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Daily Light Integral, Prevernalization Photoperiod, and Vernalization Temperature and Duration Control Flowering of Easter Cactus

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Abstract. **Experiments were performed on *Hatiora gaertneri* (Regel) Barthlott 'Jan' and 'Rood' and *H.* ×*graeseri* (Wedermann) Barthlott 'Evita' to determine their flowering responses to 1) daily light integral (DLI) before and during vernalization; 2) 0 to 6 weeks of short-day (SD) or long-day (LD) photoperiods before vernalization at 10, 12.5, or 15 °C; 3) propagation from April to July; 4) timing of leveling before or during inductive treatments; and 5) SD photoperiods before vernalization under darkness at 0 to 10 °C. 'Jan' grown under elevated DLI before vernalization and low DLI during vernalization flowered more prolifically than plants grown under low DLI before vernalization or high DLI during vernalization at 15 °C. Six weeks of SD photoperiods before vernalization increased the number of buds per flowering phylloclade after vernalization at 10 °C and increased flowering uniformity when vernalization duration was insufficient at 10 °C or vernalization temperature was 12.5 or 15 °C. For plants flowering in January, propagation the previous April produced better flowering than propagation in May, June, or July. Removal of apical phylloclades during prevernalization SD or during vernalization was deleterious to flowering. Vernalization in the dark produced marginal flowering, but SD treatment before vernalization increased the percentage of apical phylloclades flowering, buds per flowering apical phylloclade, and percentage of plants flowering after dark vernalization. 'Evita' flowered more poorly than either 'Jan' or 'Rood'. Collectively, the most uniform flowering in January occurred when plants were exposed to a sequence of 4 to 6 weeks of SD, vernalization at 7.5 to 15 °C for 8 weeks, then growth under LD for 7 weeks.**

Easter cacti (*Hatiora gaertneri* and *H.* ×*graeseri*) belong to a group of epiphytic cacti native to the southeastern Brazilian states of Paraná and Santa Catarina near lat. 26°S (Barthlott, 1983; Barthlott and Taylor, 1995). *Hatiora* ×*graeseri* is a hybrid of *H. gaertneri* and *H. rosea* (Barthlott and Taylor, 1995). Flowering may be achieved through photoperiod manipulation (photoinduction); *Hatiora* sp. are classified as short–long-day plants for flowering from 15 to 20 °C (Boyle, 1991; Boyle et al., 1988; Peters and Rünger, 1971; Rünger, 1960). Easter cacti are sold as flowering potted plants from January to June in northern Europe. Uniform flowering in January has been difficult to achieve (Hans de Vries, personal communication), most likely because of noninductive temperature or photoperiod conditions during and before the early stages of induction in early to mid-October.

Vernalization from 10 to 15 °C may substitute for the short-day (SD) phase (thermoinduction) depending on cultivar. Thermoinduction at 10 °C is optimal, whereas 15 °C is marginal for *H.* ×*graeseri* regardless of photoperiod (Rünger, 1960). For *H. gaertneri*, the optimum temperature for vernalization under SD is 10 to 15 °C; under long-day (LD) photoperiods, 10 °C is optimum (Peters and Rünger, 1971). Flowering is generally greater after thermoinduction than photoinduction, especially in *H.* ×*graeseri* (Boyle, 1991, 1995). The critical photoperiod for the SD phase of photoinduction in *H. gaertneri* is 11 to 12 h (Boyle, 1991), and daylength, including civil twilight on 1 Oct., is 12 h 41 min and 12 h 47 min at lat. 25°N and 55°N, respectively (Astronomical Almanac for the Year 2002, 2000). In early October, consistently achieving the 8 to 12 °C night temperatures recommended for thermoinduction (Boyle and Stimart, 1989; Nell, 1988) also may not be possible because of higher ambient temperature.

Extending the duration of inductive periods for *Hatiora* enhances flowering. For example, increasing the duration of the SD phase (8- to 11-h photoperiods) of photoinduction from 2 to 8 weeks increased the percentage of flowering apical phylloclades (PFAP), number of buds per flowering apical phylloclade (BFAP), and number of buds per plant for photoperiods of 8 to 11 h in *H. gaertneri* 'Crimson Giant' (Boyle, 1991).

Treatment with SD followed by vernalization creates a longer inductive period and improves flowering in *Hatiora*. *Hatiora gaertneri* given a 30-d SD treatment at 15 or 20 °C before a 70-d vernalization at 15 °C had a greater PFAP (78% to 81%) than plants grown under LD until vernalization (62% to 63%) (Peters and Rünger, 1971). *Hatiora* ×*graeseri* given 50 SD before vernalization for 60 d at 5 to 15 °C showed a larger proportion of apical phylloclades flowering than plants given 50 LD before vernalization (Rünger, 1960). It was postulated that three *Hatiora* cultivars had more flowers if artificial photoinduction began on 24 Nov. than if photoinduction began on 21 Sept. because of natural SD before 24 Nov. (Boyle, 1995). This response to prevernalization SD has been shown in other plants that respond to vernalization (Napp-Zinn, 1984).

Leveling, pinching, twisting, and pruning are synonyms for the removal of apical phylloclades in *Hatiora* or the related *Schlumbergera* cacti to increase uniformity, branching, and bud count and to create a more compact plant. To our knowledge, no research has been performed on timing of leveling for *Hatiora*. Leveling the plants during vernalization is not recommended, and additional cooling is suggested if plants are leveled during vernalization (Boyle, 1997; Nell, 1988). The closely related SD plant *Schlumbergera* benefits from leveling 1 to 10 d after SDs are started (Boyle, 1997).

Vernalization in a cooler may provide a means for extending the season or cooling the plants when greenhouse temperatures are insufficient for vernalization. Celery (*Apium graveolens* L.), ajuga (*Ajuga reptans* L.), and carnation (*Dianthus caryophyllus* L.) were insensitive or less responsive to low temperature when no light was provided (Eltzroth and Link, 1970; Ramin and Atherton, 1994), but flowering in carrot (*Daucus carota* L.) was enhanced by vernalization in the dark compared with vernalization under 12- to 20-h photoperiods (Atherton et al., 1984). Previous research indicates that vernalization of *Hatiora* in darkness does not lead to flowering (Peters and Rünger, 1971), but prevernalization SDs may condition the plants for successful dark vernalization.

Specific combinations of prevernalization SD treatment and vernalization duration and temperature may increase reliability and uniformity of Easter cactus flowering, especially for early-season crops. Reducing the total crop time through later propagation would increase available space for growers in the spring and reduce production costs. Vernalization of *Hatiora* in a refrigerated chamber could save space, allow extension of the market dates, and prevent insufficient

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vernalization caused by unpredictable weather in the fall and spring. The objectives of this research were to 1) study the effects of photoperiod before vernalization and daily light integral (DLI) before and during vernalization on flowering induction; 2) identify combinations of SD treatments before vernalization and vernalization treatments that increase uniformity and BFAP; 3) observe differences in flowering after exposure to two different photoperiods of SD prevernalization treatment; 4) identify propagation and leveling treatments that increase uniformity and BFAP; and 5) determine the effects on flowering of SD treatment followed by vernalization in a refrigerated chamber.

Materials and Methods

Phylloclades were harvested from vegetative cacti on 15 to 20 Apr. 2000 in Expt. 1; 15 to 20 Apr. 2001 in Expts. 2, 3, and 5; or as specified in Expt. 4. Phylloclades were rooted under natural daylengths [lat. 42°45′N, 13.4 h on 15 Apr. (Astronomical Almanac for the Year 2002, 2000)] in a 50 peat:50 perlite (by volume) mix in 55-cell (23 mL per cell) plug trays. Air and bench temperature were set at 23 and 25 °C, respectively. Plants were grown under intermittent mist until transplant. Mist duration was 4 s every hour or when accumulated light integral reached 0.2 mol·m^{-2}, whichever occurred first. Rooted plugs were transplanted into 10.2-cm (0.46-L) plastic pots containing 70 peat:30 perlite (SureMix Perlite; Michigan Grower Products, Galesburg, MI). Plants were irrigated with well water (containing 95, 34, and 29 mg·L^{-1} Ca, Mg, and S, respectively) supplemented with water-soluble fertilizer to provide the following (mg·L^{-1}): 125 N; 12 P; 125 K; 13 Ca; 1.0 Fe, B, and Mo; and 0.5 Mn, Zn, and Cu (MSU Special; Greencare Fertilizers, Chicago) acidified to a titratable alkalinity of 140 mg·L^{-1} $CaCO_3$. Fertilization was ended during vernalization treatments and resumed during forcing.

Plants were maintained in a greenhouse under 16-h LD from propagation until the beginning of SD or vernalization treatments. In Expt. 1, LDs were provided by pulling blackout cloth over the plants from 1700 to 0800 HR and lighting with incandescent lamps [(5 µmol·m^{-2}·s^{-1} photosynthetic photon flux (*PPF*)] from 1700 to 0000 HR. Long-day photoperiods in Expts. 2 through 5 were provided by high-pressure sodium (HPS) lamps (80 µmol·m^{-2}·s^{-1} *PPF*) for 16 h as needed from 0600 to 2200 HR to maintain a minimum of 80 µmol·m^{-2}·s^{-1}. Prevernalization SD photoperiods (10-h) were achieved by pulling blackout cloth over the plants from 1700 to 0800 HR and lighting (5 µmol·m^{-2}·s^{-1} incandescent irradiation) from 1700 to 1800 HR. Plants were grown under natural daylengths during vernalization in Expts. 2 through 5 and as described in Expt. 1. Long days during forcing were provided by pulling blackout cloth over the plants from 1700 to 0800 HR and providing incandescent irradiation (5 µmol·m^{-2}·s^{-1}) from 1700 to 0000 HR (16-h photoperiod). Temperature in each greenhouse was measured in an aspirated chamber every 10 s, and hourly averages were recorded by a CR-10 datalogger (Campbell Scientific, Logan, UT). Plants were grown at 21.5 ± 2.7 °C (setpoint = 20 °C) from propagation until vernalization and during forcing.

A randomized design was used in all experiments. Data were collected on percentage of plants flowering, days from the beginning of forcing (after vernalization) to visible anthers (time to flowering), number of apical phylloclades, number of apical phylloclades with flowers, and number of flower buds. Percentage of plants flowering was analyzed using 1-sample binomial tests (SPSS, 1999) in each treatment to test for difference from 99% flowering. Data for PFAP and BFAP were transformed [arcsin√PFAP and log(BFAP), respectively] and analyzed with a univariate general linear model in SPSS (SPSS, Chicago; SPSS, 1999). Days to flowering was analyzed using survival analysis (Cox regression; Dubois et al., 2003; SPSS Inc., 1997) treating flowering as a failure event with a cutoff of 80 d. Backward stepwise selection was used to include covariates for Cox regression analysis. Reported data for all experiments are raw means.

Expt. 1

Prevernalization daily light integral and photoperiod and vernalization daily light integral and temperature. Hatiora gaertneri 'Jan' was grown at 20 °C under 16-h LD or 10-h SD (provided by incandescent lighting under blackout cloth from 1700 to 1800 HR) at high (≈12 mol·m^{-2}·d^{-1}, provided by supplementary HPS lighting as previously described) or low (≈4.5 mol·m^{-2}·d^{-1}; without supplementarty HPS lighting) DLI for 6 weeks starting 19 Sept. 2000. The plants were then vernalized for 4 or 8 weeks at 7.5, 10, 12.5, 15, or 17.5 °C with a high (≈10 mol·m^{-2}·d^{-1}) or low (≈4 mol·m^{-2}·d^{-1}) DLI. During vernalization, plants were given 10 h of continuous supplementary irradiation from 0700 to 1700 HR provided by HPS lamps at ≈170 (high DLI) or 80 (low DLI) µmol·m^{-2}·s^{-1}. Plants given low DLI were grown under 50% shadecloth. All plants were leveled 7 d after the beginning of vernalization by removing a minimum number of apical phylloclades to achieve a uniform plant appearance, typically leaving three to four tiers of phylloclades. After vernalization, plants were forced under 16-h LD as described previously.

Expt. 2

Photoperiod before vernalization and vernalization duration and temperature. On 20 Sept. 2001, *H. gaertneri* 'Jan' and 'Rood' were moved into 10-h SD as described in Expt. 1. More plants were moved into this SD treatment on 4 Oct. and 18 Oct. On 1 Nov., plants from these SD treatments (6, 4, and

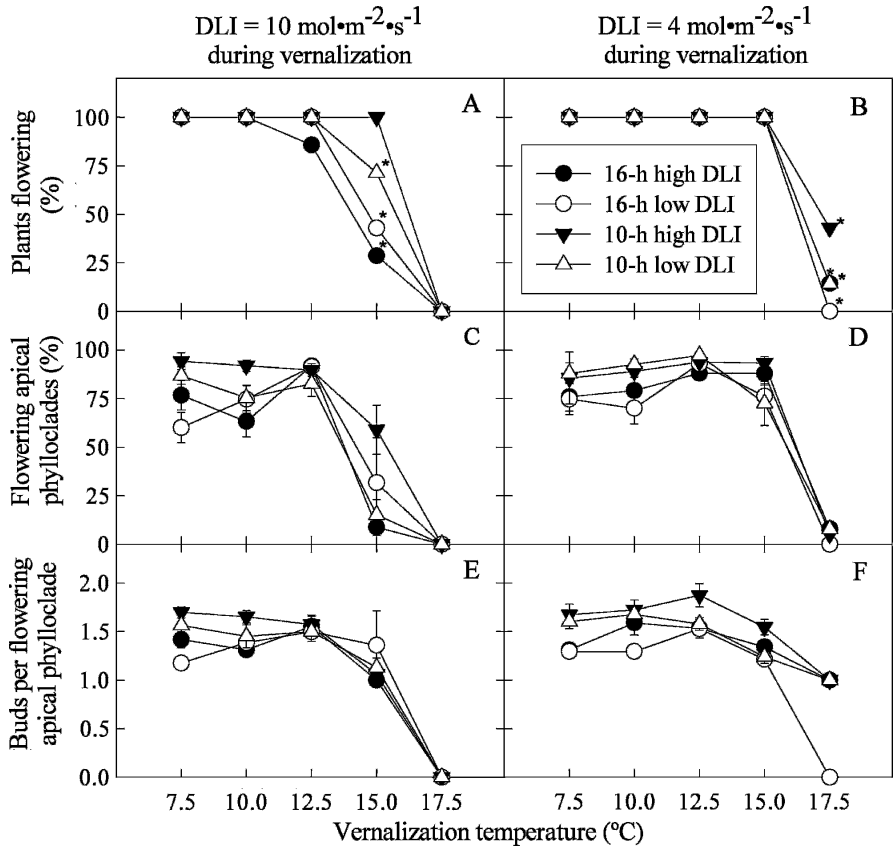

Fig. 1. Flowering of *Hatiora gaertneri* 'Jan' given short-day (10-h) or long-day (16-h) treatment at high daily light integral (DLI ≈12 mol·m^{-2}·d^{-1}) or low DLI (≈4.5 mol·m^{-2}·d^{-1}) for 6 weeks followed by vernalization at ≈10 or ≈4 mol·m^{-2}·d^{-1} DLI and 7.5, 10, 12.5, 15, or 17.5 °C for 8 weeks. Vertical bars represent ± 1 SE. Labeled treatments in graphs (A) and (B) are significantly different from 99% flowering according to a one-sample binomial test.

2 weeks of SD), along with plants from 16-h LD (0 weeks of SD), were exposed to vernalization treatments in greenhouses set at 10, 12.5, or 15 °C (actual temperatures were 10.9 ± 1.8, 12.7 ± 1.3, and 15.0 ± 2 °C, respectively) under natural photoperiods [10 h 18 min on 1 Nov. at lat 42°45′N (Astronomical Almanac for the Year 2002, 2000)]. Apical phylloclades were removed 14 d after vernalization was begun to increase plant uniformity. Vernalization treatments were for 2, 4, 6, or 8 weeks followed by forcing under 16-h LD at 20 °C as previously described.

Average proportion of flowering apical phylloclades (PrFAP) on all plants was multiplied by the percentage of plants flowering to illustrate flowering uniformity. This flowering index ranged from 0 if no plants flowered to 100 if all plants and all apical phylloclades flowered. The flowering index for each SD treatment and vernalization duration combination was compared with the maximum value in each cultivar and temperature by single degree-of-freedom χ^2 tests considering the flowering index as an observed frequency and an expected proportion of 0.5. There were seven plants per treatment.

Expt. 3

Short-day prevernalization photoperiod. On 22 Sept. or 6 Oct. 2001, *H. gaertneri* 'Jan' and *H.* ×*graeseri* 'Evita' were moved to 10- or 11-h SD provided by extending 9-h daylengths with incandescent lamps under blackout cloth as previously described. On 3 Nov. (after 6 or 4 weeks of SD), the plants were moved to 12.5 °C and vernalized for 4 or 8 weeks. Plants were leveled on 10 Nov. and forced as described previously.

Days to flower was analyzed separately for each cultivar as a result of multiple significant cultivar interactions. There were seven plants per treatment.

Expt. 4

Propagation and leveling date. Hatiora gaertneri 'Jan' and *H.* ×*graeseri* 'Evita' were propagated on 15 Apr., May, June, or July 2001. These plants were maintained under the propagation conditions described for ≈6 weeks. They were then moved to the 16-h LD (from HPS lamps) growing conditions previously described. Plants were moved to 10-h photoperiods (as described in Expt. 1) for 6 weeks beginning on 22 Sept., vernalized for 4 weeks at 10 °C beginning 3 Nov., and forced under 16-h LD at 20 °C. Plants were leveled on 6 Aug. (47 d before SD), 2 Oct. (10 d after SD started), 13 Nov. (10 d after vernalization started), or not at all. Plants propagated in July were not leveled on 6 Aug.

The PrFAP on all plants and the percentage of plants flowering were multiplied to determine flowering index. Each treatment value was compared with the maximum value within each main effect (cultivar, propagation date, and leveling date) by single degree-of-freedom χ^2 tests as described previously. Buds per flowering apical phylloclade was transformed [log(BFAP)] before analysis. There were five plants per treatment.

Expt. 5

Short-day treatment followed by vernalization in darkness in a cooler. Hatiora gaertneri 'Jan' and *H.* ×*graeseri* 'Evita' were grown for 6 or 3 weeks (starting 29 Nov. or 20 Dec. 2001, respectively) under 10-h SD as described in Expt. 1. On 10 Jan., these plants and plants given no SD treatment (continuously under 16-h LD) were moved into dark refrigerated chambers set at 0, 2.5, 5, 7.5, or 10 °C and held for 23 or 56 d. Because of a cooler malfunction, the final 7 d of the 56-d 10 °C treatment were carried out at 7.5 °C. After vernalization, plants were forced as described previously.

Days to flower was analyzed separately for each cultivar because the proportional hazards assumption was not met for cultivars (SPSS, 1997). There were seven plants per treatment.

Results

Expt. 1

Temperatures from 7.5 to 15 °C and low DLI (≈4 mol·m^{-2}·d^{-1}) during the 8 weeks of vernalization, combined with SD before vernalization, produced the greatest flowering response (Fig. 1). High DLI during vernalization reduced the percentage of flowering plants (Fig. 1A versus Fig. 1B), PFAP (Fig. 1C versus Fig. 1D), and BFAP (Fig. 1E versus Fig. 1F) when vernalization temperature was 15 °C or greater. The PFAP was greater on average when plants were vernalized under low DLI compared with high DLI (vernalization DLI $P < 0.001$ in global analysis of variance). Optimal vernalization temperature under the low vernalization DLI was 7.5 to 15 °C (100% of plants flowering, greater than 70% of apical phylloclades flowering, and greater than 1.2 BFAP), but the optimal range under the high vernalization DLI was 7.5 to 12.5 °C (86% or more of plants flowering, 60% or more of apical phylloclades flowering, and 1.2 or more BFAP). Short-day treatment (10-h) before vernalization generally increased the PFAP (Fig. 1C–D) and BFAP (Fig. 1E–F) for plants vernalized at 7.5 to 12.5 °C.

Plants given prevernalization under LD and vernalized for only 4 weeks flowered poorly (58% to 73% plants flowering after 7.5 to 12.5 °C vernalization) compared with

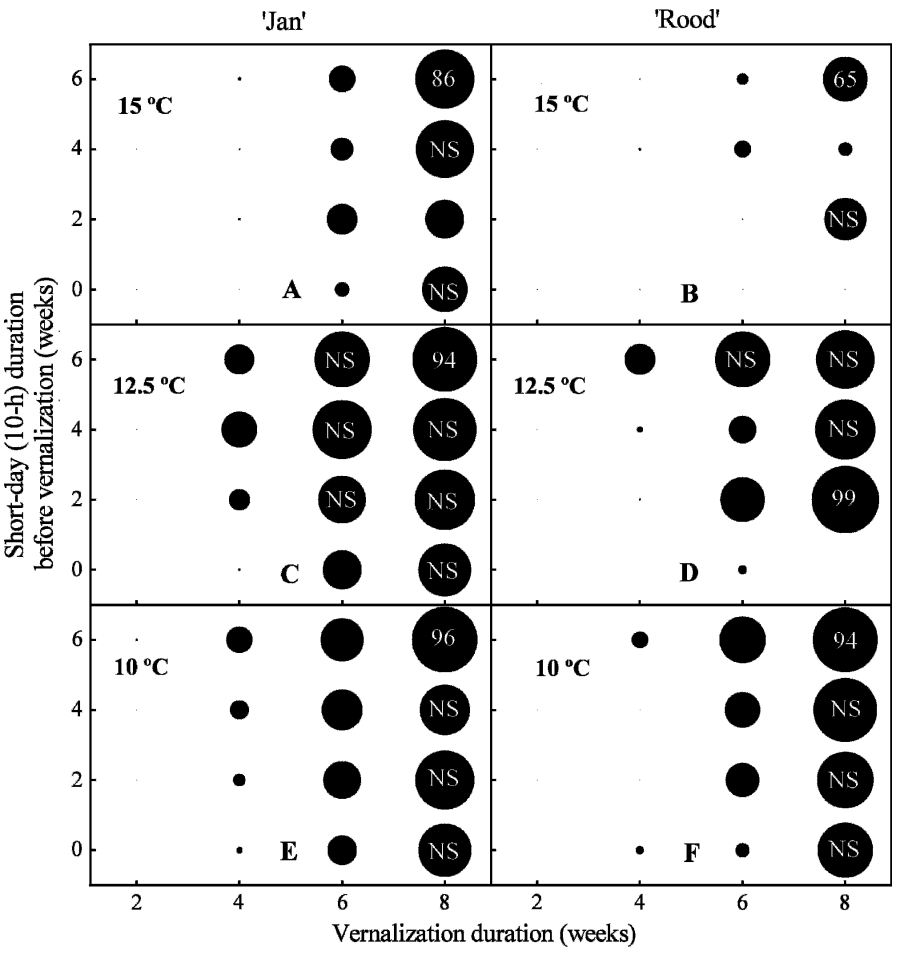

Fig. 2. Effects of vernalization duration, temperature, and a 10-h short-day prevernalization treatment on flowering uniformity in *Hatiora gaertneri* 'Jan' and 'Rood'. Bubble size was determined by (percentage of plants flowering) × (proportion of apical phylloclades flowering). NS = not significantly different from the labeled maximum within each temperature and cultivar according to single degree-of-freedom χ^2 ($\alpha = 0.05$). Unlabeled bubbles were significantly different from the labeled maximum. Treatments without a bubble did not have flowering plants.

plants given SD before 4 weeks of vernalization (93% to 100% of plants flowering after 7.5 to 12.5 °C treatment, data not shown). A maximum of 83% PFAP and 1.45 BFAP were recorded after 4 weeks of vernalization for plants given a prevernalization treatment of high DLI and SD and then vernalized under low DLI at 7.5 °C. Because of the reduced flowering of plants provided with 4 weeks of vernalization, data for these treatments are not provided.

Expt. 2

Flowering uniformity generally increased as duration of prevernalization SD treatment and vernalization increased (Fig. 2). The maximum flowering index was typically found in plants given 6 weeks of SD in combination with 8 weeks of vernalization. Vernalization at 10 or 12.5 °C for a duration of 8 weeks elicited the greatest flowering uniformity regardless of prevernalization photoperiod treatment. 'Jan' vernalized at 12.5 °C for 8 weeks with no prevernalizaion SD flowered with uniformity similar to plants given 4 or 6 weeks of SD before 6 weeks of vernalization at 12.5 °C. Flowering index was low for plants vernalized at 15 °C, especially for plants not previously receiving an SD treatment. 'Jan' flowered more uniformly than 'Rood', especially at 15 °C or at 12.5 °C with fewer than 8 weeks of vernalization.

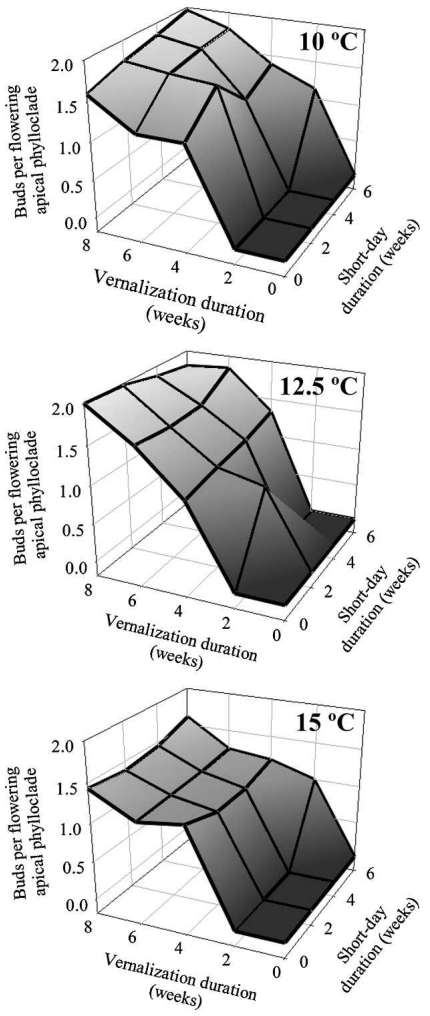

Fig. 3. Buds per flowering apical phylloclade (BFAP) on flowering *Hatiora* as a function of short-day (10-h) duration before vernalization and vernalization duration and temperature. Response is averaged over cultivar (nonsignificant at $\alpha = 0.05$).

Table 1. Effect of short-day (SD) duration before vernalization and vernalization duration and temperature on days to flower from the beginning of long days in *Hatiora gaertneri* Jan and Rood.

	Jan			Rood		
	Vernalization temperature (°C)					
Vernalization duration (weeks)	10	12.5	15	10	12.5	15
			0 wk of SD			
2 weeks of vernalization	—[z]	—	—	—	—	—
4 weeks	59	59	—	53	60	—
6 weeks	54	52	56	60	61	—
8 weeks	50	50	52	50	—	—
			2 weeks of SD			
2 weeks	—[z]	—	—	—	—	—
4 weeks	55	57	63	—	71	73
6 weeks	53	52	53	56	57	59
8 weeks	47	46	52	52	53	57
			4 weeks of SD			
2 weeks	—[z]	—	—	—	—	—
4 weeks	56	56	56	59	64	65
6 weeks	52	50	52	56	58	60
8 weeks	48	45	51	51	54	58
			6 weeks of SD			
2 weeks	—[z]	—	—	—	—	—
4 weeks	57	56	57	61	59	66
6 weeks	50	51	53	56	57	60
8 weeks	46	48	51	53	53	57
Significance						
Vernalization duration (VD)		***			***	
Short-day duration (SD)		NS			*	
Temperature (T)		***			NS	
VD × SD		***			*	
VD × T		NS			***	
SD × T		NS			NS	
VD × SD × T		NS			*	

[z]No flowering plants in this treatment within 80 d at 20 °C after vernalization.
[NS,*,***]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Table 2. Effects of prevernalization photoperiod and vernalization duration (at 12.5 °C) on flowering of *Hatiora gaertneri* Jan and *H.* ×*graeseri* Evita.[z]

Prevernalization		Vernalization	Plants	Apical phylloclades	Buds per flowering	Days to flower[x]	
Duration (weeks)	Photoperiod (hours)	duration (weeks)	flowering (%)	flowering (%)[y]	apical phylloclade	Jan	Evita
4	10	4	86	20	1.2	57	59
		8	100	57	1.7	47	47
	11	4	71[w]	14	1.0	60	58
		8	100	60	1.6	46	48
6	10	4	79[w]	33	1.1	56	52
		8	100	67	1.6	47	44
	11	4	54[w]	27	1.2	56	58
		8	100	58	1.5	48	50
Significance[v]							
Vernalization duration (VD)				***	***	NS	NS
Prevernalization duration (PD)				*	NS	***	NS
Prevernalization photoperiod (PP)				NS	NS	NS	*
Cultivar (CV)				NS	NS	—	—
VD × CV				NS	*	—	—
VD × PP				NS	NS	NS	***
VD × PD				NS	NS	***	***
PD × PP				NS	NS	***	NS
PD × PP × CV				*	NS	—	—
VD × PD × PP				NS	NS	NS	***

[z]Data are pooled by cultivar except for time to flower.
[y]Data include flowering plants only.
[x]Days to flower from start of forcing (long days at 20 °C), flowering plants only. Statistical analysis includes all plants.
[w]Significantly less than 99% flowering by a one-sample binomial test ($\alpha = 0.05$).
[v]Nonsignificant interactions ($P > 0.05$) are not shown.
[NS,*,***]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

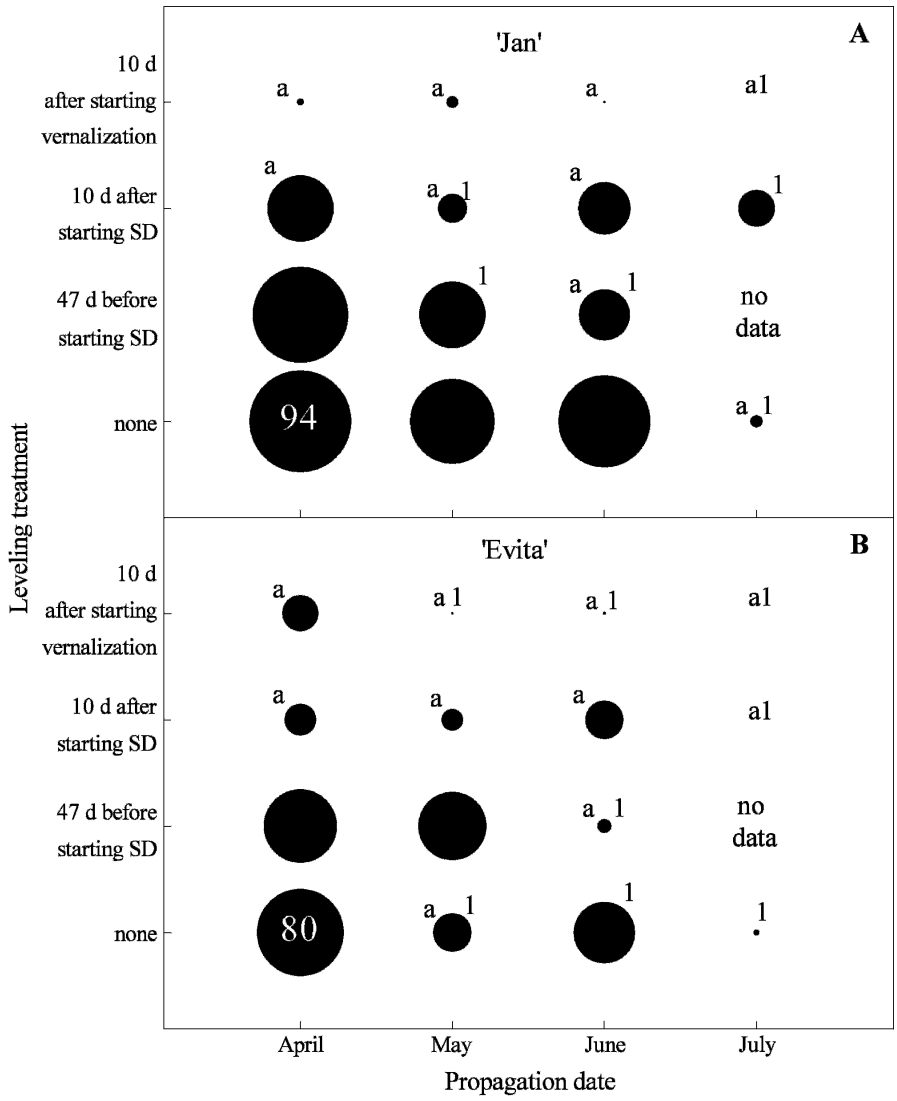

Fig. 4. Effect of propagation date and leveling treatment on flowering uniformity in *Hatiora gaertneri* 'Jan' and *H.* ×*graeseri* 'Evita'. Bubble size was determined by (percentage of plants flowering) × (percentage of apical phylloclades flowering). The maximum value in each cultivar is labeled as a reference. SD = short-day photoperiods. [a]Treatment value is significantly different from maximum value within the cultivar and column (χ^2, α = 0.05, 1 degree of freedom). [1]Treatment value is significantly different from maximum value within the cultivar and row (χ^2, α = 0.05, 1 degree of freedom).

Number of BFAP increased as the duration of vernalization increased at all three temperatures (Fig. 3). The effect of SD on BFAP before vernalization was significant only on 10 °C vernalization treatments. Plants given SD for 6 weeks and vernalized for 6 or 8 weeks at 10 °C had ≈0.4 more BFAP than if no SD treatment was provided before vernalization.

Time to flower was influenced by vernalization duration and temperature (Table 1). 'Jan' vernalized at 10 or 12.5 °C for 6 or 8 weeks flowered on average 3 d earlier than plants vernalized at 15 °C for 6 or 8 weeks. 'Jan' given 2 to 6 weeks of SD before vernalization flowered an average of 2 d earlier than plants given no SD before vernalization, but there was a significant interaction with duration of vernalization. Plants vernalized at 10 °C for 8 weeks flowered 8 to 21 d earlier than plants vernalized at 15 °C for 4 weeks.

Expt. 3

All 'Jan' and 'Evita' plants flowered after 8 weeks of vernalization at 12.5 °C with a higher PFAP and more BFAP than plants vernalized for 4 weeks (Table 2). Plants prevernalized in SD for 6 weeks had a higher PFAP than plants prevernalized for 4 weeks. Plants vernalized for 8 weeks tended to flower earlier than plants vernalized for 4 weeks, although there were significant cultivar-specific interactions. 'Evita' flowered more than 3 d earlier when prevernalization photoperiod was 10 h compared with 11 h.

Expt. 4

Plants propagated earlier in the year generally had higher flowering uniformity as shown by a larger flowering index (Fig. 4). Plants not leveled or leveled before SD flowered most uniformly. Uniformity was very low for plants leveled during vernalization. 'Jan' flowered more uniformly than 'Evita'.

The number of buds per flowering apical phylloclade (BPFAP) was generally highest for plants propagated in April (Table 3). 'Evita' had fewer buds per flowering phylloclade than 'Jan', although the difference was small. Number of buds per flowering phylloclade was generally highest for plants leveled before SD or not at all. Plants propagated in July flowered later than plants propagated earlier for comparable leveling treatments.

Expt. 5

Dark vernalization at 0 or 2.5 °C killed the plants (data not shown) or did not substantially promote flowering (Table 4). 'Jan' had a higher PFAP (48%) than 'Evita' (32%) and 'Jan' took an average of 2 d longer to flower. Three, and especially 6 weeks, of short days before dark vernalization increased the percentage of plants flowering in most treatments, PFAP, and BFAP. Vernalization temperature did not affect the percentage of phylloclades flowering or BPFAP. Maximum flowering (100% of plants flowering and 38% to 46% of apical phylloclades flowering) was achieved with 3 weeks of SD followed by 56 d of vernalization at 5 °C or 6 weeks of SD followed by 56 d of vernalization at 10 °C.

Discussion

Our first objective was to study the effects of photoperiod before vernalization and DLI before and during vernalization on flowering of *Hatiora*. We accomplished this by treating *H. gaertneri* 'Jan' with LD or SD photoperiods for 6 weeks before vernalization, five vernalization temperatures (from 7.5 to 17.5 °C), and low or high DLI before and during vernalization. Our research supports previous reports of *Hatiora* flowering as a short–long-day plants (Boyle, 1991; Peters and Rünger, 1971; Rünger, 1960), but flowering was enhanced after a 10 to 15 °C treatment during or instead of the SD phase (Fig. 1).

Phylloclade temperature may exceed vernalizing air temperature under high irradiance. A thermocouple placed in the apical areole of a single *H.* ×*graeseri* plant recorded average hourly temperatures consistently above the measured air temperature throughout an 8-d period in June 2002. The difference between plant and air temperature increased as *PPF* increased with a maximum difference of 14.7 °C (data not shown). The shoot temperature of many cacti has been recorded to be 15 °C or greater above ambient air temperature because of the closed stomata of crassulacean acid metabolism plants during the daytime and high-heat storage capacity caused by succulence, among other factors (Nobel, 1988). In our experiments, high DLI during vernalization, provided with HPS lamps, reduced all flowering responses at 15 °C compared with 12.5 °C or less (Fig. 1). The results of Expt. 5 show that light is not an absolute requirement during vernalization, and we have shown that supplemental light

Table 3. Effects of propagation date and leveling date on buds per flowering apical phylloclade and days to flower in flowering *Hatiora gaertneri* Jan and *H.* ×*graeseri* Evita.[z]

Propagation date and leveling treatment	Buds per flowering apical phylloclade		Days to flower[y]	
	Jan	Evita	Jan	Evita
April				
Control	1.5 (94)	1.4 (80)	56	52
47 d before SD[x]	1.6 (88)	1.2 (67)	56	55
10 d into SD	1.2 (61)	1.4 (29)	56	54
10 d into vernalization	1.3 (10)	1.3 (33)	58	55
May				
Control	1.4 (78)	1.2 (44)	55	53
47 d before SD	1.3 (61)	1.1 (63)	56	53
10 d into SD	1.4 (33)	1.1 (24)	57	56
10 d into vernalization	1.0 (13)	1.0 (4)	60	61
June				
Control	1.5 (85)	1.2 (57)	53	54
47 d before SD	1.5 (47)	1.3 (16)	58	55
10 d into SD	1.2 (48)	1.0 (35)	57	58
10 d into vernalization	1.0 (3)	1.0 (4)	56	53
July				
Control	1.3 (18)	1.0 (12)	58	61
10 d into SD	1.3 (41)	1.0 (2)	56	67
10 d into vernalization[w]	0.0 (0)	0.0 (0)	—	—
Significance				
Propagation date (P)	*		*	
Leveling treatment (L)	*		***	
Cultivar (CV)	*		NS	
P × L	NS		NS	
P × CV	NS		NS	
L × CV	NS		*	
P × L × CV	NS		*	

[z]Values in parentheses indicate the percentage of apical phylloclades flowering in the treatment.
[y]Days to flower from the start of forcing (long days at 20 °C), flowering plants only. Statistical analysis includes all plants.
[x]Six weeks of short-day (10-h) photoperiods given before vernalization.
[w]No flowering plants in this treatment.
[NS,*,***]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

during vernalization does not increase horticultural quality (Fig. 1). Therefore, reducing the *PPF* intercepted by the plants during vernalization may improve flowering by limiting the increase of plant temperature above air temperature caused by increased solar gain.

Our second objective was to identify combinations of SD treatments before vernalization and vernalization treatments that increase flowering uniformity and BFAP. We accomplished this by treating *H. gaertneri* 'Jan' and 'Rood' with 0, 2, 4, or 6 weeks of SD followed by 2, 4, 6, or 8 weeks of vernalization at 7.5, 10, or 12.5 °C. Our research supports previous reports (Boyle, 1991; Peters and Rünger, 1971; Rünger, 1960) that extending the duration of inductive conditions, either with SD or low temperatures, enhanced flowering uniformity in *Hatiora* (Fig. 2). Marginal thermoinductive conditions (15 °C) yielded poor flowering uniformity unless an extended SD prevernalization treatment was given (Fig. 2). This illustrates the necessity of SD before vernalization under natural SD photoperiods if temperatures are higher than those for optimum vernalization (12.5 °C or greater).

The response to vernalization is considered quantitative in many plants (Lang, 1965), including *Hatiora*. Seventy-five percent of apical phylloclades flowered on *H. gaertneri* vernalized for 80 d at 10 °C, and only 46% flowered on plants vernalized for 60 d (Peters and Rünger, 1971). An increase in the duration of vernalization at 10 °C from 50 to 70 d increased the percentage of plants flowering from 79% to 96% and increased the PFAP from 8% to 55% in *H.* ×*graeseri* (Rünger, 1960). Within a *Hatiora* crop, flowering response to vernalization is certainly quantitative. If a plant flowers, it may flower on a single phylloclade or it may flower on all phylloclades. If a phylloclade forms flowers, it may have one flower or it may have numerous flowers. The horticultural quality of a plant improves as the PFAP and the number of BFAP increase. Increased horticultural quality increases the value of the plants, and increasing vernalization or inductive treatments increases horticultural quality of *Hatiora*.

Prevernalization SD treatment under optimal vernalization conditions improved flowering by increasing 1) flowering uniformity (Figs. 1 and 2); 2) the number of BFAP (Fig. 3); and 3) the number of buds above the minimum possible (data not shown). In Expt. 2, plants with more than 90% of apical phylloclades flowering and more than two BFAP (one more bud than the minimum, 37 plants total) were vernalized for 6 or 8 weeks at 10 or 12.5 °C with the exception of one plant vernalized at 15 °C (data not shown). The majority (62%) of these plants with favorable horticultural flowering characteristics were given 4 or 6 weeks of SD before vernalization, and 86% were given 2, 4, or 6 weeks of SD.

Our third objective was to observe differences in flowering after exposure to two different photoperiods of SD treatment before vernalization. We accomplished this by treating *H. gaertneri* 'Jan' and *H.* ×*graeseri* 'Evita' with 10- or 11-h SD before 4 or 8 weeks of vernalization. Differences in flowering responses were mainly the result of differences in duration of vernalization. Numerous treatment interactions affected time to flower.

It is likely that *Hatiora* responds to low *PPF* during part or all of civil twilight, effectively extending natural daylengths beyond sunrise to sunset. Photon fluence rates have been measured from ≈13 to 0.007 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during civil twilight (the period starting in the morning or ending in the evening when the sun reaches 6° below the horizon) depending on weather conditions (Kishida, 1989). Similar low fluence rates cause photoperiodic responses in many plants (Cockshull, 1984; Hughes et al., 1984; Whitman et al., 1998). Daylength, including civil twilight, does not reach 12 h until ≈16 Oct. or 11 h until ≈8 Nov. at lat. 42°45′N (East Lansing, MI) (Astronomical Almanac for the Year 2002, 2000). Given that the critical photoperiod for photoinduction is 11 to 12 h (Boyle, 1991), naturally photoinductive conditions for *Hatiora* are probably not reached until mid-October to early November in East Lansing, MI. If vernalization is to begin before this time, i.e., for early-season crops, or if temperatures are insufficient for vernalization, there are apparent benefits of SD treatment before vernalization to extend the induction period.

Our fourth objective was to identify propagation and leveling treatments that increase uniformity and BFAP. To accomplish this, we propagated *H. gaertneri* 'Jan' and *H.* ×*graeseri* 'Evita' over a span of 4 months and leveled the plants during different developmental stages. We then prevernalized the plants under SD for 6 weeks and vernalized them for 4 weeks. The plants were leveled before or during prevernalization SD or during vernalization.

It has been recommended to level *Hatiora* before induction for uniformity or a more compact shape if necessary (Boyle and Stimart, 1989; Nell, 1988), allowing a new set of phylloclades to reach 75% maximum size before vernalization begins (Boyle, 1997). Our data support the recommendation that additional vernalization is necessary if plants are leveled during vernalization (Nell, 1988). The low uniformity observed in 'Jan' and 'Evita' leveled during 4 weeks of vernalization (Fig. 4) suggests that apical phylloclades respond to vernalization more quickly than subtending phylloclades or that the process of leveling significantly damages meristems in subtending phylloclades. Flower primordia do not form on photoinduced *H. gaertneri* until after the SD phase of photoinduction (Boyle et al., 1994), so leveling during vernalization probably does not remove flower buds directly.

Table 4. Flowering of *Hatiora gaertneri* Jan and *H.* ×*graeseri* Evita vernalized in a dark cooler at 0, 5, 7.5, or 10 °C for 23 or 56 d.

Vernalization conditions and SD duration (weeks)[z]	Plants flowering (%)[w]		Apical phylloclades flowering (%)[y]		Buds per flowering apical phylloclade		Days to flower[x]	
	Jan	Evita	Jan	Evita	Jan	Evita	Jan	Evita
0 °C								
23-d vernalization								
0 weeks' SD	0	0	0	0	0.0	0.0	—[v]	—
3 weeks' SD	0	0	0	0	0.0	0.0	—	—
6 weeks' SD	14	29	37	4	1.1	1.3	—	—
56-d vernalization								
0 weeks' SD	0	0	0	0	0.0	0.0	—	—
3 weeks' SD	14	0	9	0	1.0	0.0	53	—
6 weeks' SD	43	0	45	0	1.1	0.0	52	—
5 °C								
23-d vernalization								
0 weeks' SD	0	14	0	4	0.0	1.0	—	—
3 weeks' SD	43	14	5	27	1.0	1.2	61	51
6 weeks' SD	86	86	32	13	1.1	1.2	55	55
56-d vernalization								
0 weeks' SD	71	17	17	5	1.1	1.0	51	49
3 weeks' SD	100	100	46	38	1.3	1.4	51	47
6 weeks' SD	100	71	54	35	1.4	1.2	51	46
7.5 °C								
23-d vernalization								
0 weeks' SD	29	0	7	0	1.0	0.0	57	—
3 weeks' SD	86	57	29	8	1.5	1.2	51	55
6 weeks' SD	86	71	43	17	1.3	1.2	52	52
56-d vernalization								
0 weeks' SD	86	14	31	5	1.2	1.0	50	50
3 weeks' SD	100	83	39	33	1.2	1.3	51	45
6 weeks' SD	100	57	39	32	1.2	1.2	49	48
10 °C								
23-d vernalization								
0 weeks' SD	0	0	0	0	0.0	0.0	—	—
3 weeks' SD	100	57	36	18	1.2	1.1	54	55
6 weeks' SD	100	86	43	18	1.3	1.3	52	52
56-d vernalization								
0 weeks' SD	17	29	20	11	1.1	1.3	56	52
3 weeks' SD	100	86	33	22	1.4	1.5	50	51
6 weeks' SD	100	100	46	39	1.3	1.4	48	44
Significance[u]								
Cultivar (CV)			*		*		—	
SD duration (SD)			***		*		***	*
Vernalization duration (VD)			*		*		*	NS
Temperature (T)			NS		NS		***	*

[z]Plants were given 0, 3, or 6 weeks of short days (SD) before vernalization. No plants flowered after 2.5 °C vernalization.
[y]Data include flowering plants only.
[x]Days to flower from the start of forcing (long days at 20 °C), flowering plants only. Statistical analysis includes all plants.
[w]All treatments with less than 100% flowering are significantly less than 99% flowering by a one-sample binomial test ($\alpha = 0.05$).
[v]No flowering plants or flowering took longer than 70 d.
[u]No interactions were significant for any response at $\alpha = 0.05$.
[NS,*,***]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Hatiora gaertneri 'Jan' that were leveled 14 d after vernalization began and were vernalized for 8 weeks at 10 °C showed similar uniformity (Fig. 2) to 'Jan' leveled 47 d before prevernalization SD were begun or not leveled at all and vernalized for only 4 weeks (Fig. 4). We can conclude that fewer than 8 weeks of vernalization would be necessary in growing conditions similar those in Expts. 1, 2, and 3 to achieve a strong flowering response similar to that in Expts. 1, 2, and 3 if the plants are not leveled or are leveled before SDs are begun.

Our fifth objective was to determine the effects on flowering of SD treatment followed by dark vernalization in a cooler. To accomplish this, we treated *H. gaertneri* 'Jan' and *H.* ×*graeseri* 'Evita' with SD for 3 or 6 weeks and then we vernalized the plants from 0 to 10 °C in darkness for 23 or 56 d. Data presented here show that *Hatiora* flowered marginally when cooled in darkness (Table 4) in contrast to previous work that showed *H. gaertneri* failed to flower if vernalized for 60 to 80 d in constant darkness at 10 °C (Peters and Rünger, 1971). Prevernalizing the plants with SD increased the PFAP and BFAP after dark vernalization (Table 4). Increasing the prevernalization SD and vernalization duration also increased the percentage of plants flowering in most dark treatments. Vernalization at 5, 7.5, and 10 °C was equally ineffective at creating horticulturally desirable plants. Although many plants flowered, the horticultural quality of all plants was low after dark vernalization in a cooler. Future research may show that flowering of *Hatiora* vernalized in a cooler is improved by vernalization in the light of a greenhouse before or after the dark vernalization period or by providing a minimum *PPF* in the cooler.

Poor flowering in coolers at 0 to 10 °C vernalization may be a result of suboptimal temperatures in combination with no light. In previous research, a vernalization temperature of 11 or 14 °C was more effective than 5 or 8 °C (Peters and Rünger, 1971). It is possible that 5 to 10 °C is suboptimal for dark vernalization of *Hatiora*, although 'Jan' vernalized in a greenhouse at 7.5 °C under low DLI ($\approx$4 mol·m^{-2}·d^{-1}; Fig. 1) flowered completely and uniformly, especially when grown under SD before vernalization. It was previously shown that *H.* ×*graeseri* vernalized at 5 °C flowered (Rünger, 1960), but this treatment was preceded by 50 d of 15 °C, which may have vernalized or preconditioned the plants for vernalization at 5 °C. The differences between our research and

previous reports are likely the result of cultivar differences and experimental conditions, including light intensity and photoperiod.

High irradiance or availability of adequate nutrition and sucrose may substitute for or act similarly to vernalization in some plants (Napp-Zinn, 1984; Roldán et al., 1999). In some plants, flower initiation is profoundly influenced by availability of accumulated assimilates (Bernier et al., 1993; Bodson and Bernier, 1985). For example, onion (*Allium cepa* L.) with high carbohydrate levels before vernalization initiated flowers more rapidly after vernalization than plants with low prevernalization levels of carbohydrates (Brewster, 1985). It has been suggested that new vegetative growth in *H. gaertneri* is supported by translocation of carbon from older tissue (Boyle, 1992). We have shown that high irradiance in combination with SD before vernalization increases PFAP and BFAP in *Hatiora* (Fig. 1). Flowering after vernalization in darkness could be improved by high irradiance before vernalization, after it, or both, but additional studies are warranted to test this theory. SDs before vernalization improved the flowering response in a greenhouse or in a dark cooler. Short days may act as a preconditioning treatment by directing assimilates to storage rather than growth processes.

Increased duration of vernalization and prevernalization SD, to a lesser extent, generally hastened flower initiation, evocation, or development under LD (Tables 1, 2, and 4). Plants given 6 weeks of 10-h prevernalization SD flowered 4 d faster than plants given 11-h SD (Table 2). These data show that subsequent forcing time may be reduced by extended induction duration and sufficiently short photoperiods.

Hatiora gaertneri and *H.* ×*graeseri* performed differently in our experiments. *Hatiora gaertneri* 'Jan' flowered more uniformly or with a higher PFAP than *H.* ×*graeseri* 'Evita' in Expts. 4 and 5 (Table 4; Fig. 4) and with more BFAP in Expt. 4 (Table 3). *Hatiora* ×*graeseri* is an interspecific hybrid between *H. gaertneri* and *H. rosea* (Barthlott and Taylor, 1995). *Hatiora rosea* is native to higher altitudes than *H. gaertneri* (Barthlott and Taylor, 1995) and has a greater requirement for vernalization than *H. gaertneri* (Boyle, 1990, 1995). Three late-flowering *H.* ×*graeseri* cultivars ('5805', 'Phoenix', and 'Capella') also flowered poorly under nonideal inductive conditions (data not presented). The *H. rosea* parentage of 'Evita' helps explain the relatively weaker flowering of 'Evita' compared with that of 'Jan' and supports previous research indicating strong genotype × environment interactions for flowering in *Hatiora* (Boyle, 1995).

Flowering requirements of *Hatiora* are comparable to a number of noncactus plants. Other plants with similar short–long-day flowering activity in which SD may be replaced or enhanced by vernalization include *Campanula medium* (Wellensiek, 1960, 1985), *Coreopsis grandflora* (Ketellapper and Barbaro, 1966; Runkle, 1996), *Echinacea purpurea* (Heide, 2004), *Dactylis glomerata* (Heide, 1987), *Festuca rubra* (Heide, 1990), and other temperate grasses (Heide, 1994). The critical temperature for heading in *Festuca pratensis* was 15 °C under SD and 12 °C under LD (followed by LD) (Heide, 1988), which is very similar to *Hatiora*. *Trifolium repens* (Thomas, 1961) and *Echeveria harmsii* (Rünger, 1962) also have shown short–long-day flowering requirements.

These data, in combination with previous research, confirm that uniform flowering of *Hatiora* requires a rather specific sequence of environmental conditions and cultural practices. First, the flowering response of older plants is greater than younger plants, although *Hatiora* are vegetatively propagated and juvenility should not be an issue. Short days for 4 to 6 weeks followed by vernalization at 7.5 to 12.5 °C promote flower induction. Flower development is then favored by forcing plants under LD at moderate temperatures of 17 to 20 °C for 7 weeks. Sale of uniform flowering plants requires 17 to 21 weeks from the start of the SD inductive process.

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