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Manipulation of bolting and flowering in celery (*Apium graveolens* L. var. dulce). III. Effects of photoperiod and irradiance

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SUMMARY

Photoperiods of 8 and 16 h during chilling at 5°C had no effect on bolting and macroscopic flower appearance in celery cv. New Dwarf White. Eight hour photoperiods during chilling however markedly increased the number of plants forming sessile flowers. Short photoperiods (8 h) after chilling decreased the proportion of young, but competent plants that bolted and flowered. Total darkness during chilling completely prevented any subsequent vernalization response either as bolting or as flowering. Reducing irradiance receipt by the plants during chilling from 85 to W m^{-2} (PAR) had no effect on their vernalization response. After chilling, a reduction in mean daily total irradiance in the glasshouse from 4.05 to 1.57 MJ m^{-2} d^{-1} had no effect on bolting and flowering. Confinement of competent plants to darkness for 4–8 d at 20°C just prior to chilling resulted in a highly significant delay ($P<0.001$) to bolting and reduced the number of plants flowering. Two days of darkness had no significant effect. The inhibitory effects of dark treatments prior to chilling was greater in plants chilled subsequently for six weeks than for nine weeks.

LIGHT conditions prevailing before, during and after vernalization may influence subsequent shoot extension and flowering. Short photoperiods during chilling generally advance, whereas long photoperiods then may delay or prevent flower initiation and bolting (Lang, 1965; Vince-Prue, 1975). After chilling, however, long photoperiods usually promote, and short photoperiods suppress, flowering (Pierik, 1967b; Elers and Wiebe, 1984). For celery, Spector (1965) and Hanisova and Krekule (1975) claimed that photoperiod did not affect the vernalization response and thus classified it as day neutral with a cold requirement for flower initiation. Consistent with these reports, Roelofse *et al.* (1989) found that at a maintained temperature of 10°C, bolting and flowering occurred regardless of photoperiod. They did not attempt to distinguish possible shifts in photoperiodic sensitivity depending on whether the plant was already vernalized. When this was done previously (Pressman and Negbi, 1980) celery was seen to behave as a quantitative short-long day plant with a vernalization requirement. Part of the present study examines this question again, using temperatures for flower induction that were near optimum (Ramin and Atherton, 1991a).

Irradiance has not been examined previously as a potentially interactive factor with low temperature on bolting and flowering in celery. With other species, for example onion, low irradiance during chilling reduced flower initiation only when plants had previously been grown at high temperatures (25°C) and low irradiance (Brewster, 1985). Plants from cooler, brighter conditions showed no change in their vernalization response to chilling attributable to light intensity. Earlier investigations with *Lunaria annua* by Pierik (1967a and b) and with cauliflower by Wiebe (1974) found irradiance during chilling to have no influence on flowering. Reduction in carbohydrate reserves below

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a critical level in previously competent plants may lead to a reversion of the adult to the juvenile form which would abolish sensitivity to flower induction (Allsopp, 1954). Low irradiance prior to chilling would therefore be expected to reduce the competence of young celery plants to perceive chilling as a vernalization stimulus.

The purpose of this investigation was to study the effects of photoperiod and irradiance on chilling induced bolting and flowering in celery cv. New Dwarf White. This is desirable not only for assisting in commercial crop production, but also for suggesting environmental controls for manipulating juvenility and vernalization generally.

MATERIALS AND METHODS

Experiment 1

Seeds of celery cv. New Dwarf White were sown on 28 October 1987 in a glasshouse maintained above a minimum temperature of 18°C. The mean temperature during germination was 20°C. Germination and general husbandry were as described earlier (Ramin and Atherton, 1991b). 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, when a total of 17 leaves had been initiated, (Ramin and Atherton, 1991), chilling treatments at 5 ± 1 °C combined with two photoperiod treatments were applied under growth room conditions. Transfer from the glasshouse to the growth rooms was on 5 January 1988. Nine plants were arranged at random for each treatment. Photoperiod treatments during chilling were: 8 h high intensity light (40 W m^{-2}, PAR) from HLRG lamps then 16 h darkness; 8 h high intensity light followed by 8 h low intensity light (1.5 W m^{-2}) from tungsten filament lamps and then darkness. On completion of nine-week chilling treatments, nine plants were transferred to short (8 h) photoperiods and nine to long photoperiods (16h) under growth room conditions at 16 ± 2°C for two weeks to stabilize any vernalization effect (Ramin and Atherton, 1991b). The plants were next moved on 23 March 1988 to a glasshouse maintained above a minimum temperature of 18°C under two photoperiods of 8 h natural daylight alone or 8 h natural day light followed by 8 h from incandescent lamps (1.5 W m^{-2}) until end of the experiment. Eight hours natural daylight was maintained by drawing blackout cloth over the plants from 1700 hours to 0900 hours each day. The incandescent lamps had a negligible heating effect on the leaves (<0.5°C). The experiment ended on 22 June 1988 and the number of days taken to visible bolting, number of leaves initiated below the flower and stem length were recorded. Microscopic examinations were made to determine whether flowers had initiated and to count the primordia in vegetative plants.

Experiment 2

Seeds were sown on 13 June 1988 under natural daylight (16.5 h) conditions and at 20°C in the glasshouse following methods described earlier. Chilling treatments began on 19 August together with different light levels from 350 W SON/H lamps at 5°C given to plants when they had initiated 22 leaves, including primordia. Lighting in the growth rooms was provided for 8 h each day. Different light levels were obtained in a growth room by positioning the plants at different distances from the lamps or by shading with plastic sheets (Table I). Treatments 4 and 5 were separated from the direct lighting by white plastic sheets to further reduce the irradiance. In treatment 6 plants were covered with black plastic sheets to provide darkness. Plants were chilled under the different irradiance regimes for nine weeks and then stabilized for two weeks at 16°C in a growth room as described previously. After stabilization, plants were transferred to a glasshouse maintained above 18°C, on 4 November 1988, to natural light of 9.3 h in a glasshouse supplemented using SON/T lamps providing 40 W m^{-2} (PAR) at plant height for 16 h each day until the end of the experiment. Temperatures in the glasshouse ranged from 18°C at night to a maximum of 24°C during the day. A randomized block design was used with three blocks and four replicate plants in each plot. Days to bolting from the end of chilling were counted at 2 d intervals and then all plants were harvested on 15 December 1988.

Experiment 3

Sowing dates, chilling treatments and transfer times were as described for Experiment 2.

TABLE I
Light and temperature conditions during chilling in growth rooms

Treatment	Distance from lamps (cm)	Irradiance (Wm^{-2}, PAR)	R/FR ratio	Temperatures (°C ± SE)
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	I.L	6	2.5	4.4 ± 1.4
5	I.L	0.2	2.5	4.4 ± 1.4
6	Darkness	—	—	4.8 ± 1.6

I.L. = Indirect lighting.

After nine weeks' chilling, the plants were moved to the glasshouse at a minimum 18°C under a range of irradiance treatments. Natural daylight in the glasshouse (10.0 h) was supplemented using SON/T lamps providing an additional 40 W m^{-2} (PAR) at plant height for 16 h each day. Reduction in total irradiance was achieved by shading with layers of green plastic netting (Rokolene) known to have no effect on spectral energy distribution (Ramin, unpubl.). Lower levels of irradiance were obtained by increasing the number of netting layers above the canopy. Irradiance was thereby reduced to between 25 and 77% of ambient and a control treatment remained unshaded (Table II). The total mean daily irradiance within each treatment was determined at the top of the canopy using tube solarimeters connected to integrators (Delta-T-Devices, Cambridge, UK).

Experiment 4

Seeds were sown on 2 March 1988; germination and plant maintenance were as described earlier. At the termination of juvenility (17 leaves initiated, Ramin and Atherton, 1991), plants were transferred to darkness at a temperature of 20°C in a growth room for periods of 2, 4 and 8 d by covering with a black plastic sheet. Control plants remained uncovered at 20°C and were illuminated for 12 h daily from warm white fluorescent tubes giving 40 m^{-2} PAR at plant height. Prior to chilling a sample of five plants from each treatment was randomly selected and dissected to determine leaf number, leaf area and shoot dry weight. 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 W HLRG lamps each day to give an irradiance of 40 W m^{-2} at plant level. Plants were then chilled for six or nine weeks before transfer to a warm glasshouse (18°C) to complete their development. The experiment was arranged in a randomized block design with three replications and three plants in each replicate. All plants were harvested on 5 September 1988 when they were dissected and the total number of leaves, and the stage of flowering were recorded.

RESULTS

Photoperiod

The effects of photoperiod during vernalization on bolting (macroscopic visibility of internodes) and flowering of young yet competent plants of celery cv. New Dwarf White

TABLE II
Total incoming solar radiation in the glasshouse after vernalization. Each value is a mean of six, ± standard error of mean

Treatment	Relative light intensity (% total)	Total irradiance integrated above canopy (MJ m^{-2})	Mean daily irradiance (MJ m^{-2})	Mean air temperature (°C)
1	100 (control)	113.5	4.05	18.6 ± 3.0
2	82	93.5	3.34	18.5 ± 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

TABLE III

Effects of photoperiod during and after chilling on bolting and flowering in young, competent plants. Each value is a mean of nine, ± standard error of the mean

	Photoperiod (h)	Days to bolting from the end of chilling	Percentage of plants bolting	Percentage of Percentage of		Leaf number (including leaf primordia)		Stem length (cm)
				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
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

are shown in Table III. No effect was apparent on time to bolting or macroscopic flower appearance in this cultivar or on the number of leaves subtending the flower in reproductive plants. Percentages of plants bolting and showing normal flowering were also unaffected by photoperiod during chilling. There were however marked increases in the number of plants which formed sessile flowers without bolting (abnormal flowering) after vernalization at 5°C under short photoperiods. Stem elongation was not influenced by photoperiod during vernalization.

Time from the end of chilling to bolting was reduced by long (16 h) photoperiods after vernalization and a decrease was evident in the number of leaves subtending the inflorescence (Table III). The flowering shoot also extended more in plants under LD than in SD, with stem length at harvest approximately six times greater in plants growing under long days. Moreover, short days after vernalization markedly decrease the proportion of both bolting and flowering plants. It would appear therefore that long photoperiods following vernalization are necessary for normal flower appearance in young celery plants.

Irradiance

Darkness during chilling completely prevented any vernalization response, even after nine weeks at 5°C. No floral differentiation was observed at the shoot apex at the time of harvest for these plants (Table IV). A promotive effect of vernalization appeared when plants were chilled under a very low irradiance of 0.2 W m^{-2} for 12 h (Treatment 5). Data in Table IV shows that vernalization at this light level was enough to induce 41% bolting and 33% flowering. Normal bolting and flowering occurred in plants chilled under conditions of 6 W m^{-2} or more. Vernalization under higher light intensities of 45 and 85 W m^{-2} at plant height slightly delayed flowering in terms of days to visible flowering and the leaf number below the inflorescence compared with treatments 3 and 4 ($P<0.05$). This small delay was probably related to higher temperatures around the shoot tip during vernalization in the growth room under the higher light levels (Table I).

TABLE IV

Effects of irradiance during chilling at 5°C on bolting and flowering

Treatments (irradiance Wm^2. PAR)	Days to bolting (from end of chilling)	Percentage bolting	Percentage flowering	Leaf no. in plants		Stem length (cm)
				flowering	vegetative	
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		***				

*** = significant at $P<0.001$

TABLE V
Effects of total incoming solar radiation in the glasshouse after vernalization on bolting and flowering

Treatments	Irradiance (MJ $m^{-2}d^{-1}$)	Percent bolting & flowering	Days to bolting	Leaf number to flower
1	4.05	100	21	24
2	3.34	100	23	24
3	3.13	100	24	25
4	2.42	100	24	25
5	2.01	100	24	25
6	1.57	100	26	26
LSD at $P<0.05$			n.s.	1.3

n.s. = Not significant at $P<0.05$

Effects of irradiance following vernalization on leaf number below the inflorescence and days to macroscopic bolting are shown in Table V. All plants bolted and flowered under total irradiances from 43.9 to 113.5 MJ m^{-2} (mean daily irradiance of 1.57 to 4.05 MJ 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 of 1.57 MJ m^{-2} d^{-1}. More leaves were initiated before the flower when irradiance was reduced to 1.57 MJ m^{-2} d^{-1}. At this point 26 leaves were formed below the flower compared with 24 leaves in control.

Dark treatments prior to chilling

Plants confined to darkness for 2–8 d at 20°C had significantly smaller shoots than control plants at the start of vernalization (Table VI). Generally, as the duration of darkness increased, leaf number, leaf area and shoot dry weight decreased. Leaf number was in no case reduced below the minimum number required for competence to perceive vernalization (Ramin and Atherton, 1991b).

Keeping competent plants in darkness at 20°C before chilling significantly delayed bolting and flower initiation ($P<0.001$). This was seen in an increase in both the time to macroscopic internode visibility and in the number of leaves initiated below the inflorescence (Table VII). Generally, the effectiveness of dark treatments prior to chilling was greater in plants chilled at 5°C for six rather than nine weeks. Two days' dark treatment prior to chilling had no effect on the proportion of plants bolting and flowering, but four and eight days' darkness significantly delayed the onset of bolting and flowering ($P<0.001$). Four and eight days in darkness prior to chilling for six weeks completely inhibited bolting and flowering and all plants remained vegetative, at least to the time of final harvest (Table VII).

DISCUSSION

In celery studied here, photoperiod during vernalization had no effect on bolting, macroscopic flower appearance or the number of leaves initiated below the flowers. Flower initiation without bolting however was clearly promoted by short photoperiods during chilling. The flower initiation response was consistent with previous reports from Pressman and Negbi (1980) and Roelofse *et al.* (1989) who found long photoperiods during vernalization to delay flower initiation in celery, but the bolting response was different in both previous

TABLE VI
Shoot size prior to chilling in controls and plants in darkness. Each value is a mean of 5

Treatments	Leaf number (including primordia)	Leaf area (cm^2)	Shoot dry weight (g)
Control	22	716	5.13
2 d dark	21	680	4.87
4 d dark	20	637	4.56
8 d dark	18	465	3.40
LSD $P<0.05$	0.95	56	0.51

TABLE VII
Effects of dark treatments immediately before chilling on bolting and flowering

Treatments	Duration of chilling (weeks)	Days to bolting (from end of chilling)	Percent of plants bolting	Percent of plants flowering	Leaf number in	
					flowering plants	vegetative plants
Control	6	54	55	55	28	32
	9	28	100	100	22	—
2 d dark	6	59	55	11	28	34
	9	32	100	100	23	—
4 d dark	6	—	0	0	—	40
	9	34	88	88	24	28
8 d dark	6	—	0	0	—	42
	9	41	66	44	28	32
LSD $P<0.05$	7	***	***	2.0	3.5	

*** = Significant at $P<0.001$.

studies where clear delays to bolting were evident in plants exposed to long photoperiods during vernalization. The inconsistency could have been due to the different temperature regimes used for vernalization. In the present study, optimal temperatures for vernalization of celery of 5°C (Honma, 1969; Kinet *et al.*, 1976) were used whereas in the previous studies, plants were vernalized at supra-optimal temperatures of ca. 10°C. Intense vernalization treatments are known to suppress responses to photoperiod in other plants (Barendse, 1964; Pierik, 1964a; Vince-Prue, 1975).

After chilling, long photoperiods promoted bolting and flowering, whereas short photoperiods applied then inhibited all vernalization responses. These results agree with those of Pressman and Negbi (1980) but at first sight appear to conflict with Roelofse *et al.* (1989) who showed that night-break lighting applied to celery grown at 10°C delayed flower initiation and bolting. This discord is probably attributable to differences in the environmental conditions under which the plants were grown. The young, competent plants in the present study and in the experiments of Pressman and Negbi (1980) were grown at non-inductive temperatures after vernalization. Roelofse *et al.* (1989) however, grew plants throughout at vernalizing temperatures which probably caused all plants to initiate flowers regardless of photoperiod. This explanation is consistent with observations on a range of plants where long chilling treatments remove requirements for long photoperiods for flower initiation (Bernier *et al.*, 1981).

Absolute darkness during chilling prevented vernalization in celery. This contrasted with vernalization of carrots where darkness during chilling enhanced subsequent bolting and flowering (Atherton *et al.*, 1984). The possible importance of irradiance during vernalization may depend on the condition of the plants at the time chilling treatments began (Pierik, 1967a; Brewster, 1985). For example, plants with high levels of stored carbohydrates in the shoot may be insensitive to irradiance during chilling but those with low reserves may need light to enable nutrient availability to the stem apex (Brewster, 1985). A regulatory role for light rather than a direct photosynthetic function is further indicated by the observation that only very low irradiance ($0.2\ Wm^{-2}$) was required to enable full vernalization and no enhancement of flowering was observed with increasing irradiance. Insensitivity of flower induction to increasing irradiance during vernalization has been demonstrated also for *Lunaria* (Pierik, 1967b), in cauliflower (Wiebe, 1974) and in onion (Brewster, 1985).

Once vernalization has taken place, bolting and flowering were not influenced by irradiance. All plants initiated flowers normally, including those grown at the minimum mean daily irradiance of $1.57\ MJ\ m^{-2}\ d^{-1}$. This agrees with previous reports from Harrington, Verkerk and Doorenbos (1959) for endive and Pierik (1967b) for *Lunaria*. Pressman and Shaked (1988), however, working with Chinese cabbage, found the rate of bolting decreased under high irradiance. This could

have been due to a temperature increase around the canopy to supra-optimal levels for extension growth or to high-temperature devernalization effect.

Dark treatments prior to chilling reduced the responsiveness to vernalization of previously competent celery plants. This phenomenon has been reported for other plants previously and has been termed 'predevernalization' (Sadik and Ozbun, 1968; Fontes and Ozbun, 1972; Brewster, 1985). For outdoor celery crops, predevernalization by high temperatures of 30°C for 20 d prior to field planting delays bolting and flowering (Sachs and Rylski, 1980). In temperate countries the costs of subjecting celery transplants to such high temperatures for so long would be prohibitively expensive. Confining young plants to darkness for short periods of 4–8 d before transferring them to potentially vernalizing conditions in the field could reduce bolting and should be a cheaper alternative. Night break lighting is likely to remain the most economic way of constraining bolting in early celery crops grown at vernalizing temperatures under glass (Roelofse *et al.*, 1990).

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