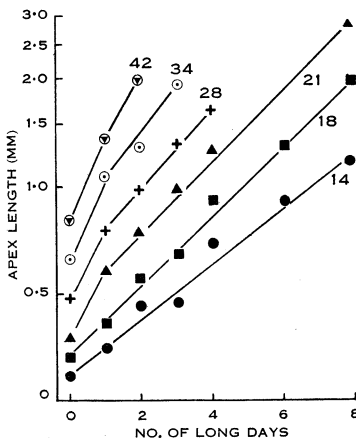


Fig. 2

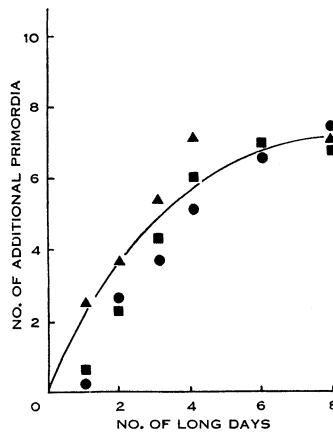


Fig. 3

Fig. 2.—Effect of plant age on apex length 2 weeks after exposure to the first of a number of days of continuous light. Age of plants in days indicated on the figure.

Fig. 3.—Number of primordia differentiated in excess of the number in plants not exposed to long days, 2 weeks after exposure to the first long days. Age of plants: ● 14 days; ■ 18 days; ▲ 21 days.

being up to 3 days, about twice the interval in the series described. The rate of leaf appearance was less affected, the slowest rate being one every 9.6 days, compared with 6.4 days in the series described.

Since all series were grown under the same conditions of temperature, photoperiod, and nutrient culture, the differences between them are probably due to seasonal changes in the intensity or quality of daylight.

Bases other than chronological age were therefore used to compare the results of the various series. Total leaf area, number of primordia initiated, and number of expanded leaves were used, but only with the last were the results at all

comparable. In fact, the change in sensitivity to photoperiodic induction with increase in the number of expanded leaves on the primary shoot was almost identical in all series. This suggests that it is the expansion of the later-formed leaves which most affects the sensitivity of *L. temulentum* plants to induction by long days, a conclusion which is supported by the results given below.

(c) *Minimum Leaf Area Required for Induction by One Day of Continuous Light*

The plants were sown in early April, and grown for 41 days until leaf 6 on the primary shoot was fully expanded. All other leaf blades were then removed from the plants, and the blade of leaf 6 was reduced to varying degrees, in groups of 8–10 plants, just before exposure to a single day of continuous light. The plants were dissected after a further 3 weeks in the standard short-day conditions, with the results shown in Figure 4. Exposure of only 6 cm² of leaf 6 to one long day was

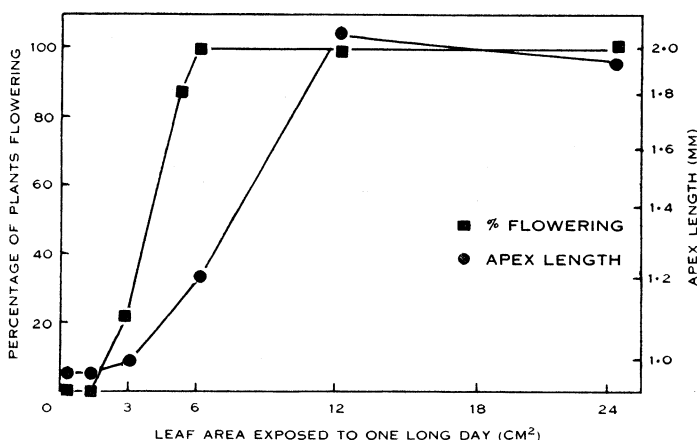


Fig. 4.—Effect of the area of leaf 6 exposed to one day of continuous light on the percentage of plants initiating inflorescences (■) and on increase in length of the shoot apex (●).

apparently sufficient for the initiation of inflorescences in all plants, and exposure of 12 cm² resulted in the maximal rate of inflorescence development under these conditions. Since the minimum effective leaf area is comparable to the leaf area of plants 14 days old, the increase in photoperiodic sensitivity with age cannot be ascribed to increasing leaf area *per se*.

(d) *Effect of Reduced Leaf Areas on the Photoperiodic Sensitivity of Mature Plants*

A large number of plants was sown late in April to 8-hr photoperiods at 25°C/20°C and subsequently divided at random into three groups. Group A comprised an age-sensitivity series, like those already described, for comparison with the other two groups. Lots of eight plants were removed at intervals from the short-day conditions, exposed to a number of days of continuous light, and returned to short days until dissection 2 weeks after the first exposure to long days.

The group B plants were kept under short-day conditions until 35 days old, by which time leaf 6 was fully grown. Their leaf areas were then reduced to areas equivalent to those of the younger plants in group A at the time of their exposure to long days, and the plants were then given the same long-day treatments as the group A plants, in lots of 8. In the group B plants the reductions in leaf area were made by removal of the younger leaves, with the result that the same leaves were left on the main shoots as were present on the younger plants at the equivalent age.

TABLE 2
PERCENTAGE OF PLANTS WITH INITIATED INFLORESCENCES 14 DAYS AFTER THE INITIAL EXPOSURE TO LONG DAYS

Age of Plant (days)	Leaf Area Exposed to Long Days (cm ²)	Leaves or Parts of Leaves Left	Number of Long Days at 25°C/20°C				
			0	1	2	3	4
14	5.0	All (leaf 1, leaf 2)	0	0	0	0	75
35	5.0	Lower (leaf 1, leaf 2)	0	0	0	37.5	100
35	5.0	Upper (leaf 6)	0	87.5	100	—	—
18	8.6	All (leaves 1-3)	0	0	0	37.5	100
35	8.6	Lower (leaves 1-3)	0	0	12.5	37.5	87.5
35	8.6	Upper (leaf 6)	0	100	100	—	—
21	13.2	All (leaves 1-3)	0	0	62.5	100	—
35	13.2	Lower (leaves 1-3)	0	0	37.5	100	—
35	13.2	Upper (leaf 6)	0	100	100	—	—
28	36.3	All (leaves 1-5)	0	0	100	100	—
35	36.3	Lower (leaves 1-5)	0	0	100	—	—
35	36.3	Upper (leaf 5, leaf 6)	0	100	100	—	—
35	95.5	All (leaves 1-6)	0	100	100	100	—

In the group C plants, on the other hand, all the lower leaf blades were removed, and the required leaf areas were derived from the two uppermost fully expanded leaves of the main stem. Otherwise, the treatment of the plants was the same as that for group B.

Additional leaf areas developing during the long-day treatments were removed daily. The primary shoots of the plants were dissected 14 days after the beginning of the long-day treatment, and some of the results of these dissections are given in Table 2.

The increase in sensitivity to long-day induction with advance in age of the group A plants is closely similar to that already described. So too, is that for the mature plants in which only the lower leaves were exposed to long days (group B), there being only minor differences between the two groups despite the increased age of both the leaves and the differentiating shoot apex in the latter. On the other hand, as would be expected from the results given in Section III(c), the equivalent

areas of the upper leaves were apparently far more effective in induction, since exposure to only one long day was sufficient for inflorescence initiation in virtually all of the group C plants.

IV. DISCUSSION

The progressive increase in sensitivity to photoperiodic induction with age of plants of *L. temulentum* could have several explanations, and the evidence bearing on some of these will now be considered. Lona (1949) and Zeevaart (1958) have previously discussed the results for short-day plants.

(a) Increase in the Perceptive Leaf Area of the Whole Plant

In *Oenothera biennis* (Chouard 1950) there is evidence that the total leaf area of the plants may limit sensitivity to photoperiodic induction. However, plants of *L. temulentum*, of an age just to have attained full sensitivity to photoperiodic induction, may retain that sensitivity even when their leaf area is reduced by 95 per cent. Hence, as in the several other species known to behave similarly in this respect, it cannot be the total leaf area which limits sensitivity to photoperiodic induction in young plants.

(b) Increase in the Photoperiodic Sensitivity of Individual Leaves as they become Older

From their experiments with *Xanthium*, Khudairi and Hamner (1954) and Salisbury (1955) suggest that although leaves may increase in their sensitivity to photoperiodic induction until they are almost fully expanded they tend thereafter to decline in sensitivity with increased age. However, since they took the position of a leaf as the criterion of its age, effects due to the age of a leaf and those due to its position are confounded.

From grafting experiments with *Perilla*, Zeevaart (1958) found that fully expanded leaves retain their photoperiodic sensitivity for a considerable time, and that the age of leaves was far less important than their position on the plant. It seems likely that, in *L. temulentum* also, fully expanded leaves retain their photoperiodic sensitivity for some time, since the response to a number of long days of mature plants with only their basal leaves remaining was almost identical to that of young plants with the same, but much younger, leaves.

In no species is there any evidence of an increase in the photoperiodic sensitivity of fully expanded leaves with age.

(c) Greater Photoperiodic Response in later-formed Leaves

With a few exceptions (Zieriacks 1952; Kujirai and Imamura 1958), cotyledons appear to be unable to induce plants to flower under the appropriate photoperiodic conditions, and it is possible that the first-formed leaves may also be less sensitive than later ones to photoperiodic induction. In a series of elegant grafting experiments with *Perilla*, in which he could exclude effects due to the age of leaves or growing points, Zeevaart (1958) found that the lower leaves required exposure to more short days than did the later-formed ones before they could initiate flowering in vegetative stocks.

Since grafting experiments are precluded in *L. temulentum*, comparisons of the inductive efficiencies of various leaves are confounded with differences in their age. However, it was concluded above that leaf age did not appear to have a major effect on the sensitivity of the leaves to long-day induction, in which case the very great differences found between the sensitivity of the lower and that of the upper leaves is likely to be due to the position of the leaves on the plant, a conclusion which agrees with Zeevaart's results, and with the analysis of seasonal changes in the rate at which *L. temulentum* plants attain full sensitivity to long-day induction.

(d) *Increase in the Ability of the Growing Point of the Potential Inflorescence to Respond to the Floral Stimulus*

Crucial experiments to establish the contribution of increasing bud age to the increasing sensitivity to photoperiodic induction have not been done, and are precluded in the grasses because one would have to graft induced leaves of equal ontogenetic rank, age, and area to vegetative stocks of various ages. It is possible that plants with terminal inflorescences differ from those with axillary ones in this respect.

In soybeans, Borthwick and Parker (1940) found that neither the distance nor the direction of the induced leaf from the differentiating bud was of much account, which excludes effects due to minor differences in bud age and in distance over which the stimulus must be translocated.

In *L. temulentum*, the fact that the results obtained with mature plants on which had been left only the first-formed leaves agreed closely with those for the younger plants with the same leaves suggests that the shoot apex had not increased in responsiveness with age, unless the leaves had at the same time decreased in photoperiodic sensitivity to an equivalent degree.

It would seem, then, that it is the expansion of leaves of higher ontogenetic rank which contributes most to the increased sensitivity of older plants of *L. temulentum* to induction by long days, although an effect due to the increased age of the shoot apex is not altogether excluded.

V. ACKNOWLEDGMENTS

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