THE BOLTING AND FLOWERING OF *CHONDRILLA JUNCEA* L. AS INFLUENCED BY TEMPERATURE AND PHOTOPERIOD

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Summary

C. juncea plants were grown in a variety of controlled conditions to determine effects of temperature, photoperiod, and gibberellic acid treatment on stem elongation (bolting) and flowering.

The results permit the following conclusions. *C. juncea* is a quantitative long-day plant, with a quantitative requirement for vernalization. Bolting and flower development are two separate processes. Low temperatures before as well as during the photoperiodic induction lower the minimal inductive photoperiod. Vernalization renders the plant independent of day length for bolting when it is grown at low temperatures (15/10°C). Treatment of plants in 16- or 8-hr photoperiods with gibberellic acid induces rapid bolting but flower formation does not follow on plants in short days. The minimal inductive photoperiod for bolting is approximately 12 hr for unvernalized plants grown at 15/10°C while at 27/22°C it is about 12 hr for vernalized and about 14 hr for unvernalized plants. Short days before long-day treatments do not accelerate bolting but do reduce the number of long days required to induce bolting. There is an effect of the size of the plant in relation to the development of flowers.

I. Introduction

Chondrilla juncea L. ("skeleton weed"), a member of the family Compositae, is a plant of Mediterranean origin and in Australian conditions is a relatively long-lived perennial. During its life cycle a leafy, vegetative, rosette stage is followed in late spring or early summer by the bolting of flowering stems which are tall and branched, with numerous small heads of yellow flowers.

Most investigations of this plant have been directly concerned with its control as a weed (Greenham 1940; Greenham and Wilkinson 1942; Tindale 1954; Moore and Robertson 1963) and very few have been related to its physiology, especially to processes associated with its flowering. In the first study of factors influencing flowering (Ballard 1956) the results suggested that skeleton weed was an obligate long-day plant and some evidence for a cold requirement was obtained. Ballard estimated the critical photoperiod to lie between 8 and 14·5 hr. Cuthbertson (1965, 1966) studied the interaction between vernalization and day length and concluded

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that vernalization was not an absolute requirement for floral initiation in skeleton weed, although it accelerated initiation and reduced the dependence on day length. According to his results, the critical photoperiod was about 12 hr. Also, he found evidence of a juvenile phase during which initiation could not occur.

As part of a general study of the physiological behaviour of *C. juncea*, the interaction of day length and temperature in the regulation of flowering processes, and particularly of the bolting process, was investigated. Also an attempt was made to ascertain the critical photoperiods for the initiation of bolting and the opening of flowers within close limits. The general physiological interest of this study lies in the expression of interactions between a variety of environmental factors, in the regulation of bolting and flowering. Most research on the physiology of flowering is done on plants with an absolute requirement for some environmental condition. Most plants, however, are less absolute in their requirements and flowering is often controlled by the complex interaction of several factors.

II. Materials and Methods

All experiments were conducted in the controlled conditions of the CERES phytotron in Canberra (Morse and Evans 1962). Seeds for the experiments on the effect of vernalization were harvested from a field located close to the Canberra Airport, during January 1964. Seeds for the other experiments were harvested from a single plant, grown in the phytotron at 24/19°C, with a 16-hr photoperiod. All plants were grown singly in plastic pots (12·5 or 15 cm in diameter), filled with a mixture of equal volumes of vermiculite and perlite. Seeds were germinated at 21°C in darkness for 2 days, then, in most cases, plants were kept for 2 weeks in 8-hr days, at 21/16°C, the temperature at which skeleton weed grew best and most uniformly. Seedlings were then thinned to one per pot and after being selected for uniformity were sorted into the particular conditions of an experiment.

During the first 4 weeks, plants were irrigated three times weekly with Hoagland nutrient solution and at other times with demineralized water. After the fourth week nutrient solution was used daily.

The plants were kept in controlled-environment cabinets with a photoperiod of 8 hr under natural illumination. When required, the photoperiod was extended with tungsten filament lamps providing about 40 f.c. of illumination to the plants. Further details of the methods are given with each experiment.

III. Results

(a) *Effects of Short-day and Vernalization Pretreatments upon Bolting and Flower Opening in Long Days*

In this experiment, *C. juncea* plants were subjected to short days and vernalization for varying periods prior to being exposed to long days at two temperatures. Times to the initiation of bolting and the opening of the first flower were noted. The long-day treatments were given at two temperatures to observe whether vernalization effects were evident in plants subsequently grown at high temperatures.

After germination, plants were held at 21/16°C in 8-hr light periods for 0, 3, 6, and 12 weeks before vernalization. The youngest group was transferred to vernalization conditions 2 days after germination at 21/16°C. Sowings were staggered so that vernalization treatments commenced simultaneously. The vernalization conditions were 10/5°C with 8 hr of light for 0, 2, 4, or 8 weeks. After vernalization, the plants were subjected to a long-day regime (16 hr of light), either at 21/16°C or 27/22°C, until the first flower opened. The number of long days to the initiation of bolting, and the number of days from bolting to the first open flower were recorded. Plants were considered to have bolted when the stem was between 1·5 and 2·5 cm long. There were six plants in each group, and the experiment was conducted from October 1964 to May 1965.

None of the plants transferred to 27/22°C when younger than 6 weeks survived. The number of long days to the initiation of bolting for the groups grown at 21/16°C and the surviving groups grown at 27/22°C are given in Figures 1(*a*) and 1(*b*). Bolting

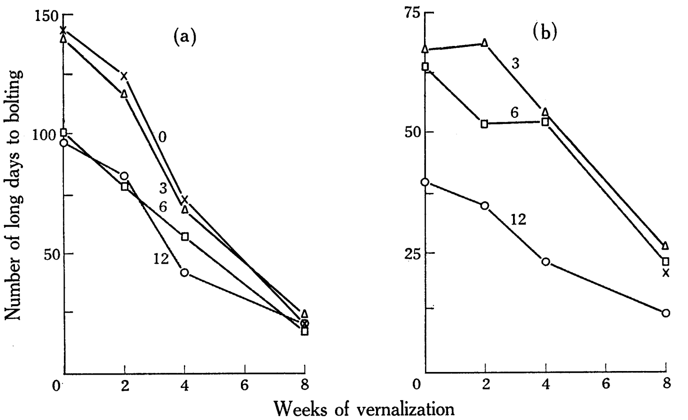

Fig. 1.—Number of days in 16-hr photoperiods at 21/16°C (*a*) or 27/22°C (*b*) required for the bolting of *C. juncea* plants following 0, 2, 4, or 8 weeks of vernalization. Vernalization treatments followed 8-hr photoperiod treatments of 0, 3, 6, or 12 weeks, as shown.

occurred in both temperature regimes on unvernalized plants, but bolting was hastened by vernalization and the number of long days required for bolting decreased with increasing vernalization periods up to 8 weeks. The short-day pretreatments decreased the number of long days necessary for the bolting of unvernalized plants and those vernalized for 2 or 4 weeks. At 21/16°C, bolting occurred after 140 long days on unvernalized plants which entered long-day treatment at germination or when 3 weeks old, but after only 100 days on plants that entered long days when 6 or 12 weeks old. The same relationship held for plants vernalized for 2 weeks, but plants vernalized for 8 weeks, which may be fully vernalized, all bolted after about 20 days. A similar effect of short-day treatments was found for plants grown in long days at 27/22°C. However, if in all these cases the total time from germination is counted, the short-day treatments do not produce a clear hastening of bolting. The reduction in the number of long days required for bolting following short-day treatments may be an age effect rather than a direct effect upon the bolting process.

With respect of flowering, the data in Table 1 show that, for plants either not vernalized or vernalized for 2 weeks only, the interval from bolting to flower opening at 27/22°C decreased progressively with increasing age of plant at commencement of vernalization, over the range studied. This effect, probably due to age or size of plant, rather than to length of the short-day pretreatment, was not apparent in plants vernalized for 4 or 8 weeks. At 27/22°C, the effect of vernalization period on the interval from bolting to flower opening was slight.

Table 1

EFFECTS OF PRIOR VERNALIZATION AND SHORT-DAY TREATMENT ON TIME FROM BOLTING TO FLOWER OPENING FOR *C. JUNCEA* PLANTS HELD IN LONG DAYS AT 27/22 OR 21/16°C

Plants were held at 21/16°C in 8-hr photoperiods for the times shown, prior to vernalization at 10/5°C in 8-hr photoperiods for 0, 2, 4, and 8 weeks. Plants then passed to 16-hr photoperiods at 27/22 or 21/16°C, and the number of days from bolting to the first open flower was recorded. Values given are means ± standard errors

Weeks at 21/16°C Prior to Vernalization	Temperature Regime for Long-day Treatment	No. of Days from Bolting to Flower Opening for Vernalization Periods (weeks) of:			
		0	2	4	8
0	27/22°C	—	—	—	49·4±0·4
3	27/22°C	55·2±0·4	49·4±2·0	47·7±2·6	47·2±0·9
6	27/22°C	43·5±3·0	43·1±2·7	46·8±1·6	45·2±1·6
12	27/22°C	39·5±2·4	38·7±2·8	44·0±1·0	43·3±0·8
0	21/16°C	82·8±3·1	82·7±2·6	87·7±0·7	90·6±4·0
3	21/16°C	74·5±2·9	77·0±1·9	78·8±1·75	67·0±1·6
6	21/16°C	75·0±2·3	72·7±1·5	68·7±2·9	66·3±1·8
12	21/16°C	70·0±5·0	73·2±1·7	69·4±2·9	64·5±2·5

The results were different for the plants grown at 21/16°C (Table 1). Here, the group which received the vernalization treatment at the seedling stage opened their first flower after about the same number of days, irrespective of the length of the vernalization period. The small increase in the number of days noted for the longer vernalization periods may be related to the different time of the year (differences in light intensity and quality) in which they started the long-day regime. The plants vernalized as seedlings required significantly more days for the opening of the first flower than other groups of plants. In the other groups, the time from bolting to the first open flower was unaffected by the vernalization period or by the age at which the long-day regime started. However, the longer the vernalization period in all three groups, the less variable was the period of time required for the first flower to open.

(*b*) *Bolting of Unvernalized Plants under Long- and Short-day Conditions*

Further evidence that *C. juncea* can bolt without exposure to a cold period was obtained with the following experiment. Plants were grown for 10 days at 21/16°C, with a photoperiod of 8 hr. At the end of this establishment period, plants were transferred to 15/10, 21/16, 24/19, and 30/25°C in photoperiods of 16 or 8 hr. There were eight plants in each condition. The number of days to initiation of bolting in 16-hr photoperiods is shown in the following tabulation:

Temperature regime (°C)	15/10	21/16	24/19	30/25
Time to initiation of bolting (days)	79·1	134·9	105·9	80·4

Bolting occurred in about the same number of days at 15/10 or 30/25°C, and was slower at the intermediate temperatures. Growth of the plants is slower at the higher temperatures, being optimal at 21/16°C where bolting took longer to occur. Thus the effect of the high temperatures in hastening bolting is not due to an increased rate of assimilation.

Bolting occurred also in those plants kept in 8-hr photoperiods at 15/10°C. In these conditions, some plants bolted after about 200 days, but they produced a short stalk with axillary rosettes formed on several nodes, as shown in Figure 2. There was no formation of flower buds in these plants, and some of the stalks died a few weeks after bolting.

(*c*) *Effect of Night Temperature on Bolting*

Plants were grown at 21/16°C in short days for 10 days. Plants selected for uniformity at their second true leaf stage were transferred to a day temperature of 30°C, and night temperatures of 25, 22, 16, or 10°C. In all groups the photoperiod was 16 hr, made up of 8 hr of natural light and 8 hr of artificial illumination. There were eight plants per condition, and the number of days to commencement of bolting was recorded. The results are shown in the following tabulation:

Night temperature (°C)	25	22	16	10
Time to initiation of bolting (days)	84	122	145	194

Time to the initiation of bolting was longer the lower the night temperature. The best growth in this experiment was obtained with the medium night temperatures (22 and 16°C), being very poor at both 25 and 10°C.

(*d*) *Effect of Gibberellic Acid on Bolting*

The ability of gibberellic acid (GA_3) to replace the effects of cold and long days was studied in the following experiment.

Plants were grown at 24/19°C, both in short-day (8 hr of light) and long-day (16 hr of light) conditions. Treated plants, 4, 8, or 12 weeks old, received one drop (18 μl) of a solution (1000 p.p.m.) of potassium gibberellate daily. Treatments ceased when the bolting stalk was macroscropically visible.

The younger plants (4 and 8 weeks old) started to bolt in both short days and long days after 6 drops of GA_3 had been applied (about 100 μg GA_3 per plant). The 12-week-old plants required 2–4 drops to initiate bolting (36–72 μg GA_3 per plant) when they were growing in long-day conditions, and 6 drops (about 100 μg GA_3 per plant) in short-day conditions. Control plants in long days bolted at the same time as the last group of treated plants, an average of 92·0 days from planting. Untreated plants in short days did not bolt and on plants treated with GA_3 in short days,

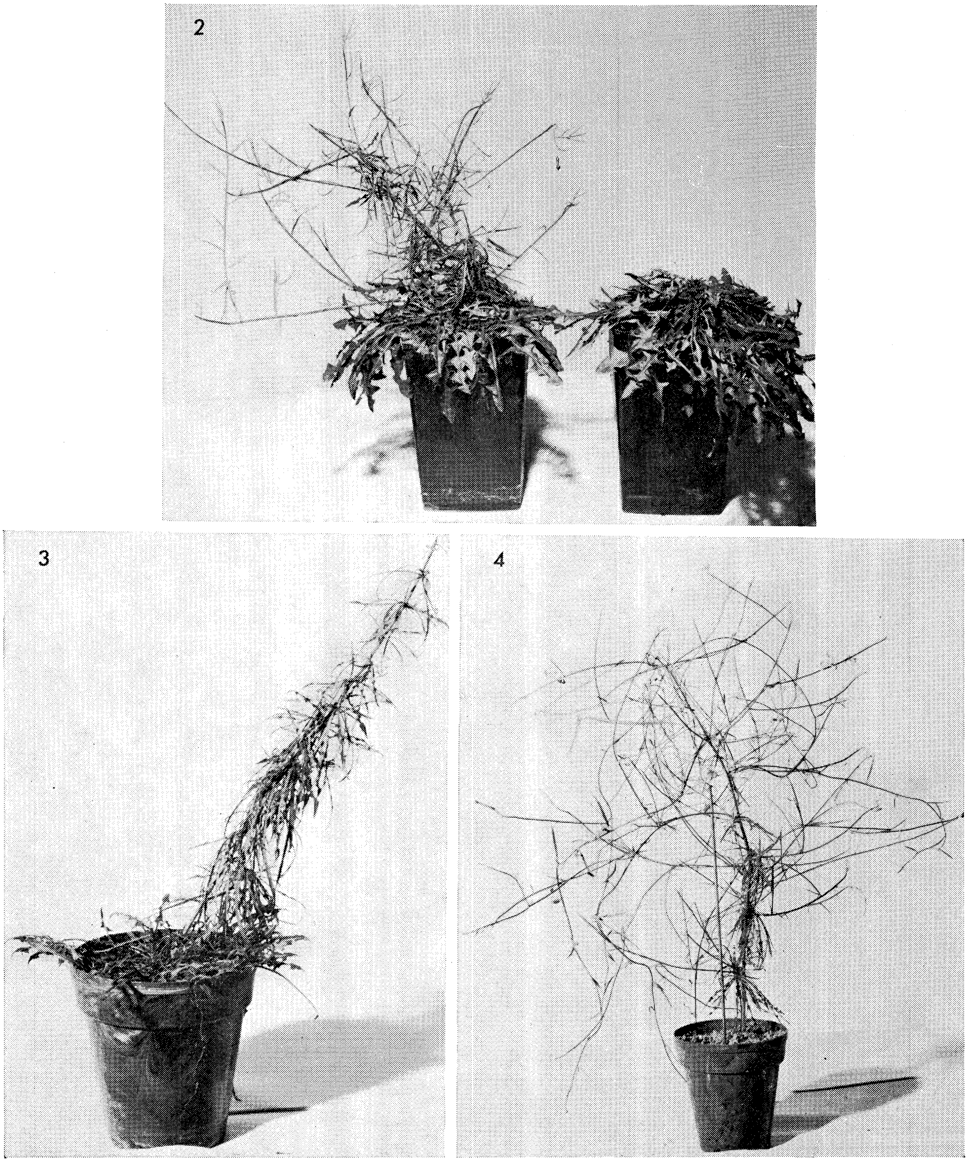

Fig. 2.—Form of bolted (left) and unbolted (right) *C. juncea* plants grown for 210 days at 15/10°C, 8-hr photoperiod. Photographed 15 days after initiation of bolting.

Fig. 3.—Bolting of *C. juncea* plant grown for 8 weeks in 8-hr photoperiod and treated with gibberellic acid.

Fig. 4.—Bolting and flowering of plant of same age as that in Figure 2 but treated with gibberellic acid in 16-hr photoperiod.

although bolting occurred, there was no formation of flower buds, and small rosettes of leaves were formed at some nodes of the stalks (Figs. 3 and 4). When the time from the initiation of bolting to the first open flower is considered, the results in Table 2 show that a longer period was required for the plants induced to bolt by GA_3 treatment when they were 4 and 8 weeks old than for untreated plants and those treated when 12 weeks old.

GA_3 could replace the need of long days and of a cold period for the initiation of bolting, but it could not replace the long-day requirement for flower development, as could be seen by the failure of plants of all age groups to develop flower buds when kept in short days, although bolting in these plants took place almost simultaneously with the plants kept in long days.

TABLE 2

EFFECTS OF GIBBERELLIC ACID ON TIME TO BOLTING AND OPENING OF FIRST FLOWER

C. juncea plants grown at 24/19°C, 16-hr photoperiod, were treated daily with GA_3 (potassium salt) commencing at ages of 4, 8, and 12 weeks. The times (days) from germination to bolting and the opening of the first flower are shown

	Untreated Plants	Plants Treated with GA_3 at Age: 4 Weeks	8 Weeks	12 Weeks
Days in 16-hr photoperiod:				
To bolting	92	35	63	92
To first open flower	150	127	129	148
From bolting to first open flower	58	92	66	56

(*e*) *Minimal Inductive Photoperiod and the Effect of Temperature*

The effect of temperature prior to and during the duration of an inductive photoperiod was investigated as follows. Seedlings, grown for 2 weeks at 21/16°C with 8 hr of natural light per day, were vernalized for 8 weeks at 10/5°C in 8-hr photoperiods. Three weeks before the end of the vernalization period other seedlings were established at 21/16°C, also with 8-hr photoperiods, to serve as unvernalized plants of similar size. Then, after selecting for uniformity, 12 plants of both categories were placed in each of the following photoperiods: 8, 10, 12, 14, 16, and 18 hr, either at 27/22 or 15/10°C. The photoperiod was obtained by adding the necessary number of hours of artificial light to 8 hr of natural light. From the behaviour of the plants in these conditions it was possible to determine the effect of vernalization temperatures prior to photoinduction, as well as the effect of temperature differences during the photoinduction, on the minimal inductive photoperiod for initiation of bolting. After bolting occurred on at least some plants in all groups, three to six were chosen from each group, and for these, the number of days from bolting to the first open flower was also recorded.

The number of days from the beginning of the photoinduction to the initiation of bolting are given in Figures 5(*a*) and 5(*b*). Exposure to a cold period prior to an inductive photoperiod decreased the minimal inductive photoperiod. This reduction was observed at both temperature levels used during photoinduction. At 15/10°C the vernalized plants bolted in all the photoperiods, that is, in this temperature regime previous vernalization rendered the plants independent of a photoperiodic requirement for bolting, although they bolted earlier in the longer photoperiods. In the unvernalized plants at 15/10°C, the minimal inductive photoperiod was 12 hr. At 27/22°C, the vernalized plants bolted with a 12-hr photoperiod, but a photoperiod of 14 hr was required by the unvernalized ones.

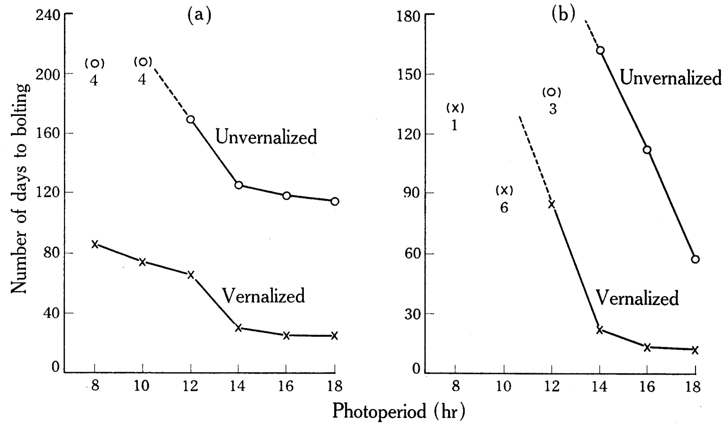

Fig. 5.—Critical photoperiod for the bolting of *C. juncea* as affected by prior vernalization and by the growing temperature during photoperiodic treatment. All plants were established at 21/16°C with 8-hr photoperiods for 2 or 3 weeks. Vernalized plants were treated at 10/5°C, 8-hr photoperiod, for 8 weeks; then vernalized and unvernalized plants received photoperiods of 8, 10, 12, 14, 16, or 18 hr at 15/10°C (*a*) or 27/22°C (*b*). The number of days from the commencement of photoinduction to the initiation of bolting are shown. If only some of the 12 plants in each treatment bolted, the point is shown in parentheses with the number bolted underneath.

The rosettes of vernalized plants which did not bolt, i.e. those at 27/22°C with 8- and 10-hr photoperiods, were larger and greener than those of the unvernalized plants of the same photoperiodic treatments. The bigger rosettes were due to a small elongation of the internodes of the main rosette (no more than 4–5 mm between nodes) and the formation of several axillary rosettes. The bolting stalks of the plants kept at 15/10°C were very leafy and, in some cases, small rosettes of long leaves developed at the lower nodes.

The experiment was continued for 200 days after the first plants bolted but during this time flower buds did not form on plants kept at 15/10°C and in photoperiods less than 16 hr. In photoperiods of 16 or 18 hr the few flowers that opened did so sporadically. The results for flower opening at 27/22°C are given in Figure 6. Vernalized plants held at 27/22°C opened flowers in photoperiods of 10 hr or more. On unvernalized plants, some flowers opened in those photoperiods that had induced bolting. Although bolting occurred in only 50% of the plants that were vernalized and kept in 10-hr photoperiods, these plants opened their first flower only 47 days after bolting.

For unvernalized plants, only 3 out of 12 plants kept in the 12-hr photoperiod bolted, and of these 3 plants one failed to show open flowers before the termination of the experiment. On both vernalized and unvernalized plants, increasing photoperiod hastened bolting more than flowering, thus the time from bolting to flower opening increased with increasing photoperiod. The differences in the number of days from bolting to flower opening between vernalized plants kept at 12- and 14-hr photoperiods, and at 16-hr photoperiods, are statistically significant. In the unvernalized plants, the differences between plants kept at 14-, 16-, or 18-hr photoperiods are also significant. Another differential effect on bolting and flower opening may be noted. In the shorter photoperiods, the number of days from bolting to the first open flower was lower for unvernalized plants than for vernalized plants. However, without data obtained by dissection, it is difficult to evaluate the effect of the length of the photoperiod on the development of the flower buds after induction.

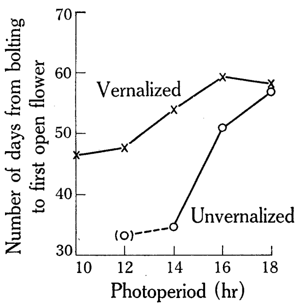

Fig. 6.—Critical photoperiod for the opening of flowers on *C. juncea* plants as affected by prior vernalization when grown at 27/22°C during photoperiodic treatment. Details given in legend to Figure 5. The numbers of days that elapsed between bolting and the opening of the first flowers on those plants that bolted are shown. The point in parentheses represents a treatment in which only one of three bolted plants produced an open flower.

IV. Discussion

It is evident that skeleton weed, unlike most other rosette plants (Chouard 1960), does not have a cold requirement for flowering. It flowered in our experiments, as well as in those reported by Cuthbertson (1966), without vernalization prior to long-day induction. Nevertheless, bolting was accelerated when plants were vernalized, and the promotion was greater the longer the vernalization period. Moreover, there was also a promotion of bolting when the plants were grown at cool temperatures (15/10°C) in conjunction with long days (16 hr). Further evidence of the acceleration of bolting by vernalization was obtained in the experiment described in Section III(*e*). Here bolting was initiated earlier in vernalized than in unvernalized plants subject to a variety of photoperiods and temperature regimes [Figs. 5(*a*) and 5(*b*)].

The present experiments produced no evidence of the existence of a "juvenile phase" for vernalization, as has been postulated by Cuthbertson (1965, 1966). Fully vernalized plants bolted after the same number of long days irrespective of their age at the commencement of vernalization [Fig. 1(*a*)]. Skeleton weed would appear to become receptive to induction by cold treatment at an early age because vernalization was commenced on one group of plants immediately after germination. Age therefore does not limit the initiation of vernalization (Lang 1965) and once this is optimal flowering may occur. Age may, however, affect the bolting response to day length. A period of short days prior to long-day treatment reduced the number of long days required for bolting without obviously changing the time from sowing to bolting. Thus the short-day treatments did not accelerate bolting but they did reduce the amount of long-day treatment needed for bolting to be induced.

The evidence did not suggest the operation in *C. juncea* of a dark-induced process inhibitory to bolting, such as Evans (1960) postulated for flowering in *Lolium temulentum*. The effects of temperature upon plants in long-day conditions may all be interpreted in terms of effects upon a light reaction which promotes bolting. Except for a 15/10°C regime, which was partially vernalizing, regimes with increasing day and night temperatures shortened the time to bolting [see tabulation, Section III(*b*)]. This effect was further analysed (see tabulation, Section III(*c*)] by using a common, high, day temperature of 30°C and increasing night temperatures, and it was found that the higher the night temperatures the shorter the time to bolting. This result excludes an inhibitory dark process with a positive temperature coefficient and suggests that increasing the night temperature hastens processes initiated in the light through a general promotion of the mechanisms leading to bolting.

The interaction occurring between vernalization and subsequent photoinduction in reducing the minimal inductive photoperiod for bolting, has been observed for other plants by Vlitos and Meudt (1955), Evans (1959), and Grossin and Mathon (1961). Fully vernalized plants grown at low temperatures (15/10°C) were completely independent of the day length for bolting, a response which has been described for some strains of subterranean clover (Evans 1959). Further, there was an effect on the minimal inductive photoperiod of the temperature at which plants were grown during induction. For both vernalized and unvernalized plants the photoperiod was reduced when the plants were kept at low temperatures (15/10°C). The same effect has been well studied in *Hyoscyamus niger* (Melchers and Lang 1943).

Gibberellic acid could replace cold and long days for the initiation of bolting (Table 2). However, GA_3 failed to replace long days for the development of flowers, as flower formation did not occur on plants grown in short-day conditions. There are several reports in the literature (Lang 1965) of the failure of GA_3 to induce flower formation after succeeding in replacing long days for stem elongation. It has been observed that stem elongation precedes flower differentiation in some rosette plants, while in others the sequence is reversed (Wellensiek 1960). Although there is no direct evidence in the present experiments, skeleton weed seems to belong to the first group of plants for the following reasons. While GA_3 could replace the cold and long-day requirements for the initiation of bolting, it failed to replace the long days needed for the development of flowers. Furthermore, although GA_3 induced normal flowering in the treated plants irrespective of the age at which they were treated, more days were required by the younger plants to open the first flower. If the bolting and flower differentiation processes were not occurring in that sequence a similar number would be required for all plants. Bolting appears as a process separate from flower differentiation and with not necessarily the same requirements for induction.

As further support for this contention, the data suggest that bolting is less vernalization-dependent and has a lower critical photoperiod than flower differentiation.

The opening of flowers was the criterion used for skeleton weed flowering and this may not be a useful index of flower initiation or the rate of flower development, but some interesting relations were established. High temperatures hastened bolting and decreased the time between bolting and flower opening. This is seen in Table 1 and in the tabulation in Section III(*b*); the former showed that plants grown at 27/22°C produced flowers earlier than those grown at 21/16°C. In the experiment reported in Section III(*e*) few flowers developed in a temperature regime of 15/10°C while flowers developed on plants at 27/22°C in most photoperiods. In this experiment it was also noted that fewer days elapsed between bolting and flowering in unvernalized plants than in vernalized plants. This was probably an expression of a well-known relationship between plant size and age and the rate of flower development (Borthwick and Parker 1938, 1940; Chouard 1950; Evans 1960). The unvernalized plants were older and larger when they commenced bolting than vernalized plants.

While bolting and flower development in *C. juncea* are clearly responsive to day length, temperature, and plant age, and particularly to interactions between these factors, there is not an absolute requirement for any of them. The adaptive value of responses to these climatic factors may be presumed to have influenced the evolution of the plant but none of the factors is able to obstruct bolting or flowering completely. Therefore, by demonstrating the great breadth of the climatic limits for bolting and flowering and hence the geographical limits for these phases of the life cycle, the present results emphasize the large potential of *C. juncea* as a weed. The results do not indicate boundaries for the spread of the weed nor do they suggest points of weakness for attack in weed control.

V. Acknowledgments

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