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EFFECT OF PHOTOPERIOD AND LIGHT INTENSITY ON BOLTING AND FLOWERING IN CELERY

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ABSTRACT

Expriments under controlled environments were carried out to examine the responses of celery cv. New Dwarf White to photoperiod and light intensity, during and following vernalization, on the flowering process. Photoperiods of 8 and 16 h during vernalization at 5°C had no effect on bolting and flowering. Short photoperiods (8 h) after vaenalization markedly decreased the proportion of plants bolting and flowering in young mature plants. Light intensity in the range of 6 to 85 Wm^{-2} (PAR) at plant height during chilling (5°C) had no effect on vernalization. After vernalization a reduction in mean daily irradiance from 1.57 to 4.05 MJ m^{-2} d^{-1} had no effect on bolting and flowering. Exposing competent plants to darkness just prior to chilling resulted in a highly significant delay in bolting and reduced the number of flowering plants ($P<0.001$). Two days of darkness had no significant influence, but 4 and 8 days of darkness at 20 °C caused a very significant inhibition of bolting and flowering ($P<0.001$). The in plants chilled for 6 weeks than those chilled for 9 weeks.effectiveness of dark treatments prior to vernalization was greater in plants chilled for 6 weeks than those chilled for 9 weeks.

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اثر فتو پریود و شدت نور بر تولید ساقه و گل در کرفس

علی اکبر رامین و ج. جی. اترتون

به ترتیب دانشجوی سابق دوره دکترا (اکنون استادیار دانشکده کشاورزی دانشگاه صنعتی اصفهان) ومدرس ارشد بخش کشاورزی و باغبانی دانشگاه ناتینگهام انگلستان.

چکیـــده

آزمایش های زیادی در محیطهای کنترل شده بمنظور بررسی اثر فتوپریود و شدت نور در حین سرما و پس از مرحله سرما دهی گیاه، بر تولید گل در کرفس رقم نیـودوارف وایت صورت پذیرفت. طول روز ۱۶ و ۸ ساعت در خلال سرما دهی در دمـای ۵ درجـه سانتیگراد تـأثیر معنـی داری بر تولید ساقه و ظهور گل ها نداشت ولـی بعـد از مرحلـه سـرما دهـی، طـول روز کوتـاه (۸ ساعت) بطور چشمگیری موجب کاهش گیاهان گلدار گردید ($P<0.05$). شدت نوردر زمـان سـرما دهی و همینطور بعد از سپری شدن سرما، تأثیر معنی داری بر تولید سـاقه و تشـکیل گـل نداشـت. قرار دادن گیاهان بالغ در تاریکی برای مدت ۲ ، ۴ ، ۸ روز در دمای ۲۰ درجه سـانتیگراد پیـش از سرما دهی، بطور معنی‌داری موجب تأخیر در زمان ظهور گل هـا و کـاهش گیاهـان گلـدار گردیـد ($P<0.001$). تاریکی پیش از سرما دهی برای گیاهانی که مدت ۶ هفته سرما دریافت کرده بودند (۵ درجه سانتیگراد) به مراتب بیشتر از گیاهانی که ۹ هفته سرما دریافت کرده بودند اثر داشت.

INTRODUCTION

Numerous studies have been reported on the effects of light conditions on flower initiation and development in cold-requiring plants. Short

photoperiods during vernalization generally enhance flowering, whereas long photoperiods delay or reduce the number of plants bolting and flowering (11,23). On the other hand, long photoperiods after vernalization promote bolting and flowering whereas short photoperiods suppress flowering (7, 13). Spector (21), Vince-Prue (23) and Hanisova and Krekule (9) reported that photoperiod does not affect the vernalization response of celery. They classified celery as a day-neutral plant with a cold requirement for flower initiation. But, Pressman and Negbi (14) later classified celery as a short-long day plant (SLDP) with vernalization requirement. However, Thompson (22) and Roelofse *et al.* (18) reported that at a maintained temperature of 10° C, bolting and flowering occurred regardless of the photoperiod. They did not determine possible photoperiodic sensitivity of plants separately during and following vernalization. Additional work was needed then to define any photoperiodic requirement under chilling condition that were near to the optimum temperature for vernalization in the celery.

Brewster (5) demonstrated with onion that low light intensity during vernalization reduced subsequent flower initiation when plants had previously been grown at high temperatures (25 °C) and low light intensity. Plants that were grown under cooler , brighter condition showed no change in their flower initiation response to chilling attributable to light intensity. Earlier investigation with other plants by Pierik (12,13)and Wiebe (24)showed that light intensity during vernalization had no influence on flowering. In some plants, flower initiation following vernalization depends on the light intensity after vernalization (12,15). There is no published work describing the effects of light intensity during and following vernalization on bolting and flowering in the celery.

In an earlier investigation, the number of leaves initiated by the plant was used as a marker for phase transition (17). Leaf number was probably related to the supply of nutrients by the leaves to the shoot apex (3,4). There is evidence, however, that reduction in storage of nutrients in adult plants

before thermoinduction, either by high temperatures in celery (19) and onions (5) or by chemical compounds in cauliflower (8), can reduce or delay the flower initiation response. Reduction in the storage of nutrients below a certain level in previously competent plants by starvation or by growing mature plants at a high temperature may therefore, lead to a reversion of the adult to the juvenile form which would abolish sensitivity to flower induction (1).

The purpose of this investigation was to study the effects of light (photoperiods and irradiance) on bolting and flowering in celery cv. New Dwarf White. For modelling purposes, it is essential to know if there is any effect of light together with low temperature on flower induction and initiation. An attempt was made also to investigate the effects of a short period of high temperature and darkness on response to vernalization in this cultivar.

MATERIALS AND METHODS

In the first experiment , seeds of celery cv. New Dwarf White were sown on 28 October, 1987, at 20 °C in a glasshouse. Germination and general culture conditions were as described earlier (16). Natural glasshouse irradiance was supplemented by SON/T lamps providing an additional 40 W m^{-2} (PAR) incident at plant height for 12 h each day. On attainment of maturity, chilling teatments at 5 °C combined with two different light treatments were given to the plants under growth room conditions. Photoperiod treatments during chilling were:8 h photoperiod comprising 8 h high-intensity light (40 W m^{-2} , PAR) from HLRG lamps, 16 h photoperiod comprising 8 h high-intensity light followed by 8-h low-intensity light (1.5 W m^{-2}) from tungsten filament lamps.

At the completion of growth room treatments (9 weeks) , all plants were assigned at random into two groups. Half of the plants were shifted to short photoperiod (8 h) and an equal number was transferred to long photoperiods

(16 h) under growth room conditions of 16 °C for two weeks. The 8-h regime in the growth room comprised high intensity light from HLRG lamp of 50 W m^{-2} at plant height. Sixteen-hour photopreiods comprised 8-h lighting from HLRG lamp followed by a day extension to 16-h by incandescent lamps alone (1.5 Wm-2). Following the stabilization of any vernalization response (17), the plants were moved on 23 March 1988 to a warm glasshouse (20 °C) under either 8 h natural daylight alone or 8 h natural daylight followed by 8 h of light from incandescent lamps (1.5 W m^{-2}) until the end of the experiment. The experiment ended on 22 June 1988, having recorded the number of days taken to visible bolting, number of leaves initiated below the flower, and stem length. Microscopic examination was made to determine whether flowers had initiated and to count the primordia in vegetative plants. The experiment was arranged in a randomized block design with three replications and 4 plants in each replicate. In the second experiment , seeds of cv. New Dwarf White were sown on 13 June 1988 under natural daylight (16.5 h) at 20 °C in the glasshouse following the methods described earlier. Chilling treatments together with different light levels from 350 Watt (SO N/H) at 5 °C were given to plants when they had initiated 22 leaves, including primordia. Different light levels were achieved in a growth room by putting the plants at different distances from the lamps (Table 1). Treatments 4 and 5 were separated from the direct lighting by white plastic sheets to further reduce the irradiance. Plants in treatment 6 then were covered with black and white plastic sheets to provide for chilling in darkness. Plants were chilled under different irradiance regimes for a period of 9 weeks and then stabilized for two weeks at 16 °C in growth room as described previously. After stabilization, plants were transferred to a warm glasshouse (20 °C) on 4 November, 1988. Natural light of 9.3 h in glasshouse was supplemented using SON/T lamps of 40 W m^{-2} (PAR) at plant height for 16 h each day until the end of the experiment. A randomized block design was used with 3 replicates for each treatment and each replicate

consisted of 4 plants. Days to bolting from the end of chilling were measured at 2-day intervals and then all plants were harvested on 15 December, 1988.

Table 1. Light and temperature conditions during chilling for celery cv. New Dwarf White in growth rooms (Experiment 2).

Treatment No.	Distance from Lamps (cm)	Irradiance (Wm^{-2}, PAR)	R/FR ratio	Temperatures (° C)
1	60	85	2.6	6.8 ± 1.8
2	100	44	2.4	6.2 ± 1.2
3	140	26	2.4	4.8 ± 1.5
4	Ind.L† (150)	6	2.5	4.4 ± 1.4
5	Ind.L (200)	0.2	2.5	4.4 ± 1.4
6	Darkness	--	--	4.8 ± 1.6

† Ind. L = Indirect Lighting.

In the third experiment, sowing and chilling treatments were the same as those described for experiment 2. After 9 weeks of chilling, the plants were moved to the glasshouse at a temperature of 20 °C with 6 different light intensities. The natural light in glasshouse (10.0 h) was supplemented using SON/T lamps providing an additional 40 Wm^{-2} (PAR) at plant height for 16h each day. Reduction in total irradiation was achieved by shading with layers of Rokolene netting (Rokolene, KDA, Rokocontainers, UK). Lower levels of irradiance were obtained by increasing the number of layers of the canopy. Irradiance in the glasshouse was reduced from 25 to 77 percent and the control treatment remained unshaded (Table 2). The total mean daily irradiance within each treatment was determined at the top of the canopy using tube solarimeters connected to integrator recorders (Delta-T-Devices, Cambridge , UK). In this experiment a complete randomized design was used with 12 plants for each treatment. In the fourth experiment, seeds were sown on 2 March 1988. Germination and plant maintenance were as described earlier. At the termination of the juvenility, plants were

Table 2. Summary of irradiance treatments after vernalization in glasshouse (Experiment3).

Treatments	Relative light intensity (% total)	Total irradiance integrated above canopy (MJ m^{-2})	Mean daily irradiance (MJ m^{-2} d^{-1})	Mean air temperature (° C)±SEM§
1	100†	113.5	4.05	18.6 ± 3
2	82	93.5	3.34	18.8 ± 1.8
3	75	87.69	3.13	18.2 ± 2.5
4	57	65.57	2.42	18.0 ± 2.0
5	50	56.28	2.01	18.1 ± 1.9
6	25	43.96	1.57	17.8 ± 2.1

† Cont = Control treatment.
§ Standard error of mean.

transferred to darkness at a temperature of 20 °C in the growth room for periods of 2, 4 and 8 days by covering with a black plastic sheet. Control plants remained uncovered at 20 °C under 12 h light of 40 W m^{-2} warm white fluorescent tubes at plant height. Chilling was applied to plants at the same time for all treatments at 5 °C in a growth room. Throughout the low temperature treatments, plants received a 12 h photoperiod from 400-Watt Philips high pressure mercury lamps (HLRG) each day to give an irradiance of 40 W m^{-2} at plant level. Plants were then chilled for periods of 6 or 9 weeks and then returned to warm glasshouse (20 °C) to complete their development. The experiment was arranged in a randomized block design with three replications and 4 plants in each replicate. All plants were harvested on 5 September 1988 when they were dissected, and total number of leaves and the stage of flowering were recorded.

RESULTS

Photoperiods

The effect of photoperiod during vernalization on bolting and flowering of young mature plants of celery cv. New Dwarf White are shown in Table 3. Photoperiodic regimes of 8 and 16 h light given to plants during chilling appeared to have no great effect on time to bolting and flower appearance in this cultivar. Acceleration of bolting and flowering was measured as decreases in both days from the end of chilling to visible bolting and leaf number below the inflorescence. There were no marked differences between days to bolting and number of leaves subtending the flower in reproductive plants from 8 h and 16 h photoperiod during vernalization treatments. Percentages of both bolting and normal flowering after vernalization at 5 °C also were not affected markedly by photoperiod during vernalization treatments. Stem elongation was not influenced by photoperiod during vernalization. There were, however, marked increases in the number of plants which flowered without bolting (abnormal flowering) when plants were vernalized at 5 °C under short photoperiod condition.

The number of days from the end of chilling to macroscopic appearence of internode (bolting) was highly influenced by the photoperiod after vernalization. A promotive effect of vernalization was apparent under long photoperiod as a decrease in both the number of leaves subtending the inflorescence and also in the time to bolting (Table 3). The flowering stem was also longer in plants under long photoperiod. Stem-length was approximately 6 times greater in plants growing under long photoperiods. Moreover, short photoperiod after vernalization caused a remarkable decrease in the proportion of both bolting and flowering plants.

Table 3. Effects of photoperiod during and following vernalization on bolting and flowering in young mature plants of celery cv. New Dwarf White.

Photoperiod (h)	Days to bolting	Percentage of plants bolting	Percentage of flowering plants		Leaf number ± SEM†		Stem length (cm) ± SEM
			Normal	Abnormal	Flowering plants	Vegetative plants	
During chilling							
8	41	50	38	22	24 ± 1.8	36 ± 2.6	22 ± 3.3
16	48	44	38	5	25 ± 2.0	37 ± 1.9	18 ± 3.5
LSD	NS§				NS	NS	NS
χ^2-test (P<0.05)		NS	NS	SIG¶			
After chilling							
8	67	7	7	18	37 ± 2.5	39 ± 3.0	5.3 ± 0.9
16	48	70	66	-	26 ± 1.8	33 ± 2.5	31.8 ± 2.5
LSD (P<0.05)	8.5						
χ^2 - test		SIG	SIG	SIG			

† Standard error of mean.
§ Not significnat at P>0.05.
¶ Significnat at P<0.05.

Irradiance

Plants chilled in darkness showed no vernalization response even if chilled for 9 weeks at 5 °C. No generative differentiation was observed in shoot apex at the time of harvest for these plants (Table 4). A promotive effect of vernalization appeared when plants were chilled under a very low irradiance of 0.2 W m^{-2} for 12 h at plant height (Treatment 5).

Table 4. Effects of light intensity during chilling at 5 °C on bolting and flowering in celerycv. New Dwarf White.

Treatments (irradiance W m^{-2} PAR)	Days to bolting	Percentage of plants bolting	Percentage of plants flowering	Leaf number in		Stem length (cm)
				FLO†	VEG§	
1 (85)	30	100	100	25	--	14.5
2 (45)	29	100	100	24	--	17.4
3 (26)	26	100	100	23	--	18.9
4 (6)	27	100	100	23	--	18.5
5 (0.2)	31	41	33	25	30	5.9
6 (Dark)	--			--	35	1.5
LSD P<0.05	3.8			1.5	2.2	5.1
χ^2-test			SIG¶			

† Flowering plants
§ Vegetative plants
¶ Significant at p<0.001

Vernalization at this very low light level was enough to produce 41 percent bolting and 33 percent flowering. Normal bolting and flowering occurred in plants that were chilled under low light condition of only 6 W m^{-2} or more. Vernalization of plants at the low light intensity of 6 W m^{-2} or more resulted in 100 percent bolting and flowering. Vernalization under higher light intensities of 45 and 85 W m^{-2} at plant height slightly delayed flowering in terms of increasing both the time to visible flowering and the leaf number below the inflorescence compared to treatments 3 and 4

(P<0.05). However, the small delay was probably related to higher temperatures around the shoot tip during vernalization in growth room which was cooler under the lower light levels (Table 1).

Effects of irradiance following vernalization on inflorescence initiation in terms of days to macroscopic bolting and leaf number subtending the flower were minimal (Table 5). All plants bolted and flowered under different levels of light from total irradiance of 44.0 to 113.5 M J m^{-2} (mean daily irradiance of 1.57 to 4.05 M J m^{-2} d^{-1}). There was no significant difference between treatments for days to visible bolting under different light levels, even for those that remained in low irradiance.

Table 5. Effects of irradiance after vernalization on bolting and flowering in celery cv. New Dwarf White.

Treatments (M J m^{-2})	Percent of plants bolting	Percent of plants flowering	Days to bolting	Leaf number at flowering	Stem length (cm)
1 (113.4)	100	100	21	24	15.4
2 (93.5)	100	100	23	24	14.4
3 (87.69)	100	100	24	25	14.3
4 (65.57)	100	100	24	25	14.2
5 (56.28)	100	100	24	25	14.2
6 (43.96)	100	100	26	26	13.4
LSD at P<0.05			NS†	1.3	NS

† Not significant (P > 0.05).

Bolting was delayed by 4 days in plants transferred to 75 percent shading with average mean daily irradiance of 1.57 M J m^{-2} d^{-1} compared with unshaded treatment. Generally low levels of light after vernalization at 5 °C caused a small delay in bolting. There was no significant difference between treatments for the number of leaves initiated below the inflorescence except for those plants transferred in to 75 percent shading (1.57 M J m^{-2} d^{-1}). Leaves initiated below the flower however increased with decreasing

irradiance to 1.57 M J m^{-2} d^{-1}. At this point 26 leaves were formed below the flower compared with 24 leaves in control plants. The changes in leaf number below the canopy after chilling was not more than 1 or 2 leaves, suggesting that flower initiation was only slightly influenced by the light levels following vernalization. There was no significant difference in stem length for shaded and unshaded treatments (Table 5).

Dark Treatments prior to Chilling

Keeping mature plants of celery cv. New Dwarf White in darkness at 20 °C before chilling resulted in a significant delay in bolting ($P<0.05$). This was seen both as an increase in the time to macroscopic internode visibility and in the number of leaves initiated below the inflorescence (Table 6).

Table 6. Effects of short dark treatments just before chilling on bolting and flowering of celery cv. New Dwarf White.

Teratments	Duration of chilling (weeks)	Days to bolting	Percent of plants bolting	Percent of plants flowering	Leaf number in	
					FLO†	VEG§
Control	6	54	55	55	28	32
	9	28	100	100	22	--
2 days darkness	6	59	55	11	28	34
	9	32	100	100	23	--
4 days darkness	6	--	0	0	--	42
	9	34	88	88	24	28
8 days darkness	6	--	0	0	--	42
	9	41	66	44	28	32
LSD $P<0.05$		7			2.0	3.5
χ^2 test ($P< 0.05$)			SIG¶	SIG		

† Flowering plants.
§ Vegetative plants.
¶ Significant at $P< 0.001$.

Generally, the effectiveness of dark treatments prior to chilling was greater in plants when chilled at 5 °C for 6 weeks than those getting 9 weeks of cold

treatment. Two days of dark treatment prior to chilling had no great influence on the proportion of plants bolting and flowering, but 4 and 8 days dark caused a very significant delay in the onset of bolting and flowering compared with control plants ($P<0.001$). Despite the 6 weeks of chilling at 5 °C in growth room, the 4 and 8 days in darkness prior to chilling completely inhibited bolting and flowering and all of the plants remained vegetative until final harvest (Table 6). The 4-day dark treatment was as effective as that of 8-day treatment, except for small differences in the number of leaves below the flower.

DISCUSSION

Photoperiod during vernalization of young but non-juvenile plants of celery was found to have no great effect on bolting and flowering. The photoperiodic sensitivity of celery during vernalization at supra-optimal temperatures was examined earlier by Pressman and Negbi (14). They found celery to have a quantitative reponse to short days during vernalization. Conversely , in some other plants such as onions, long photoperiods during vernalization are more favorable for flower induction than short photoperiods (6). There are several reports indicating that prolonged vernalization of plants at or near optimal temperatures suppresses the requirement for the short photoperiod and plants will flower irrespective of photoperiod. The same may be true for young plants (2 ,7 ,12). After chilling, long photoperiods promoted bolting and flowering with a marked increase in flowering stem length, whereas short photoperiods after chilling inhibited vernalization. These results agree with the report of Pressman and Negbi (14), but are in conflict with claims of Roelofse *et al.* (18). This discord may be due to the environmental conditions in which plants were grown. The young mature plants of celery in the present study and in the

experiment of Pressman and Negbi (14) were grown at non-inductive temperatures after vernalization. In the investigation of Roelofse *et al.* (18), plants remained at temperatures which would allow vernalization throughout. This probably caused all plants to initiate flowers regardless of photoperiod. This explanation is further supported by reports of very long chilling treatments suppressing the requirement for long photoperiod (3, 23).

Irradiance during chilling appeared not to be important for bolting and initiation of flowers in celery. Plants bolted and flowered after chilling at a very low light intensity of only 0.2 W m^{-2}. Insensitivity of flower induction to irradiance during vernalization has been demonstrated also in *Lunaria* (13), cauliflower (24) and onion (5). The possible importance of irradiance during vernalization may depend on the condition of the plants at the time of the treatments (5 ,12). Both size and environmental conditions before vernalization could be directly related to stored nutrients in the plants which are essential for the onset of flower induction and initiation. For example, plants with high levels of stored nutrients in the shoot may be insensitive to irradiance during chilling but those with low reserves may need nutrients to be available to the stem apex (5).

Once vernalization had taken place, bolting and flowering were not influenced by irradiance. All plants initiated flowers normally even those grown at the minimum mean daily irradiance of 1.57 M J m^{-2} d^{-1} This is in agreement with previous works with endive (10) and with *Lunaria* (13) but disagrees with results in Chinese cabbage (15) in which the rate of bolting was decreased under higher light intensity more than under lower light intensity. This sort of irradiance effect could have been due to an increase in temperature around the canopy.

Dark treatment prior to chilling significantly reduced vernalization response of previously competent celery plants. Growing plants at high temperatures and low light levels before vernalization has been reported to delay or reduce bolting and flowering in other plants (5 ,8 ,20). Previous

attempt to prevent bolting in autumn celery growth by use of night break treatments was unsuccessful (18). Pre-devernalization by high temperature of 30 °C for 20 days prior to planting is also reported to delay bolting and flowering (19). Under commercial celery production, however, this extra heating for 20 days continuously in the glasshouse during winter, especially in the temperate regions is practically and economically difficult. Using blackout covers in the glasshouse for short periods of 4 to 8 days could have commercial advantage by reducing growing costs compared to high temperature technique as Sachs and Rylski (19). However, it appears from the present study that the short period of dark treatment of seedlings before transferring them to vernalization conditions can reduce bolting, especially in the spring.

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