when root systems were cut from the plant.

The maintenance of cellular membranes is considered to be dependent upon energy from aerobic respiration (1, 9, 16). Root cells have been shown to release their contents to their environment during brief anaerobiosis (7). Anaerobic conditions would be expected to cause membrane disorganization by reducing the source of energy from respiration. Retention of selectively permeable membranes may be considered essential for separation of cyanogenic glycosides and their hydrolytic enzymes. It is therefore suggested that, under anaerobic conditions during waterlogging, respiration and resultant energy transfer are inhibited initially. With a deficient supply of energy for maintenance of membranes, cellular disorganization occurs. As a result, the cyanogenic glycoside and its hydrolytic enzymes come in contact and hydrolysis takes place. The HCN so released may cause additional inhibition and cellular damage, thus increasing severity of plant response in an autocatalytic manner. The lower sensitivity of plum than of peach and apricot might be explained by differences in respiratory mechanisms, with secondary effects due to cyanogenesis. The characteristics of plum responsible for its overall greater tolerance to waterlogging are probably of a quantitative rather than qualitative nature. This is indicated by the variability in sensitivity among individual seedlings (Fig. 1) and the high amount of glycoside hydrolysis in the plant that died during treatment in the controlled-environment room.

Cyanogenesis appears to be a highly sensitive indicator of cellular damage and relative sensitivity to waterlogging. Measurement of HCN evolution under limiting availability of O_2, and as influenced by temperature, should be useful in selecting rootstocks of species containing cyanogenic glycosides which might provide increased tolerance to waterlogging.

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Analysis of Low Temperature Stimulation of Floral Initiation in Poinsettia cv. Paul Mikkelsen[1]

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Abstract. The floral initiation response of 'Paul Mikkelsen' poinsettia to low temperature under long days was saturated after exposure to constant temperatures of 60°F for 10 days. Low temperature was perceived by the shoots but not the roots. As has been reported by others, high temperatures (80°F) during and after short days inhibited floral initiation. Gibberellin A_3 was an effective inhibitor of low temperature stimulated floral initiation under long days and Cycocel promoted flowering under long days at 70°F but not at 80°. Neither light source nor intensity greatly influenced low temperature stimulated floral initiation. These findings are discussed in relation to a possible mechanism by which low temperatures stimulate floral initiation in this short day plant and in relation to cultural practices.

Poinsettia (*Euphorbia pulcherrima* Willd.) is a short day plant in which the critical daylength for floral initiation can be altered by temperature (11). The cv. Paul Mikkelsen is particularly sensitive to temperature and when grown at 60°F night temperature will initiate floral primordia regardless of photoperiod treatment (10). A similar promotive effect of low temperature on flowering of short day plants under long day conditions has been observed in *Pharbitis* (9) and *Fragaria* (2). In both species floral initiation in long days is promoted by treatment with the growth retardant Cycocel (3,16) as well as by low temperature. Thompson and Guttridge (14) have reported that floral initiation in *Fragaria* is inhibited by applications of gibberellin A_3 (GA_3). A GA_3 induced delay of floral initiation in poinsettia under short days has been reported by Guttridge (4).

In contrast to the photoperiodic control of flowering, alternate environmental controls of floral initiation (such as low

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temperature) have been studied very little in short day plants. The objective of this investigation was to characterize the low temperature stimulation of floral initiation in 'Paul Mikkelsen' poinsettia and to define more precisely the interaction of temperature and photoperiod in the control of floral initiation in this cultivar.

Materials and Methods

Methods used to culture plants prior to imposing experimental conditions were essentially the same as those of Kofranek and Hackett (10). At the time of treatment, the shoots were about 10 cm long and had 8 to 10 leaves plus 11 or 12 leaf primordia in the shoot tip. During the experimental periods the plants were grown at constant temperatures (±2°F) in controlled environment growth rooms. A light intensity of 1000 ft-c from a mixture of Gro-Lux fluorescent and incandescent (10% of input wattage) lamps was provided for 8 hours per day. Plants under short days received this light only in order to insure that the length of the dark period was not limiting (11). Because of the reported influence of temperature on the critical daylength of poinsettia, short day treatments were administered at both 70 and 80°F. Except where noted in the results, supplementary light to extend the daylength to 16 hours was provided by incandescent lamps at 10 ft-c intensity. A constant temperature of 60°F was used for the low temperature long day floral initiation treatment because previous work (10) showed that 60°F night temperature was as effective as 55°F in promoting floral initiation under long day conditions. After exposure to short days or long days at 60°F, plants were placed under long days at either 70 or 80°F to allow development of floral primordia under conditions that are not conducive to floral initiation. In one experiment soil temperatures were controlled by immersing the pots enclosed in plastic bags in thermostatically controlled water baths. Eight plants were used per treatment in all experiments.

The growth retardant Cycocel [(2-chloroethyl) trimethyl ammonium chloride], obtained from American Cyanimid Co. as an 11.8% solution, was applied as a soil drench at the rate of 1 g per 6 inch pot at the time experimental conditions were imposed. The potassium salt of gibberellin A_3 at a concentration of 40 mg/l in a 0.05% Tween 20 solution was applied to the foliage weekly.

The effect of various factors on floral initiation was ascertained by dissecting the shoot tips to determine whether plants were vegetative or reproductive and by counting the total number of leaves (nodes) on each plant. In terminally flowering plants, fewer nodes indicate that the plants have changed from the vegetative to the reproductive stage more rapidly than plants with a larger number of nodes. The height of the plants was measured to determine the effect of various treatments on vegetative growth.

Results

Sensitivity to low temperature and short days. The poinsettia 'Paul Mikkelsen' was more responsive to low temperature (60°F) than to short days with respect to floral initiation (Tables 1 and 2). Eighty-eight percent of the plants receiving 7 long days at 60° followed by long days at 80°, but only 25% of those receiving 7 short days at 80° followed by long days at 80°, formed floral primordia. There was 100% floral initiation after 10 days exposure to either treatment. However, initiation occurred at a higher node (21.6 vs 19.9) under short days than under low temperature long days. The duration of short day

Table 1. Effect of duration of exposure to 60°F under long days on floral initiation and vegetative growth in 'Paul Mikkelsen' poinsettia. Data taken 41 days after the start of treatments.

Duration of exposure to 60°F long days	Temp. of subsequent long day treatment	Plants with floral primordia	Mean nodes	Mean plant height
Days	°F	%	No.	cm
0	70	50	27.7 ± 1.6	73 ± 2
0	80	0	33.2 ± 0.7	73 ± 2
3	70	50	28.1 ± 1.7	71 ± 2
3	80	0	32.9 ± 0.7	73 ± 2
7	70	100	20.3 ± 0.5	53 ± 2
7	80	88	21.4 ± 1.2	54 ± 3
10	70	100	19.8 ± 0.2	62 ± 3
10	80	100	19.9 ± 0.1	60 ± 3
41	–	100	19.6 ± 0.2	46 ± 2

Table 2. Effect of duration of exposure to short days on floral initiation and vegetative growth in 'Paul Mikkelsen' poinsettia. Data taken 41 days after the start of treatments.

Short day treatment		Temp. of subsequent long day treatment	Plants with floral primordia	Mean nodes	Mean plant height
Duration	Temp.				
days	°F	°F	%	no.	cm
1	70	70	50	27.0 ± 1.9	71 ± 3
1	70	80	0	32.5 ± 0.5	70 ± 3
1	80	80	0	32.7 ± 0.7	71 ± 3
3	70	70	100	20.3 ± 0.3	61 ± 2
3	70	80	13	29.6 ± 1.3	53 ± 2
3	80	80	0	31.6 ± 0.7	56 ± 3
7	70	70	100	19.9 ± 0.2	63 ± 2
7	70	80	100	19.5 ± 0.2	53 ± 2
7	80	80	25	29.5 ± 1.8	56 ± 2
10	70	70	100	19.9 ± 0.3	65 ± 4
10	70	80	100	19.6 ± 0.3	55 ± 3
10	80	80	100	21.6 ± 0.4	69 ± 3
41	70	-	100	19.2 ± 0.2	56 ± 3
41	80	-	100	21.5 ± 0.2	68 ± 3

treatment required for 100% floral initiation was increased by increasing the temperature during short days and/or during the long day after treatment.

Fifty percent of the control plants held at 70°F under long days for 41 days formed floral primordia, but plants held at 80°F under long days remained vegetative (Table 1). Subsequent experiments showed that the effect of 70°F long days on floral initiation varies with a range of 0 to 50% of the plants forming floral primordia. This indicates that 70°F is a marginal temperature for floral initiation under long days.

Interactions of temperature, GA_3 and Cycocel. Cycocel promoted and GA_3 inhibited floral initiation under long days (Table 3). As expected Cycocel inhibited and GA_3 promoted shoot elongation. Repeated applications of GA_3 completely inhibited low temperature (60°F) stimulation of floral initiation under long days. This inhibition was not negated by treatment with Cycocel and neither was the GA_3 promotion of shoot elongation. At 70°F, Cycocel promoted and GA_3 inhibited floral initiation as compared to the non-treated controls at this temperature. The promotion of floral initiation by Cycocel was completely negated by GA_3 treatments. All of the Cycocel treated plants at 70°F formed primordia and initiation occurred at nearly as low a node as with untreated control plants at 60°F. At 80°F, none of the control plants and only 13% of the Cycocel treated plants formed floral primordia. These data indicate that Cycocel only partially replaces the effect of low temperature (60°F) on floral initiation, but that GA_3 completely inhibits the effect of low temperature even when plants are treated with Cycocel.

Table 3. Interaction of temperature, GA_3, and Cycocel in the control of floral initiation and vegetative growth in 'Paul Mikkelsen' poinsettia under long days. Data taken 42 days after the start of treatments.

Treatment	Plants with floral primordia	Mean nodes	Mean plant height
	%	no.	cm
60°F Control	100	20.5 ± 0.1	49 ± 2
60°F + Cycocel	100	20.3 ± 0.1	25 ± 2
60°F + GA	0	30.3 ± 0.2	86 ± 7
60°F + Cycocel + GA	0	30.8 ± 0.2	88 ± 7
70°F Control	38	28.1 ± 1.4	70 ± 3
70°F + Cycocel	100	21.0 ± 0.2	49 ± 2
70°F + GA	0	33.7 ± 0.2	109 ± 7
70°F + Cycocel + GA	0	34.5 ± 0.2	111 ± 8
80°F Control	0	34.0 ± 0.2	68 ± 3
80°F + Cycocel	13	32.1 ± 1.3	49 ± 2

Effects of light source and intensity. From data of the previous experiment, it appeared that there was a relationship between plant height and floral initiation (i.e. short plants tended to form floral primordia and tall ones did not) when plants were grown at 60 or 70°F (Table 3). At 80°F, this relationship was not apparent as neither tall nor short plants formed floral primordia to any large extent. This failure of floral initiation at 80°F could have been due to a limitation in light energy necessary for general metabolic processes. To study the possible relationship between plant height and floral initiation and to determine whether light energy was limiting at 80°F, an experiment was conducted utilizing light sources to manipulate plant height and supplementary high intensity light to nearly double the total light energy. The 3 light treatments allowed a comparison of 2 light sources (incandescent and Gro-Lux fluorescent at 10 ft-c) and 2 light intensities (Gro-Lux fluorescent at 10 and 1000 ft-c). Supplementary light treatments were given from 4 PM to midnight following 8 hours exposure to the normal daily high intensity light.

A comparison of low intensity fluorescent (10 ft-c) and incandescent light (10 ft-c) treatments (Table 4) shows that plant height had little relationship to the formation of floral primordia. Although plants given a 10 ft-c fluorescent light treatment were in all cases shorter than plants receiving incandescent light, they had no more tendency to form floral primordia than plants treated with incandescent light. Plant height was related to floral initiation only in those treatments in which plants were exposed to 60°F and in some treatments where plants had been treated with Cycocel. These data also show that a supplementary light source with a high percentage of red (fluorescent) was no more effective than a source rich in far-red (incandescent) for inhibition of floral initiation at 60°F.

High intensity supplementary fluorescent light had no qualitative influence on floral initiation (Table 4) as compared to low intensity fluorescent light (or low intensity incandescent). At 60°F initiation was 100% regardless of light intensity but cyathia of high light treated plants were considerably larger, especially on plants treated with Cycocel. At 70°F, plants receiving high intensity fluorescent light had a slightly greater tendency to initiate floral primordia than those receiving low intensity fluorescent (or incandescent) light; this was most apparent with Cycocel treated plants. At 80°F very few plants formed primordia even with high intensity supplementary light and these few plants formed cyathia at a very high node number.

Receptive site for temperature. Root temperature had neither a stimulatory nor an inhibitory effect on initiation of floral primordia under long days (Table 5). This means that the receptive site for temperature is in the above ground parts of the plant.

Discussion

'Paul Mikkelsen' poinsettia is a striking example of a plant in which low temperature provides a very effective alternate to short days as an environmental pathway to floral initiation. The effectiveness of low temperature in stimulating floral initiation is demonstrated by the fact that only 10 days at 60°F are required to obtain floral initiation in 100% of the plants. This means that the floral initiation response is saturated after this short exposure to low temperature. In *Pharbitis nil* (9) and

Table 4. Influence of long day supplementary light source and intensity on floral initiation and vegetative growth in 'Paul Mikkelsen' poinsettia. Data taken 37 days after the start of treatments.

Temp.	Light source and intensity	Control			Cycocel treated		
		Plants with floral primodia	Mean nodes	Mean plant height	Plants with floral primodia	Mean nodes	Mean plant height
°F	ft-c	%	no.	cm	%	no.	cm
60	incand. 10	100	21.0 ± 0.1	46.4 ± 1.8	100	20.3 ± 0.1	26.2 ± 1.5
60	fluor. 10	100	20.1 ± 0.1	30.3 ± 1.5	100	20.4 ± 0.2	19.5 ± 1.2
60	fluor. 1000	100	20.5 ± 0.1	28.9 ± 0.3	100	20.5 ± 0.1	17.5 ± 0.2
70	incand. 10	0	31.8 ± 0.3	68.6 ± 2.5	63	25.3 ± 1.9	44.9 ± 1.7
70	fluor. 10	0	31.9 ± 0.2	50.1 ± 1.1	88	22.4 ± 1.4	28.0 ± 1.3
70	fluor. 1000	13	30.8 ± 1.4	52.9 ± 1.3	100	21.0 ± 0.2	25.4 ± 0.2
80	incand. 10	0	34.5 ± 0.2	64.3 ± 2.8	13	32.1 ± 1.3	48.7 ± 1.8
80	fluor. 10	0	34.5 ± 0.2	51.4 ± 1.3	0	33.6 ± 0.2	32.3 ± 0.3
80	fluor. 1000	25	33.5 ± 1.1	52.1 ± 1.1	38	31.5 ± 1.3	26.6 ± 0.3

Table 5. Floral initiation and vegetative growth response of 'Paul Mikkelsen' poinsettia to various shoot and root temperatures under long days. Data taken 42 days after the start of treatments.

Treatment				
Root temp.	Shoot temp.	Plants with floral primodia	Mean nodes	Mean plant height
°F	°F	%	no.	cm
60	60	100	19.5 ± 0.2	39.1 ± 1.5
80	60	100	19.9 ± 0.2	33.4 ± 1.7
60	80	0	31.5 ± 0.2	39.8 ± 0.3
70	70	50	28.7 ± 1.2	65.4 ± 2.6
70	60	100	19.1 ± 0.2	36.8 ± 1.5
60	70	50	27.3 ± 1.0	39.5 ± 2.4
80	80	0	37.5 ± 0.2	66.4 ± 2.0
70	80	0	36.9 ± 0.3	64.7 ± 1.8
80	70	38	27.7 ± 1.5	65.5 ± 1.9

Fragaria (6) similar responses to low temperature are saturated after 30 days at 15°C and 10 days at 9°C, respectively. Ten days exposure to low temperature results in development of rudimentary cyathia in 'Paul Mikkelsen' poinsettia but longer exposure (ca 60 days) produces fully developed primary and secondary cyathia with bract formation (10). Low temperatures effectively stimulate floral initiation under long days, but high temperature (80°F) during and after short days inhibits floral initiation. These responses suggest that low temperature can substitute in part for darkness and high temperature for light in the control of floral initiation in this cultivar.

As has been reported for *Pharbitis nil* (8) and *Fragaria* (7) floral initiation at low temperature is not greatly influenced by quality or intensity of the light used to extend the daylength. Supplementary fluorescent light of 1000 ft-c did not inhibit floral initiation of 'Paul Mikkelsen' at 60°F, and unpublished data of Hackett and Kofranek show that 200 ft-c of incandescent light also is not effective. Hackett and Miller (5) showed that 4 hour light interruptions of 35 ft-c in the middle of the dark period were not effective for inhibiting floral initiation in this cultivar when the mean night temperature was 59°F.

Gibberellin A3 inhibits floral initiation at a low temperature under long days and Cycocel promotes flowering under long days at 70°F but not at 80°F. This suggests that the promotive effect of low temperatures may be mediated through the reduction in level of an endogenous gibberellin-like inhibitor of floral initiation the production of which is favored by high temperature and long days. It is known that Cycocel inhibits gibberellin biosynthesis (12) and Criley (1) has shown that gibberellin-like activity in root exudates of 'Paul Mikkelsen' is reduced in long day plants treated with Cycocel. Similar effects of GA3 and Cycocel on floral initiation have been reported for both *Pharbitis nil* and *Fragaria* (3,14,16). The failure of plants to initiate cyathia when treated with Cycocel at 80°F may be explained if it is assumed that promotive as well as inhibitory substances are involved in the control of floral initiation in poinsettia (15). If the promoter is a heat-labile substance (see Table 2, effect of temperature on initiation under short days) produced under a variety of conditions (including long days but favored by short days), it would be at a low level at 80°F under long days. Even though Cycocel might reduce the level of inhibitor at 80°F under long days, there would not be sufficient promoter to induce floral initiation.

The results of the experiments with light sources and root-shoot temperatures indicate that the promotive effect of low temperature or Cycocel on floral initiation is not an indirect one which functions via the reduction of shoot elongation.

From the cultural standpoint these results show that short exposures of stock plants or rooted cuttings to temperatures below 70°F can cause premature and unwanted flower bud formation even though plants are under long day conditions. The sensitivity to temperature is illustrated by the observation that stock plants near glasshouse doors or ventilators have a greater tendency to form premature buds than plants not exposed to occasional cold air drafts from out-of-doors. A supplementary light treatment that will prevent premature bud formation at low temperatures has not been found.

Under conditions where temperatures cannot be maintained above 70°F, GA3 could be used to prevent premature bud formation without adverse side effects other than rapid shoot elongation. Although a concentration of 40 mg/l of GA3 was used in these experiments, lower concentrations (15-20 mg/l) are very effective without excessive shoot elongation. Prolonged inhibition of premature budding would require repeated applications of GA3.

Formation of a premature floral bud breaks apical dominance and has the same effect as "pinching" the shoot tip. Short duration low temperature exposure might be used as a method of environmentally pinching 'Paul Mikkelsen'. Struckmeyer and Beck (13) have suggested using short days for this purpose with other cultivars.

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