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ABSTRACT

FLOWERING PHYSIOLOGY OF *HATIORA*

By

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Hatiora, or Easter cactus, is a tropical epiphyte sold as a flowering potted plant from mid-winter through spring. Plants can be induced to flower as early as January, but the plants may be of poor horticultural quality. Flower induction for crops sold in January must begin in October, but environmental conditions at this time may not sufficiently fulfill the unique flower induction requirements for *Hatiora*. Studies presented here examined the interactive effects of photoperiod, light sum, and daylength before vernalization, and vernalization temperature, vernalization light sum, and vernalization duration on *Hatiora* flowering. A four- to six-week short-day treatment and elevated daily light integral (≈10 $\mu mol \cdot m^{-2} \cdot s^{-1}$) before six to eight weeks of vernalization at 7.5 to 12.5 °C were optimal for uniform and rapid flowering. It was also discovered that vernalization in darkness was effective and may be a useful method to extend the season. The effects on flowering of propagation date and apical phylloclade removal were also studied. Plants vegetatively propagated in April flowered better than plants propagated in later months. Flowering was reduced by removal of apical phylloclades during inductive treatments.

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LITERATURE REVIEW

Introduction

Hatiora spp. are epiphytic cacti native to tropical Brazil. They are sold as a flowering potted crop from March to May in the United States, and are one of the few dual-photoperiod floriculture crops grown, although a vernalization-long-day sequence is more often used to induce flowering than a short-/long-day (SLD) sequence. Northern European producers grow upwards of 5 million pots of *Hatiora* for sale beginning in mid-January but sometimes encounter difficulties with nonuniformity of flowering at these early dates. This problem could be due to a combination of insufficient temperature control and insufficiently short photoperiods during the early stages of induction. Current taxonomic opinions, production methods and their scientific basis, so-called natural photoperiods, and a brief description of other SLD plants (SLDP) are presented here.

Nomenclature and Biogeography of Easter Cactus

Easter cacti (*Hatiora*), also called spring cacti, belong to a group of epiphytic shrubs native to the southeastern Brazilian states of Paraná and Santa Catarina (Barthlott, 1983; Barthlott and Taylor, 1995). These cacti are members of Cactaceae, tribe Rhipsalideae. Other genera in this tribe include *Lepismium*, *Pseudorhipsalis*, *Rhipsalis*, and *Schlumbergera* (Barthlott, 1987; Barthlott and Taylor, 1995).

Nomenclature of Easter cactus has changed in recent years. Growers often still refer to the genus as *Rhipsalidopsis* or *Rhipsalis*, as cited in *Hortus Third* (Bailey, 1976). *Hatiora* is now considered the correct genus for Easter

cactus, although *Rhipsalidopsis* is still considered an acceptable synonym (Barthlott and Taylor, 1995). *Rhipsalis* is a separate genus generally containing cacti that have more lateral flowers, which are typically whitish or yellow, unlike the predominantly terminal *Hatiora* flowers, which are typically shades of pink, orange, or red. *Rhipsalis* stems are more often terete than flat or angled, although two subgenera, *Phyllarthrorhipsalis* and *Epallagogonium*, are lateral-flowering *Rhipsalis* characterized by flat stems. *Rhipsalis* and *Schlumbergera* are closely related to *Hatiora* (Barthlott, 1979; Barthlott and Taylor, 1995).

Most recently and more accurately, Easter cacti have been properly labeled as species of *Hatiora* by botanical, scientific, and educational literature (Barthlott and Taylor, 1995; Dole and Wilkins, 1999; Karle and Boyle, 1999). *Rhipsalidopsis* is the subgenus including *Hatiora*. Therefore, referring to Easter cactus as *Rhipsalidopsis* may be correct, but this nomenclature includes *H. epiphylloides*, a nearly extinct relative. The two other species in the *Rhipsalidopsis* subgenus are *H. gaertneri* and *H. rosea* (Barthlott and Taylor, 1995).

Hybrids of *H. gaertneri* and *H. rosea* are labeled *H. ×graeseri*. *Hatiora gaertneri* and, more commonly, *H. ×graeseri*, are the typical Easter cacti cultivated today (Barthlott, 1979; Boyle, 1990; Boyle, personal communication). *Hatiora* naturally flowers in the spring (Bailey, 1976). *Hatiora rosea* typically flowers later in the season than *H. gaertneri* and may therefore be referred to as Mother's Day cactus. Phylloclades of *H. rosea* are smaller than those of *H.*

gaertneri. Flowers of *H. rosea* are usually smaller and show lighter pastel colors, unlike the red flowers of *H. gaertneri* (Barthlott and Taylor, 1995).

The native habitat of *Hatiora* species is reflected in their flowering requirements. Thermoinduction requirements are greater for *H. rosea* than *H. gaertneri* or *H.* ×*graeseri* (Boyle, 1990), although many *H.* ×*graeseri* clones also flower poorly without a vernalizing treatment (Boyle, 1995b). In its native Brazilian habitat, *H. gaertneri* is found at altitudes of 350 to 1300 m, whereas *H. rosea* is native to 1000 to 2000 m (Barthlott and Taylor, 1995). Plants native to the higher altitudes are likely to have a stronger vernalization requirement than plants native to lower, more temperate altitudes, which seems to be the case for *H. rosea* (Boyle, 1990; Wilkins and Rünger, 1985).

Photoperiodic flowering of *Hatiora* is not as strong as flowering after a vernalizing treatment, but some cultivars flower as SLDP at nonvernalizing temperatures. The photoperiodic nature of these cacti may be a remnant of photoperiodic flowering in ancestral species of desert cacti. The response to vernalization may then be considered an evolutionary adaptation to higher altitudes. This remnant short-day (SD) response is similar to the response of the high-arctic SLD grasses *Poa pratensis* and *Cerastium regelii* (Heide, 1994). The shortest civil daylength reached in the Panará and Santa Catarina region (lat. ≈26°S) is 11 h 28 min (Fig. 1, p. 22), and the most current research shows that the critical SD photoperiod for *Hatiora* is between 11 and 12 h (Boyle, 1991).

Schlumbergera truncata and *S.* ×*buckleyi*, the Thanksgiving and Christmas cacti, respectively, are also popular potted members of the

Rhipsalideae tribe (Barthlott and Taylor, 1995). *Schlumbergera* flowers are zygomorphic with a well-developed perianth tube. Vegetative stems of *S. truncata* are noticeably more serrate-dentate than those of either *S.* ×*buckleyi* or *Hatiora*. *Schlumbergera* lack dependence on long days (LD) for profuse flowering, which is contrary to the actinomorphic flowers and LD requirement of *Hatiora* (Boyle, 1991; Boyle et al., 1988; Dole and Wilkins, 1999). Optimum night temperature for flower initiation in *S. truncata* is 15 to 20 °C, which is 5 to10 °C higher than for induction in *Hatiora* (Boyle, 1991; Erwin et al., 1990; Peters and Rünger, 1971).

The *Hatiora* cultivars under experimentation at Michigan State University include 'Jan' (large red flowers, pronounced and separated stigmatic lobes, slightly elongated phylloclades, often reddish new growth), 'Rood' (small darker red flowers, stigmatic lobes often closed and erect, more rounded phylloclades, dark-red new growth), 'Evita' (pink flowers, phylloclades similar to those of 'Jan' except that new growth is often yellowish, poor branching and horizontal growth habit under insufficient light), and 'Rose' (pink flowers, small phylloclades that are easily separated from the mother plant, petals often twisted when open, prolific branching). Taxonomic status of these cultivars is unclear because of extensive breeding, but the following is estimated for each cultivar according to flower color and structure, vegetative habit, and information provided by Thomas Boyle (personal communication) and Han and Boyle (1996): 'Jan' and 'Rood' are *H. gaertneri* (Regel) Barthlott, and 'Evita' and 'Rose' are *H.* ×*graeseri* (Werdermann)

Barthlott. To the best knowledge of the author, no pure *H. rosea* (Lagerheim) Barthlott plants were studied at Michigan State University.

Production Methods for *Hatiora gaertneri* and *H. ×graeseri*

Propagation

Hatiora phylloclades are easily harvested and rooted. Rather than a single phylloclade's being propagated, a series of adjoining phylloclades may be propagated from cultivars with small phylloclades (Boyle, 1995b). Propagation typically occurs from 8 to 12 months before sale (Boyle and Stimart, 1989). Mature phylloclades are twisted off stock plants or plants that are leveled for production purposes (described later). Ethylene and ethephon [(2-chloroethyl)phosphonic acid] have been used experimentally to induce phylloclade abscission for propagation. Ethephon concentrations ≥1250 $\mu L \cdot L^{-1}$ caused phylloclade abscission (33 to 99%), and ≥2500 $\mu L \cdot L^{-1}$ caused phytotoxicity on abscised phylloclades (2 to 78%) (Han and Nobel, 1995). A 7-d treatment with ethylene at 20 $\mu L \cdot L^{-1}$ also caused phylloclade abscission and phytotoxicity on abscised pylloclades but did not affect new growth from remnant phylloclades. The ethephon caused phytotoxicity on new aerial growth, whereas the ethylene did not. Therefore, the acidity of the ethephon solution was considered phytotoxic to new growth (Han and Nobel, 1995). Propagule root length and number were also reduced by treatment with ethephon (Han and Nobel, 1995).

Stock plants require no special treatment, but keeping them disease-free is important. Stock plants are grown at 8 to 10 °C if possible to moderate their vegetative growth (Hans de Vries, personal communication). When cuttings are taken, phylloclades close to the soil should be avoided because they are more likely to carry diseases (Dole and Wilkins, 1999). Mother plants may be treated with a broad-spectrum fungicide, such as iprodine or chlorothalonil, 1 d before cuttings are harvested to reduce losses caused by *Fusarium* in storage or during propagation (Hans de Vries, personal communication). It may be advantageous to let fresh cuttings dry for about two weeks at 13°C to allow callus tissue to form. Cuttings may be stored in a cooler at 13 °C and approximately 90% relative humidity for up to six months (Hans de Vries and Jørn Hansson, personal communication). Losses to disease also may be reduced by soaking the cuttings immediately before planting in a 1.5% bleach solution (volume commercial bleach:volume water) for 15 minutes and then rinsing the pads in water (PKM, personal communication). In addition, treatment of *Hatiora* propagules with benomyl or chlorothalonil reduced infection of plants in *Fusarium*-inoculated soil (Mitchell, 1987).

Phylloclades are easily rooted under standard or relatively dry propagation conditions. Two to three phylloclades are stuck in plug trays or directly in pots. During rooting, medium temperature should be 21 to 26 °C, and watering may be provided by intermittent mist or by hand. Excess water during rooting will limit strong root growth. *Hatiora* may be propagated under natural daylengths. The

first flower bud or phylloclade to form on a cutting should be removed when it is large enough to handle to promote branching.

Depending on rooting and growing temperature, plugs may be transplanted after 6 to 16 weeks. Transplant-ready plugs should have two tiers of pads, including the original (Boyle and Stimart, 1989; Hans de Vries, personal communication). If plants are left in propagation trays too long, poor branching may result (Jørn Hansson, personal communication). Larger plants should be twisted to two tiers before transplant (Hans de Vries, personal communication).

Nutrition, water, light, and temperature

Media and nutrition requirements for *Hatiora* are not unique, but there are distinctions worth mentioning. Well-drained peat-based medium is used throughout production. Moderate fertilization (N at 125-200 ppm) should commence when roots reach the side of the container. High Mg requirements have been reported for *Hatiora* (Dole and Wilkins, 1999), and fertilizer may be supplemented with $MgSO_4$, which creates a darker green plant (Jørn Hansson, personal communication). However, twice the normal level of Mg (amount unspecified) did not increase the number of flowers or the amount of dry matter accumulation (Penningsfeld, 1972). The best dry-matter production was achieved with fertility programs of twice the level of K (amount not specified) or no added Zn (Penningsfeld, 1972). To slow vegetative growth, all fertilization may be terminated one to two months before flower induction begins (Dole and

Wilkins, 1999) and may be eliminated during induction and forcing until buds are visible (PKM, personal communication).

Micronutrient nutrition may require special attention. Media pH is maintained above 5.7 (Nell, 1988) or 6 (Hans de Vries, personal communication) to avoid micronutrient (Fe and Mn) toxicity, which manifests itself as discolored phylloclade margins. Twice the normal level of B (amount unspecified) significantly increased flower number and dry matter accumulation of *Hatiora* when used in a full fertility regimen (Penningsfeld, 1972). Compared with *Fuschia ×hybrida*, *Chrysanthemum indicum* 'Yellow Delaware', and *Primula obconica* 'Bayernblut', *Hatiora gaertneri* showed a relatively high accumulation of Zn and Mo (>100 ppm and 5.2-6.3 ppm, respectively) without noticeable toxicity (Penningsfeld, 1972). Plants grown in 50% peat and fertilized without microelements showed no significant change in number of flowers or dry matter accumulation compared with those grown under a control fertility program with micronutrients added (Penningsfeld, 1972). Therefore, commercial producers may choose not to add micronutrients (PKM, personal communication).

Plants should be allowed to dry slightly between waterings, but they should not be allowed to wilt, especially during forcing (after vernalization). Excess water will encourage weak, rapid vegetative growth (Nell, 1988; PKM, personal communication).

Shade is usually necessary for growth in the summer. A maximum of about 3500 foot-candles (700 $\mu mol \cdot m^{-2} \cdot s^{-1}$) is recommended (Dole and Wilkins, 1999). High light coupled with high temperatures will cause phylloclades to

become chlorotic and abscise (personal observation; Dole and Wilkins, 1999). Too little light causes weak and spindly branching and low bud count (Boyle and Stimart, 1989; Nell, 1988).

Growing temperatures are moderate (18-24 °C) prior to induction. Photoperiod and temperature interact during flower induction of *Hatiora*; this is explained later under "Control of Flowering." Growers of *Hatiora* typically cool plants (≤10 °C if possible) for 9 to 10 weeks, beginning in October or when temperatures are cool enough. This procedure is followed by 16-hour LDs or night-interruption (NI) lighting at 18 to 22 °C if natural daylengths are insufficient for an adequate response (daylength during forcing is described later) (Dole and Wilkins, 1999; PKM, personal communication).

Leveling and spacing

Leveling is done to increase branching and create a more uniform plant. Plants are leveled (pinched or twisted) approximately six weeks before cold treatments are begun, if necessary. A new tier of phylloclades will grow after leveling, and when these reach ≈75% of their maximum size, induction may begin (Boyle, 1997; Jørn Hansson, personal communication). Depending on the growing temperature, one new phylloclade forms in approximately six weeks under LD conditions. Plants are usually leveled to two to four phylloclades. More tiers are left on cultivars with smaller phylloclades or on plants in larger pots. It is important not to damage subtending phylloclades when leveling plants

because the areolar meristem is the location of new reproductive and vegetative growth.

Plants may be grown pot to pot for the duration of the growing season. Some growers choose to give plants 25% more space approximately four weeks before beginning flower induction if space is available (Jørn Hansson, personal communication). For a 4-inch pot, this spacing is from 97 pots/m^2 to 77 pots/m^2.

Plant growth regulators

The use of plant growth regulators in *Hatiora* production systems is limited, but the effects of gibberellic acid (GA_3) and benzyladenine (BA) have been researched. Data show that GA_3 at 5 to 500 mg•L^{-1} applied to *Hatiora gaertneri* reduced the percentage of apical phylloclades flowering, buds per flowering phylloclade, and number of buds per plant in favor of new phylloclade formation (Boyle et al., 1994). Application before or at the beginning of LDs (during SDs) was more detrimental to flowering than application after LD were started. One application of GA at 5 mg•L^{-1} hastened flower development by 5 d when applied to 1- to 2-mm-long buds (Boyle et al., 1994). Explants grown in medium supplemented with 0.3 to 289 µM GA_3 (harvested after SD treatment for flowering) also showed a reduced number of flower buds compared with untreated explants (Boyle and Marcotrigiano, 1997).

Benzyladenine increases organ formation in *Hatiora gaertneri*. It increased the number of new phylloclades in vegetative plants or explants and the number of flower buds in reproductive plants (Boyle, 1992; Boyle and

Marcotrigiano, 1997; Boyle et al., 1988). Application of BA (200-1000 $mg \cdot L^{-1}$) at 27, 37, or 47 d after planting had no influence on the number of apical phylloclades on the plant at 316 d after planting, but there were a greater number of tertiary (3°) phylloclades [propagated phylloclade = primary (1°)] in treated plants (Boyle, 1992). Multiple applications of BA at 200 $mg \cdot L^{-1}$ increased the number of secondary (2°) phylloclades more than single applications of higher concentrations. Benzyladenine applied to three- or six-month-old plants more successfully increased branching and the number of apical phylloclades than application to recently rooted phylloclades (Boyle, 1992). Application of BA at >50 $mg \cdot L^{-1}$ to plants 12 d after forcing treatments were begun increased the number of buds per plant (from 48 to 89 maximum), number of buds reaching anthesis (from 45 to 71 maximum), number of buds per flowering phylloclade (from 2.1 to 3.4 maximum), nonapical phylloclades flowering (from 1.3 to 1.9 maximum), and percentage of aborted buds (from 6 to 20% maximum) (Boyle, 1995a). Most aborted buds were reported to be small (<1 cm). Benzyladenine did not increase the percentage of apical phylloclades flowering, and BA at 10 $mg \cdot L^{-1}$ had little effect (Boyle, 1995a). Abortion of flower buds on BA-treated plants was not reduced with silver thiosulfate treatment (Boyle et al., 1988). Silver thiosulfate (2 mM) was shown to decrease bud abscission in plants with small buds (<2.6 cm) or medium buds when applied one week before exposure to ethylene (0.5 $\mu L \cdot L^{-1}$).

Control of Flowering in Easter Cactus

Botanically, Easter cacti are short-long-day plants (SLDPs) for flowering (Dole and Wilkins, 1999; Rünger, 1960). Using photoperiod to control flowering is termed *photoinduction*. The SD phase of induction may be substituted with a cold treatment (Boyle, 1991; Boyle and Stimart, 1989; Dole and Wilkins, 1999), a process called *thermoinduction*. Photoinduction, although useful for breeding purposes, is generally weaker than thermoinduction.

Photoinduction

Easter cactus is considered an SLDP for flowering at 15 to 20 °C (Boyle, 1991; Boyle et al., 1988; Dole and Wilkins, 1999; Peters and Rünger, 1971 Rünger, 1960). *Hatiora gaertneri* 'Crimson Giant' given two, four, six, or eight weeks of SDs (starting 11 Sept.) followed by 14-h LDs at 18 °C night temperature responded with 100% of plants flowering, 1.3 to 1.7 buds per flowering apical phylloclade (BPFAP), and 71 to 81% of apical phylloclades flowering (Boyle et al., 1988). Plants grown first under LDs and then SDs flowered, with a maximum of 80% of plants flowering, 1.0 BPFAP, and 32% of apical phylloclades flowering. Continual SDs did not produce flowering plants (Boyle et al., 1988). Continual LDs created the longest time to flower (89 d from the start of LDs) and the most intermediate levels of BPFAP and percentage of apical phylloclades flowering (PAPF) (Boyle et al., 1988). Previous experiments with *H. gaertneri* showed no substantial flowering for plants given 80 d of 8-h SDs followed by 16-h LDs at ≥ 20 °C (Peters and Rünger, 1971), indicating inhibition of flowering at temperatures ≥ 20 °C.

Photoinduced *H.* ×*graeseri* and *H. rosea* may flower more poorly than *H. gaertneri*. There was no substantial flowering at up to 90 d of 9-h SDs followed by 15-h LDs for *H.* ×*graeseri* grown continually at ≥20 °C (Rünger, 1960), but again this result may have been caused by high-temperature inhibition. Some cultivars of *H. rosea* and *H.* ×*graeseri* flowered poorly or not at all following six weeks of 8-h SDs followed by 14-h LDs at 18 °C night temperatures, while 100% of *H. gaertneri* 'Crimson Giant' grown under the same conditions flowered, although with only 47% apical phylloclades flowering and 4.3 buds per plant (Boyle, 1995b).

Short-day phase

A minimum of four weeks of SDs is desired for horticultural flowering of *H. gaertneri*. For *H. gaertneri* 'Crimson Giant', increasing duration of SDs at 20/18 °C (day/night) from two to eight weeks increased the percentage of apical phylloclades flowering, number of BPFAP, and number of buds per plant for SD photoperiods of eight to 11 h, although days to flowering increased (from start of SD treatment on 4 Dec.) (Boyle, 1991). Minimum days to flower and maximum BPFAP and percent apical phylloclades flowering were statistically achieved following a minimum of 4 weeks of SDs (Boyle et al., 1988).

The critical SD photoperiod for photoinduction of *H. gaertneri* is between 11 and 12 hours. Eight weeks of 12-h photoperiods produced plants that averaged 58% apical phylloclades flowering, 1.1 BPFAP, and 16.2 buds per plant. Plants given the same duration of 11-h photoperiods had 82% apical

phylloclades flowering, 1.3 BPFAP, and 30.8 buds per plant (Boyle, 1991). Number of BPFAP was significantly higher following eight weeks of 8-h SD (BPFAP = 1.5) than eight weeks of 11-h SDs (BPFAP = 1.3) (Boyle, 1991).

Long-day phase (forcing)

Photoinduced *H. gaertneri* 'Crimson Giant' do not flower or flower poorly under continual SD (Boyle et al., 1988). The same is true for *H. ×graeseri* (Rünger, 1960). However, after a minimum of eight weeks of SDs, plants grown at photoperiods >12 h or given 4-h NI treatments (beginning 17 Jan.) flowered. Maximum BPFAP and percent apical phyllcoaldes flowering (≈2.5 and 99%, respectively) were achieved with photoperiods ≥14 h or NI. Plants flowered 15 to 25 d faster at these photoperiods than at 12 h (Boyle et al., 1988). Therefore, the critical photoperiod for the LD phase is considered to be between 12 and 14 h, and NI is equally sufficient. Microscopic analysis of the areolar meristem showed that flower primordia were not present at the beginning of LDs following an SD treatment (Boyle et al., 1994).

Thermoinduction

Response to photoinduction vs. thermoinduction is genotype dependent. Although *Hatiora* will flower as an SLDP, maximum flowering is achieved by a cool treatment (vernalization) to supplement or substitute for the SD phase (Boyle, 1991; Boyle and Stimart, 1989; Dole and Wilkins, 1999). *Hatiora gaertneri* 'Crimson Giant' showed 91% apical phylloclades flowering after six

weeks of 10 °C (night temperatures) and natural daylengths (beginning 24 Nov., preceded by natural daylength conditions and followed by 14-h LD at 21/18 °C day/night). The same cultivar showed 72% apical phylloclades flowering after 18 °C treatment (under natural daylengths beginning 24 Nov.) and similar forcing. However, *H.* ×*graeseri* 'Evita' flowered with 72% and 18% apical phylloclades flowering, and *H.* ×*graeseri* 'Red Pride' flowered with 90% and 22% apical phylloclades flowering after the same respective treatments (10 °C vs. 18 °C) (Boyle, 1995). *Hatiora rosea* flowered weakly after 16 weeks of photoinduction (33% of plants flowering, 3.2 buds per plant) but flowered much better after 16 weeks of thermoinduction at 10 °C (100% plants flowering, 110.1 buds per plant) (Boyle, 1990).

Prevernalization period

Environment during the prevernalization affects flowering in *Hatiora*. Before vernalization, 50 d of 9-h SDs effectively promoted flowering (greater percentage of apical phylloclades flowering) than 50 d of 15-h LDs when *H.* ×*graeseri* were vernalized for 60 d at 5, 10, or 15 °C. This effect was especially apparent if vernalization was at 15 °C. In addition, prevernalization was also more effective at 15 °C than 25 °C (Rünger, 1960), possibly because of the thermoinductive nature of 15 °C. Only 38% of plants given 25 °C prevernalization under 15-h photoperiods and then vernalized at 10 °C flowered, with only 16 to 18% apical phylloclades flowering. On the other hand, 95% of plants flowered when prevernalization was at 25 °C under 9-h photoperiods, with

32 to 34% of apical phylloclades flowering. Plants were damaged if prevernalization temperature was 25 °C followed by a vernalization temperature of 5 °C, most likely because of the strong temperature change. These data emphasize the importance of SDs before cooling if vernalization temperatures are ≥15 °C. Maximum flowering (100% flowering, 63% of apical phylloclades flowering) was achieved with a 50-d SD pretreatment at 15 °C followed by SD vernalization at 10 °C for 60 d (Rünger, 1960).

Hatiora gaertneri benefited from SD pretreatment similarly to *H ×graeseri*. Plants had significantly more apical phylloclades with flowers (maximum 81%) if they were given 30 SDs instead of 30 LDs (starting 13 Oct.) at 15 to 20 °C before a 50- or 70-d vernalization at 15 °C. Optimum temperature of the SD-pretreatment was 10 to 20 °C over the range of 10 to 30 °C (Peters and Rünger, 1971).

Vernalization period

Vernalization is the "acquisition or acceleration of the ability to flower by a chilling treatment" (Chouard, 1960). This definition applies to the cold treatment given to *Hatiora*, during which initiation occurs or signals that allow initiation and evocation during the subsequent LD treatment are made. Temperatures below 14 to 15 °C are vernalizing for *Hatiora*.

Hatiora gaertneri 'Crimson Giant' all flowered when given zero to eight weeks of 18 or 10 °C (night temperatures under natural daylength beginning 4 Dec.) followed by LDs. However, vernalization at 10 °C yielded a greater

percentage of apical phylloclades flowering than induction at 18 °C after two or five weeks of vernalization. After vernalization at 10 °C for durations beyond four weeks, BPFAP and number of buds per plant were higher (2.3 BPFAP and 49 buds per plant at eight weeks) than at 18 °C (1.7 BPFAP and 33 buds per plant) (Boyle, 1991). Days to flowering from the beginning of inductive treatment (4 Dec.), percentage of apical phylloclades flowering, number of buds per plant, and BPFAP all increased with increasing duration of induction at 10 or 18 °C (Boyle, 1991).

Photoperiod was generally unimportant when vernalization was 90 d at 10 °C for *H. ×graeseri*. Percentage of apical phylloclades flowering at 10 °C was slightly higher, although still poor (<65%) and not statistically significant, when photoperiod during the vernalization was continual 9-h SDs rather than 15-h LDs. Vernalization at 10 °C was better than that at 15 °C for LD photoperiods (Rünger, 1960).

Hatiora gaertneri may show a larger response to photoperiod during vernalization than *H. ×graeseri*. *Hatiora gaertneri* plants vernalized for 80 d at 10 °C under 8-h SD (beginning 22 Dec.) had 75% apical phylloclades flowering, whereas plants vernalized under 16-h LDs at 10 °C had only 43% flowering apical phylloclades (Peters and Rünger, 1971). The effect of photoperiod during vernalization was more apparent after 80 d at 14 °C (beginning 30 Sept), when 74% percentage of apical phylloclades flowered under SDs and only 39% flowered under LD (Peters and Rünger, 1971).

Response to photoperiod during vernalization may vary between temperature treatments, species, cultivars, and even experiments. There was no effect of photoperiod at 10 °C for *H. gaertneri* vernalized for 50, 70, or 90 d beginning 11 Nov. (Peters and Rünger, 1971). Increasing photoperiods from 10 h to 24 h at 15 °C decreased the percentage of apical phylloclades flowering for these same durations. Short-day photoperiods (10-h) were especially beneficial (when compared with photoperiods ≥12 h or 10 °C vernalization) at 70 d of 15 °C vernalization. Plants from these SD treatments at 15 °C had 80 to 85% apical phylloclades flowering, whereas at 10 °C and the same photoperiod (10-h), the percentage of apical phylloclades flowering was ≈40 (Peters and Rünger, 1971). These results further illustrate the tremendous variation, even using the same clones and with data presented in the same paper, in Easter cactus research. Possible reasons for this variation, especially relating to natural photoperiods and starting date for inductive treatments, will be discussed later under "Civil Twilight Effects" (p. 23).

As with some other plants, *Hatiora* respond to night temperature during vernalization. In *Xanthium*, *Perilla*, and *Kalanchoe*, supra- and suboptimal temperatures during the dark cycle in SDs reduced the effectiveness of the SD treatment (Lang, 1965). With *Hatiora*, supraoptimal temperature during the dark period in vernalization reduces effectiveness of vernalization, which is shown in plants vernalized under SD at various day/night temperature regimens. *Hatiora gaertneri* vernalized at 10/10 °C or 20/10 °C (day/night) and 8-h SDs flowered with 76 or 72% apical phylloclades flowering, respectively (Peters and Rünger,

1971). Only 9% of plants given 20/15 °C and SDs flowered, and 9% of plants given 20/10 °C and 16-h LDs flowered (Peters and Rünger, 1971). Plants grown at 10/20 °C and LDs flowered, although poorly (91% of plants flowering, 32% of apical phylloclades flowering). No flowering at any night temperature or photoperiod was seen at 25 or 30 °C (day temperature) (Peters and Rünger, 1971). Therefore, day temperatures during vernalization may rise to 20 °C with no ill effects, as long as night temperatures reach 10 °C for the duration of vernalization and photoperiods are sufficiently short.

Light has been considered necessary during vernalization of *Hatiora*. During cooling treatments, 2000 lux (≈30 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for 8 hours (≈0.86 $mol \cdot m^{-2} \cdot d^{-1}$) produced the maximum percentage of apical phylloclades flowering of *H. gaertneri* (76% after 80 d of cooling at 10 °C), although there was no statistical difference between any light treatment from 1000 to 4000 lux. Continuous darkness during cooling did not produce any flowering plants, and considerable phylloclade damage and abscission can occur under constant darkness (Peters and Rünger, 1971; personal observation).

Long-day phase (forcing)

As with photoinduction, thermoinduced *H. gaertneri* flower poorly if forced under SD photoperiods (Boyle, 1991; Boyle et al., 1988; Peters and Rünger, 1971). The same is true for the SLDPs *Festuca pratensis* and *Dactylis glomerata* (Heide, 1987; Heide, 1988), and for *Campanula medium* under certain treatments (Wellensiek, 1960). *Hatiora* ×*graeseri* thermoinduced with a 90-d

vernalization at 10 °C (beginning 15 Nov.) followed by forcing under 15-h LDs at 20 to 22 °C had a greater percentage of apical phylloclades flowering (45%) than plants forced under 9-h SDs (36% apical phylloclades flowering) (Rünger, 1960). *Hatiora gaertneri* 'Crimson Giant' vernalized for eight weeks followed by LDs had a similar number of buds, BPFAP, and PAPF as plants that were moved from LDs to 8-h SDs after five weeks of forcing, suggesting a five-week minimum period of LDs following vernalization. 'Crimson Giant' plants forced under continual LDs flowered only 3 d earlier than plants moved to SDs after five weeks of LD (Boyle, 1991). 'Crimson Giant' plants forced under continual SDs require a minimum of six weeks of vernalization, although only 5.6 buds formed per plant if eight weeks of vernalization was followed by continual SDs (Boyle, 1991).

Hatiora are typically forced at 18 to 22 °C (Dole and Wilkins, 1999). Raising the temperature after vernalization too quickly may cause the buds to drop during forcing. Raising the temperature 2 to 3 °C per week to reduce bud drop is typically recommended (PKM, personal communication; Nell, 1988), but this practice may be beneficial because it lengthens the inductive period.

Experimentation has been performed on forcing under 10- to 24-h photoperiods at 15, 20, and 25 °C. There were no differences in the percentage of apical phylloclades flowering, days to flower, or BPFAP among *H. gaertneri* vernalized at 15 °C for 70 d under naturally short photoperiods (beginning 20 Nov.) and forced at 10- to 24-h photoperiods at 15 °C for 30 d (followed by LDs at 20 to 22 °C until flowering). All apical phylloclades flowered with 2.4 to 2.8 BPFAP, and flowering took ≈66 days from the beginning of forcing. Percentage

apical phylloclades flowering decreased as forcing temperature increased to 20 °C (91-98%) or 25 °C (31-51%). Days to flower and buds per flowering phylloclade also declined with increasing forcing temperature, to a minimum of 49 days (from beginning of forcing) and 1.4 buds at 25 °C (Peters and Rünger, 1971). The advantage of forcing at 15 °C is that induction likely continues at this temperature.

Light quantity during forcing may affect flowering following thermoinduction. Data suggest that flowering in *Campanula medium*, another SLDP, is influenced by light quantity during the LD forcing phase (Wellensiek, 1960). Light, CO_2 concentration, or both affect plant assimilation directly, and assimilation before, during, and after inductive processes has been implicated in the flowering response of many photoperiodic and vernalization-requiring plants (Bodson and Bernier, 1985). Forcing of *Hatiora* may be accelerated by increasing the light levels of an LD or NI treatment (PKM, personal communication), which may be a result of increased plant temperature caused by increased irradiance and therefore more rapid development.

Civil Twilight Effects

Civil daylength is the time it takes the sun to move from 6° below the horizon before sunrise to 6° below the horizon after sunset (*The Astronomical Almanac*, 2000). Civil daylength in East Lansing, Mich. (lat. 42°45'N) does not decrease to 12 h in the autumn until approximately 15 Oct., with slight variations caused by elevation and weather conditions (data interpolated from *The*

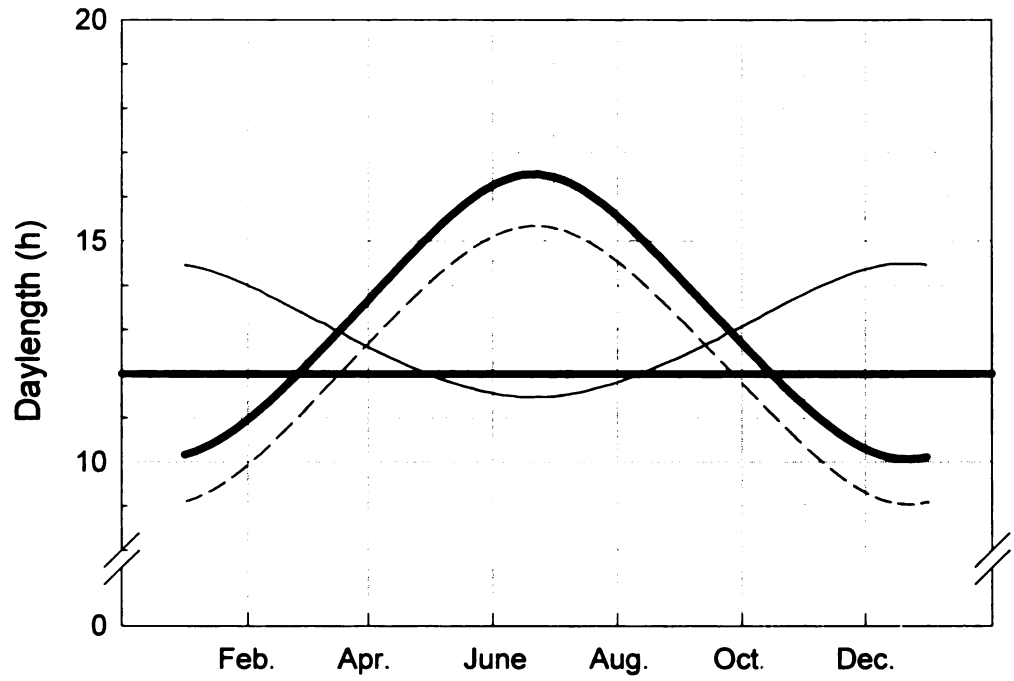

Figure 1. Daylength in East Lansing, Mich. (lat. 42°45'N) and the native range of *Hatiora* (near 26°S). The dark solid curve represents civil daylength in East Lansing, the dashed curve is actual daylength in East Lansing, and the thin solid curve is civil daylength at lat. 26°S. A reference line is shown at 12 h (data interpolated from *The Astronomical Almanac*, 2002).

Astronomical Almanac, 2000). Civil daylength is 56 minutes longer than actual daylength in March and October and 71 minutes longer in mid-June (Fig. 1).

Most plants are able to perceive some part of civil twilight (the duration of time when the sun is -0.85° to 6° below the horizon) for photoperiodic responses. Light quantity plays a role in detection of the beginning and end of night (dark) treatments in plants (Hughes et al., 1984; Cockshull, 1984). Minimum irradiance causing a response in end-of-day treatments ranged from 0.02 to 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for *Glycine*, *Pharbitis*, *and Xanthium* (Cockshull, 1984).

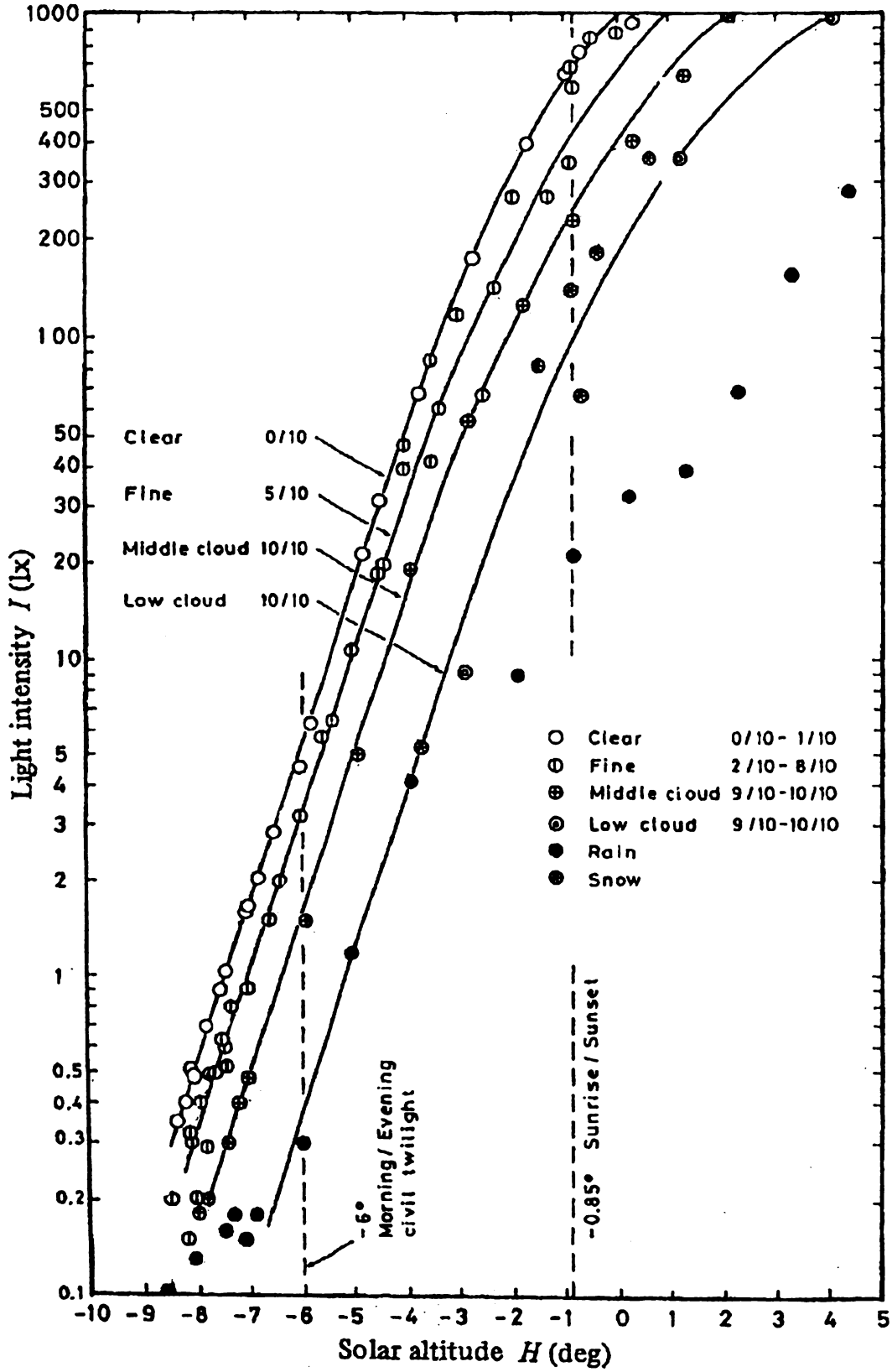

Figure 2. Twilight intensity as a function of solar angle for different weather conditions (Kishida, 1989).

Light during civil twilight is often strong enough to cause a photoperiodic response. Luminous intensity of light (I, in lux) during twilight can be expressed as a function of solar altitude (H, in degrees) and a variable β that ranges from –5.15 for a sky obscured by low clouds to –7.43 for a clear sky (Fig. 2). This relationship is defined by the equation $I = e^{[(H-\beta)/0.87]}$ from 0.2 to 50 lux (Kishida, 1989). By this equation, plants with photoperiodic sensitivity to >1 lux (0.02 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of light will respond at solar altitudes of > –5.15° to –7.43° under overcast or clear skies, respectively (Kishida, 1989). Therefore, in October in East Lansing, Mich., the duration of light at intensities >1 lx is 48 to 69 minutes longer than actual daylength, depending on weather conditions. As stated, civil daylength is 56 minutes longer than actual daylength in October. However, the data to support these conclusions were recorded on the roof of a building, not in a greenhouse. Internal greenhouse structures (or, in a natural *Hatiora* environment, forest canopy) would increase the critical value of H for a photoperiodic response, reducing perceived civil daylength.

Assuming a minimal schedule of eight weeks of induction followed by six weeks of forcing to a marketable stage on 15 Jan., induction must begin on 9 Oct. On this date, daylength is 11.4 h (in East Lansing, Mich), but *civil* daylength is approximately 12.3 h. A civil daylength of 11 h is not reached until approximately 8 Nov. (*The Astronomical Almanac*, 2000). Therefore, if night temperatures are insufficiently cold for a thermoinduction treatment (Peters and Rünger, 1971), which may be possible in October, daylength is also likely to be

insufficiently short for a full photoinductive treatment (Boyle, 1991), and the plants are not being induced to flower maximally by 15 Jan.

Other Short-Long-Day Plants

Campanula medium responds as an SLDP in much the same way as *Hatiora*. Experiments have shown that *C. medium* may also be photoinduced, but thermoinduction is stronger (Wellensiek, 1960). *Campanula pyramidalis* requires photoperiods longer than 13 or 14 h after a vernalization treatment (Zimmer, 1985). The juvenile phase, only after which flowering will occur, was shorter for photoinduction than for thermoinduction, which suggests different mechanisms for the two induction methods (Wellensiek, 1960). In addition, older plants require less vernalization than younger, although still mature, plants (Wellensiek, 1960; Wellensiek, 1985). More recently, two new *C. medium* cultivars ('Champion Blue' and 'Champion Pink') flower under continuous long days without vernalization (Cavins and Dole, 2001).

Coreopsis grandiflora responds as an SLDP. Following SDs, horticultural quality of the flowering plant is increased with an LD treatment (Ketellapper and Barbaro, 1966; Runkle, 1996), as is the case with *C. lanceolata* (Damann and Lyons, 1993). Vernalization can replace the SD phase and create a more uniform and prolific flowering response. Longer vernalization durations hastened development and increased the percentage of plants flowering (Ketellapper and Barbaro, 1966; Runkle, 1996). It was also suggested that 12.5-week-old plants

respond less strongly to vernalization than 21-week-old plants (Ketellapper and Barbaro, 1966).

Plants from a New Zealand seed stock of *Trifolium repens* responded as SLDPs, with a minimum of 3 SDs to fulfill the SD requirement. One day of continuous irriadiation saturated the LD requirement (Thomas, 1961).

Echeveria harmsii behaves as an SLDP. Plants flowered only if the photoperiod before LD was 12 h or shorter, and plants flowered after SD only if the photoperiod was 12 h or longer. A minimum of 20 SDs is required for the short-day phase, although longer durations are more beneficial for flowering (Rünger, 1962).

Some temperate grasses respond as SLDPs at temperatures above 15 °C. The responses are genotype and ecotype dependent (Heide, 1994). Ten or more weeks below 18 °C during 8-h SDs, followed by LDs, were required for heading in three *Dactylis glomerata* cultivars. These cultivars were sensitive to photoperiod at vernalizing temperatures. Approximately 12 LD (24-h) cycles at 15 °C were necessary to satisfy the LD requirement (Heide, 1987).

Festuca has a more obligate requirement for cold temperatures than some other SLD grasses, although many still respond to photoperiod during vernalization. In *F. pratensis*, critical temperature for SD vernalization was 15 °C, whereas critical temperature for long-day vernalization was 12 °C. Critical photoperiod for the long-day phase was around 13 hours (Heide, 1988). Of three SLD *Fetsuca rubra* varieties studied, one was photoperiod insensitive during vernalization. The other two favored SDs during vernalization. Few *F. rubra*

plants flowered after vernalization at 15 °C, regardless of photoperiod (Heide, 1990b).

Similarly, *Phleum alpinum* requires temperatures below 15 °C for adequate primary induction (vernalization). Short days (8-h) were substantially more effective than LDs, especially at moderate (9 to 2 °C) vernalization temperatures and short (6 to 9 week) vernalization durations. Increasing the number of LD cycles after primary induction increased the number of inflorescences, the culm height, and the development rate (Heide, 1990a).

Summary

Hatiora is one of the few mass-produced commercially profitable floriculture cacti. Growing conditions and techniques are relatively simple and space-efficient. Photoperiod and temperature treatments sufficient for flowering are less straightforward. Physiologically significant photoperiod on any given day is an objective function of the day of the year, latitude, plant characteristics, weather conditions, and greenhouse superstructures. Variable response of flowering between years within one *Hatiora* cultivar may be due to variable annual photoperiods, weather conditions, and temperature during and before induction.

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SECTION II

DAILY LIGHT INTEGRAL, PREVERNALIZATION PHOTOPERIOD, AND VERNALIZATION TEMPERATURE AND DURATION CONTROL FLOWERING OF EASTER CACTUS

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 response 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. Treatment with 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 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 prior to vernalization increased the percentage of apical phylloclades flowering, buds per flowering apical phylloclade and percentage of plants flowering after dark vernalization. Collectively, the most uniform flowering in January occurred when plants were exposed to a sequence of four to six weeks of SD, vernalization at 7.5 to 15 °C for eight weeks, then long-day forcing for seven weeks.

Easter cacti [*Hatiora gaertneri* (Regel) Barthlott and *H.* ×*graeseri* (Wedermann) Barthlott] 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). *H.* ×*graeseri* is a hybrid of *H. gaertneri* and *H. rosea* (Barthlott and Taylor 1995). Flowering may be achieved through photoperiod manipulation (photoinduction). *Hatiora* spp. are classified as short-long-day plants (SLDP) for flowering from 15 to 20 °C (Boyle, 1991; Boyle et al., 1988; Peters and Rünger, 1971; Rünger, 1960).

Vernalization from 10 to 15 °C may substitute for the short-day (SD) phase (thermoinduction), depending on cultivar. Thermoinduction at 10 °C is optimal, while 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 stronger after thermoinduction than photoinduction, especially in *H.* ×*graeseri* (Boyle, 1991; Boyle, 1995).

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

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

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 counts 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 *Schlumbergera* cacti benefit from leveling 1 to 10 d after SDs are started (Boyle, 1997).

Vernalization in a cooler may provide means for extending the season or cooling the plants when temperatures are insufficient for vernalization. Celery (*Apium graveolens* L.), ajuga (*Ajuga reptans* L.), and carnation (*Dianthus*

caryophyllus L.) were insensitive to vernalization 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 to vernalization under 12- to 20-hour photoperiods (Atherton et al., 1984). Previous research indicates that vernalization of *Hatiora* in darkness is impractical (Peters and Rünger, 1971), but prevernalization SDs may condition the plants for a dark vernalization.

Easter cacti are sold as flowering potted plants from January to June in northern Europe. Uniform flowering in January may be difficult to achieve, most likely because of non-inductive temperature or photoperiod conditions during and before the early stages of induction in early to mid-October (assuming eight weeks of vernalization followed by six weeks under LDs until a marketable stage is reached). 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, 2000). In early October, consistently achieving the 8 to 12 °C night temperatures recommended for thermoinduction (Boyle and Stimart, 1989; Nell, 1988) may be difficult.

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 cooler may save space

and allow extension of the market dates. Poor vernalization caused by unpredictable weather in the fall and spring could be avoided by vernalizing in a climate-controlled cooler. The objectives of this research were to 1) study the effects of photoperiod before vernalization and daily light integral (DLI) before and during vernalization, 2) identify combinations of SD treatments before vernalization and vernalization treatments that increase uniformity and BPFAP, 3) observe differences in flowering after exposure to 2 different photoperiods of SD pre-vernalization treatment, 4) identify propagation and leveling treatments that increase uniformity and BPFAP, and 5) determine the effects on flowering of SD treatment followed by vernalization in a cooler.

Materials and Methods

Phylloclades were harvested from vegetative cacti on 15 to 20 Apr. 2000 in Expt. 1, 15 to 20 April 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*, 2000)] in a 70:30 (vol:vol) peat:perlite mix in 55-cell (23 cm^3 per cell) plug trays. Air and bench temperature were set at 23 and 25 °C, respectively. Plants were grown under intermittent mist until transplant. Rooted plugs were transplanted into 10.2-cm (0.46-L) plastic pots containing 70:30 peat:perlite (SureMix Perlite, Michigan Grower Products, Galesburg, Mich.). Plants were irrigated with well water (containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively) supplemented with water-soluble fertilizer to provide the following ($mg \cdot L^{-1}$): 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, Ill.), acidified to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$. Fertilization was terminated during vernalization treatments and resumed during forcing.

Plants were maintained in a greenhouse under 16-h LDs from propagation until the beginning of SD or vernalization treatments. In Expt. 1, LD were provided until SD pre-vernalization or vernalization by pulling blackout cloth over the plants from 17:00 to 08:00 HR and providing incandescent irradiation [(5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux (*PPF*)] from 1700 to 0000 HR. LDs in Expts. 2 through 5 were provided by high-pressure sodium (HPS) lamps (80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux) for 16 HR as needed from 0600 to 2200 to maintain a minimum of 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Pre-vernalization SD photoperiods (10-h) were achieved by pulling blackout cloth over the plants from 1700 to 1800 HR and lighting (5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$) 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, Utah). 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 buds. Percentage of plants flowering, PAPF, BPFAP, and days to flowering were analyzed with single degree-of-freedom χ^2 tests (Hoshmand, 1988) or a mixed model procedure [PROC MIXED; SAS Institute Inc., Cary, N.C. (Khattree and Naik, 1999)] after transformation for increased normality, as described in each experiment.

Prevernalization DLI and photoperiod and vernalization DLI and temperature (Expt. 1). *Hatiora gaertneri* 'Jan' were grown at 20 °C under 16-h LDs or 10-h SDs (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 at 80 µmol•m^{-2}•s^{-1}) or low (≈4.5 mol•m^{-2}•d^{-1}) 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 and 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 to increase uniformity. After vernalization, plants were forced under 16-h LD as described above.

Statistical analyses were performed separately on the high- and low-vernalization DLI treatments because of multiple significant interactions. Data for PAPF were transformed ($\arcsin\sqrt{\text{PAPF}}$) prior to analysis. Days to flower data were transformed (d^{-2}) and analyzed separately within each cultivar due to multiple significant cultivar interactions.

Photoperiod before vernalization and vernalization duration and temperature (Expt. 2). On 20 Sept. 2001, *H. gaertneri* 'Jan' and 'Rood' were moved into 10-h SDs 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 (six, four, and two weeks of SDs), along with plants from 16-h LDs (zero weeks of SDs) were moved into 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*, 2000)]. Apical phylloclades were removed 14 d after vernalization was begun to increase plant uniformity. Vernalization treatments were for two, four, six, or eight weeks, followed by forcing under 16-h LDs at 20 °C as described.

Average proportion of apical phylloclades flowering (PrAPF) 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. Buds per flowering apical phylloclade (BPFAP) and time to flower were transformed $\{[\ln(\frac{\text{number of buds}}{\text{number of flowering phylloclades}} + 1)]$ and (d^{-2}), respectively$\}$ before analysis. There were seven plants per treatment.

Short-day pre-vernalization photoperiod (Expt. 3). On 22 Sept. or 6 Oct., 2001, *H. gaertneri* 'Jan' and *H.* × *graeseri* 'Evita' were moved to 10- or 11-h SDs provided by extending 9-h daylengths with incandescent lamps under blackout

cloth as described. On 3 Nov. (after six or four weeks of SDs), the plants were moved to 12.5 °C and vernalized for four or eight weeks. Plants were leveled on 10 Nov. and forced as described above.

Percentage of plants flowering were analyzed by χ^2 analysis. Data on PAPF, BPFAP, and time to flower were transformed {$\arcsin\sqrt{PAPF}$, [ln (BPFAP+1)]$^{-1}$ and (d^{-4}), respectively} before analysis. There were seven plants per treatment.

Propagation and leveling date (Expt. 4). 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 approximately six weeks. They were then moved to the 16-h LDs (from HPS lamps) growing conditions described. Plants were moved to 10-h photoperiods (as described in Expt. 1) for six weeks beginning on 22 Sept., vernalized for four weeks at 10 °C beginning 3 Nov., and forced under 16-h LDs at 20 °C. Plants were leveled on 6 Aug. (47 d before SDs), 2 Oct. (10 d after SDs started), 13 Nov. (10 d after vernalization started), or not at all. Plants propagated in July were not leveled on 6 Aug.

The PrAPF on all plants and the percentage of plants flowering were multiplied to determine flowering uniformity, as represented by a 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. Buds per flowering apical phylloclade and days to flower were

transformed {[ln (BPFAP + 1)]$^{-1}$ and (d^{-4}), respectively} before analysis. There were five plants per treatment.

SD treatment followed by vernalization in darkness in a cooler (Expt. 5). *Hatiora gaertneri* 'Jan' and *H. ×graeseri* 'Evita' were grown for six or three weeks (starting 29 Nov. or 20 Dec., 2001, respectively) under 10-h SDs as described in Expt. 1. On 10 Jan., these plants and plants given no SD treatment (continuously under 16-h LD) were moved into unlit coolers set at 0, 2.5, 5, 7.5, or 10 °C. Vernalization at these temperatures was 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. Following vernalization, plants were forced as described above.

Percentage of plants flowering were analyzed by χ^2 analysis. Data for PAPF and time to flower were transformed [arcsin$\sqrt{\text{PAPF}}$ and (d^{-1}), respectively] before analysis. 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 eight weeks of vernalization, combined with SD before vernalization, produced the best flowering plants (Fig. 1). High DLI during vernalization reduced the percentage of flowering plants (Fig. 1A vs. Fig. 1B), PAPF (Fig. 1C vs. Fig. 1D), and BPFAP (Fig. 1E vs. Fig. 1F) when vernalization temperature was ≥15 °C. The PAPF and buds per flowering apical phylloclade were higher on average when plants were vernalized under low DLI compared to high DLI. Plants grown under high DLI and SDs during prevernalization produced more

BPFAP than those pretreated with low DLI and LDs when plants were vernalized under high DLI at 7.5 °C or low DLI at 7.5, 10, or 15 °C (Fig. 1E and 1F). Optimal vernalization temperatures under the low vernalization DLI range from 7.5 to 15 °C (100% of plants flowering, >70% of apical phylloclades flowering, and >1.2 BPFAP), but the optimal range under the high vernalization DLI was 7.5 to 12.5 °C (≥86% of plants flowering, ≥60% of apical phylloclades flowering, and ≥1.2 BPFAP). Short-day treatment (10-h) before vernalization generally increased the PAPF (Fig. 1C and 1D) and BPFAP (Fig. 1E and 1F) on plants were vernalized at 7.5 to 12.5 °C.

Plants given prevernalization under LDs and vernalized for only four weeks flowered poorly (58-73% plants flowering after 7.5 to 12.5 °C vernalization) compared to plants given SD before 4 weeks of vernalization (93 to 100% of plants flowering after 7.5 to 12.5 °C treatment). A maximum of 83% of apical phylloclades flowering and 1.45 BPFAP was recorded after 4 weeks of vernalization for plants given a prevernalization treatment of high DLI and SDs and then vernalized under low DLI at 7.5 °C. Because of the poorer flowering of plants after four weeks of vernalization, the data for these treatments are not shown here.

Expt. 2. Flowering uniformity increased as duration of prevernalization SD treatment and vernalization increased (Fig. 2). The maximum flowering index was typically found in plants given six weeks of SDs in combination with and before eight weeks of vernalization. Vernalization at 10 or 12.5 °C for a duration of eight weeks resulted in the greatest flowering uniformity; SD before cooling did

not significantly increase flowering uniformity on plants vernalized for eight weeks at this duration and these temperatures. 'Jan' vernalized at 12.5 °C for eight weeks with no prevernalizaion SDs flowered with uniformity similar to plants given four or six weeks of SD before six weeks of vernalization at 12.5 °C. Flowering index was low for plants vernalized at 15 °C, espeically for plants not receiving an SD treatment. 'Jan' flowered more uniformly than 'Rood', especially at 15 °C or at 12.5 °C with fewer than eight weeks of vernalization.

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

Treatments that resulted in a higher PrAPF also increased the number of BPFAP (Fig. 4). The minimum number of buds per apical phylloclade (BPAP) is equal to PrAPF. For example, if half of the apical phylloclades flower (PrAPF = 0.5) on a plant with 30 apical phylloclades, the minimum number of BPAP is also 0.5 (15/30). Therefore, subtracting PrAPF from BPAP will give the number of buds per apical phylloclade above the minimum possible value. In general, the number of buds above the minimum increased as PAPF increased, although variability was larger at high PrAPF (Fig. 4).

Time to flower was influenced by vernalization duration and temperature (Table 1). 'Jan' vernalized at 10 or 12.5 °C for six or eight weeks flowered on average three days faster than plants vernalized at 15 °C for six or eight weeks.

'Jan' given two to six weeks of SDs prior to vernalization flowered an average of two days faster than plants given no SDs before vernalization. Plants vernalized at 10 °C for eight weeks flowered 11 to 21 d faster than plants vernalized at 15 °C for four weeks.

Expt. 3. All plants flowered after eight weeks of vernalization, with a higher PAPF and more BPFAP than plants vernalized for four weeks (Table 2). Plants given prevernalization SDs for six weeks had a higher PAPF than plants given four weeks of prevernalization, irrespective of photoperiod. Plants vernalized for eight weeks flowered an average of 10 d faster than plants vernalized for four weeks. Treatment with 10-h prevernalization photoperiod also resulted in more rapid flowering than 11h.

Expt. 4. Plants propagated earlier in the year generally had higher flowering uniformity, as shown by a larger flowering index (Fig. 5). Plants not leveled or leveled before SDs flowered most uniformly. Uniformity was very low for plants leveled during vernalization. 'Jan' flowered more uniformly than 'Evita.'

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

Expt. 5. Dark vernalization below 5 °C killed the plants (data not shown) or did not substantially promote flowering (Table 4). 'Jan' had a higher PAPF

(48%) than 'Evita' (32%) and 'Jan' took an average of 2 d longer to flower. Short days before vernalization increased the percentage of plants flowering in most treatments, PAPF, and BPFAP. 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 three weeks of SDs followed by 56 d of vernalization at 5 °C or six weeks of SDs followed by 56 d of vernalization at 10 °C.

Discussion

Hatiora may flower as a SLDP, but flowering is enhanced by 10-15 °C treatment during or instead of the SD phase (Boyle, 1991; Peters and Rünger, 1971; Rünger, 1960). Other plants with similar SLD flowering activity in which SD may be replaced or enhanced by vernalization include *Campanula medium* (Wellensiek, 1960; Wellensiek, 1985), *Coreopsis grandflora* and *C. lanceolata* (Damann and Lyons, 1993; Ketellapper and Barbaro, 1966; Runkle, 1996), and *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 SLD flowering requirements.

As previously shown (Boyle, 1991; Peters and Rünger, 1971; Rünger, 1960), extending the duration of inductive conditions, either with SD or cool

temperatures, enhanced flowering uniformity (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 SDs before vernalization under natural SD photoperiods if temperatures are higher than those for optimum vernalization (≥≈14 °C). Short days provided with blackout cloth before vernalization were provided in these experiments, but natural SD photoperiods are likely to have similar beneficial effects (Boyle, 1995).

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 75 to 96%, and increased the PAPF from 7.6 to 55% in *H.* ×*graeseri* (Rünger, 1960).

Flowering in *Hatiora* should be considered a quantitative response to induction. 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 PAPF and the number of BPFAP increase. Botanical flowering describes a plant with any number of flowers, while horticultural flowering describes a plant with uniform flowering and numerous buds. Increased horticultural quality increases the value of the plants.

Prevernalization SDs treatment under optimum vernalization conditions were beneficial to flowering by increasing 1) flowering uniformity (Figs. 1 and 2), 2) the number of BPFAP (Fig. 3), and 3) the number of buds above the minimum possible (Fig. 4). In Expt. 2, plants with more than 90% of apical phylloclades flowering and more than two BPFAP (one more bud than the minimum, 37 plants total) were vernalized for six or eight weeks at 10 or 12.5 °C, with one plant vernalized at 15 °C (Fig. 4). The majority (62%) of these plants with favorable horticultural flowering characteristics were also given four or six weeks of SDs before vernalization, and 86% were given two, four, or six weeks of SDs.

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 are thought to cause photoperiodic responses in many plants (Hughes et al., 1984; Cockshull, 1984). If it is assumed that most plants native to lower latitudes are more sensitive to civil twilight than plants from higher latitudes, as is the case with *Brassica* (Tarakanov, 1998), then *Hatiora* (native to lat. ≈26°S) is more sensitive to civil twilight than plants native to Europe and the northern United States. Daylength including civil twilight does not reach 12 hours until approx. 16 October or 11 h until approximately 8 Nov. at lat. 42°45'N (East Lansing, Mich.) (*Astronomical Almanac*, 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, Mich. If vernalization is to begin before this time, i.e., for early-season crops, or if temperatures are insufficient for vernalization, it is apparent that there are benefits of SD treatment before vernalization to extend the induction period. The photoperiodic sensitivity of *Hatiora* to low-fluence light and a more precise critical photoperiod need to be established to determine when photoinduction naturally begins in the fall.

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 four weeks of vernalization (Fig. 5) 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.

Hatiora gaertneri 'Jan' that were leveled 14 d after vernalization began and were vernalized for eight weeks at 10 °C showed similar uniformity (Fig. 2) to 'Jan' leveled 47 d before pre-vernalization SDs were begun or not leveled at all and vernalized for only four weeks (Fig. 5). It is therefore likely that fewer than

eight weeks of vernalization would be necessary in growing conditions similar those in Expts. 1, 2, and 3 to achieve results similar to experiments 1, 2, and 3 if the plants are not leveled or are leveled before SDs are begun.

Data presented here show that *Hatiora* will flower marginally if vernalized in darkness (Table 4), although previous work showed that *H. gaertneri* failed to flower if vernalized for 60 to 80 d in constant darkness at 10 °C, and ≈290 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during 80 d of vernalization created the highest PAPF over the range of ≈144 to 575 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Peters and Rünger, 1971). Pre-vernalizing the plants with SDs increased the PAPF and BPFAP following dark vernalization (Table 4). Increasing the prevernalization SDs and vernalization duration also increased the percentage of plants flowering in most dark treatments. Vernalization at 5, 7.5, and 10 °C were equally ineffective at creating horticulturally desirable plants. Flowering after vernalization in a cooler was generally poorer than after vernalization in a greenhouse (compare Table 4 with other Tables and Figs.). Although many plants flowered, the horticultural quality of all plants was low after 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 0-10 °C vernalization may be a result of suboptimal temperatures in combination with no light. In previous research, more *H. gaertneri* vernalized in a greenhouse for 60 to 80 d at 11 or 14 °C flowered (33-100%) than plants vernalized in a greenhouse at 5 or 8 °C (0 to 8%)

(Peters and Rünger, 1971). It may be possible that 5 to 10 °C are suboptimal for dark vernalization of *Hatiora*, although 'Jan' vernalized in a greenhouse at 7.5 °C under low DLI (≈4 $mol \cdot m^{-2} \cdot d^{-1}$, Fig. 1) flowered much better (100% flowering), especially if they were grown under SDs before vernalization (93% apical phylloclades flowering), than was previously reported for *H. gaertneri* at 5 or 8 °C (Peters and Rünger, 1971). It was previously shown that *H. ×graeseri* vernalized at 5 °C flowered (Rünger, 1960), but this treatment was preceded by 50 days of 15 °C, which may have vernalized the plants or preconditioned the plants for vernalization at 5 °C. The differences between our research and previous research are likely due to cultivar differences and experimental conditions, including light intensity and photoperiod.

Some photoperiodic and day-neutral plants will flower in total darkness, most often if sucrose is available (Lang, 1965). When given adequate glucose or sucrose, *Arabidopsis* will complete morphogenesis and flowering in total darkness (Araki and Komeda, 1993; Roldán et al., 1999), and some *Brassica napus* L. and *B. campestris* L. species will flower in total darkenss at 5 or 10 °C in medium supplemented with sucrose (Inouye and Kuo, 1981). *Hatiora* do not flower during vernalization, but sucrose availability during vernalization may affect flowering.

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), and flower initiation is profoundly influenced by availability of stored assimilates in some plants (Bernier et al., 1993; Bodson and Bernier,

1985). 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 PAPF and BPFAP in *Hatiora* (Fig. 1). Future research may show that flowering after vernalization in darkness is improved by high irradiance before vernalization, after it, or both, thereby increasing the accumulation of assimilates available for translocation during initiation. In addition, our research and previous research showed that SDs before vernalization had beneficial effects on vernalization in a greenhouse or in a dark cooler. Short days may act as a pre-conditioning treatment by favoring accumulation of assimilates over growth processes.

Phylloclade temperature may increase beyond vernalizing temperatures 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 (Fig. 6). The shoot temperature of many cacti has been recorded to be ≥15 °C above ambient air temperature because of the closed stomata of crassulacean acid metabolism (CAM) plants during the daytime and high heat storage capacity caused by succulence, among other factors (Nobel, 1988). Irradiation provided by HPS lamps increased shoot tip temperature of

vinca (Faust and Heins, 1997). In our experiments, high DLI during vernalization, provided with HPS lamps, reduced all flowering responses at 15 °C compared with ≤12.5 °C (Fig. 1). The results of Expt. 5 show that light is not an absolute requirement during vernalization, and we have shown that supplemental light during vernalization does not increase horticultural quality (Fig. 1). Therefore, reducing the *PPF* intercepted by the plants during vernalization may improve the response to vernalization by limiting the increase of plant temperature above air temperature caused by increased solar gain.

Increased duration of vernalization and prevernalization SDs, to a lesser extent, tended to hasten flower initiation, evocation, or development under LDs (Tables 1, 2, and 4). Plants given six weeks of 10-h prevernalization SDs flowered 4 d faster than plants given 11-h SDs (Table 2). These data show that 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 PAPF than *H. ×graeseri* 'Evita' in Expt. 4 and 5 (Table 4, Fig. 5) and with more BPFAP 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; Boyle, 1995). Three late-flowering *H. ×graeseri* cultivars ('5805', 'Phoenix,' and 'Capella') also flowered very poorly under non-ideal 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).

The correct taxonomy for 'Rood' is unclear. Isozyme analysis suggests that 'Rood' should be classified as *H. gaertneri* according to identity at nine loci with an *H. gaertneri* accession. There was identity with *H. rosea* at only five of the nine loci (O'Leary and Boyle, 1999). However, exact parentage of 'Rood' is unknown. In Expt. 2, there was no difference between 'Jan' and 'Rood' in buds per flowering phylloclade, but 'Jan' flowered more uniformly than 'Rood,' especially at 12.5 and 15 °C (Fig. 2), which suggests that 'Rood' may be *H.* ×*graeseri* (possibly with a diluted *H. rosea* background), as reported before isozyme analysis (Han and Boyle, 1996). Exact taxonomy of 'Jan' is also uncertain, but it is labeled here as *H. gaertneri* based on enhanced flowering relative to the other cultivars and flower and phylloclade morphology (Bailey, 1976). However, our research suggests vernalization appears to be more obligate for *H. gaertneri* 'Jan' than was previously noted for *H. gaertneri* 'Crimson Giant' (Boyle, 1991)

Horticultural significance. 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, even though *Hatiora* are vegetatively propagated and juvenility should not be an issue. Short days for four to six weeks followed by vernalization at 7.5 to 12.5 °C promote flower

induction. Flower development is then favored by forcing plants under LDs at moderate temperatures of 17-20 °C for seven weeks. Sale of uniform flowering plants requires 17-21 weeks from the start of the SD inductive process.

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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'.

Vernalization duration (weeks)	Vernalization temperature (°C) 'Jan' 10	12.5	15	'Rood' 10	12.5	15
0 weeks 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)		**			**	
VD × PD		NS			NS	
VD × T		*			NS	
SD × T		NS			NS	
VD × SD × T		NS			NS	

[NS, *, **]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

[z]No flowering plants in this treatment.

Table 2. Effects of prevernalization photoperiod and vernalization duration on flowering of *Hatiora*.

Prevernalization Duration (weeks)	Prevernalization Photoperiod (hours)	Vernalization duration (weeks)	Plants flowering (%)	Apical phylloclades flowering (%)[z]	Buds per flowering apical phylloclade[z]	Days to flower[y]
4	10	4	86	20	1.2	58
		8	100	57	1.7	47
	11	4	71[x]	14	1.0	59
		8	100	60	1.6	47
6	10	4	79[x]	33	1.1	54
		8	100	67	1.6	45
	11	4	54[x]	27	1.2	58
		8	100	58	1.5	49
Significance[w]						
Vernalization duration (VD)				**	**	**
Pre-vernalization duration (PD)				*	NS	NS
Pre-vernalization photoperiod (PP)				NS	NS	*
Cultivar (CV)				NS	NS	NS
VD × CV				NS	*	NS
PD × PP × CV				*	NS	NS

NS, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

[z]Data include flowering plants only.

[y]Days to flower from start of forcing (long days at 20 °C), flowering plants only.

[x]Significantly different from 100% flowering by χ^2 ($\alpha = 0.05$, 1 df).

[w]Non-significant interactions ($P > 0.05$) are not shown.

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'. Values in parentheses indicate the percentage of apical phylloclades flowering in the treatment.

Propagation date and leveling treatment	Buds per flowering apical phylloclade		Days to flower[z]	
	'Jan'	'Evita'	'Jan'	'Evita'
April				
None	1.5 (94)	1.4 (80)	56	52
47 d before SDs[w]	1.6 (88)	1.2 (67)	56	55
10 d into SDs	1.2 (61)	1.4 (29)	56	54
10 d into vernalization	1.3 (10)	1.3 (33)	58	55
May				
None	1.4 (78)	1.2 (44)	55	53
47 d before SDs	1.3 (61)	1.1 (63)	56	53
10 d into SDs	1.4 (33)	1.1 (24)	57	56
10 d into vernalization	1.0 (13)	1.0 (4)	60	61
June				
None	1.5 (85)	1.2 (57)	53	54
47 d before SDs	1.4 (47)	1.3 (16)	58	55
10 d into SDs	1.2 (48)	1.0 (35)	57	58
10 d into vernalization	1.0 (3)	1.0 (4)	56	53
July				
None	1.3 (18)	1.0 (12)	58	61
10 d into SDs	1.3 (41)	1.0 (2)	56	67
10 d into vernalization[y]	0.0 (0)	0.0 (0)	--	--
Significance				
Propagation date (P)	*		*	
Leveling treatment (L)	*		NS	
Cultivar (CV)	*		NS	
P × L	NS		NS	
P × CV	NS		NS	
L × CV	NS		NS	
P × L × CV	NS		NS	

NS, *Non-significant or significant at $P \leq 0.05$.

[z]Days to flower from the start of forcing (long days at 20 °C), flowering plants only.

[y]No flowering plants in this treatment.

[w]Six-weeks of short-day (10-h) photoperiods given before vernalization.

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 (%)		Apical phylloclades flowering (%)[y]		Buds per flowering apical phylloclade[y]		Days to flower[x]	
0 °C	'Jan'	'Evita'	'Jan'	'Evita'	'Jan'	'Evita'	'Jan'	'Evita'
23-d vernalization								
0 weeks'SD	0[w]	0[w]	0	0	0.0	0.0	--[v]	--
3 weeks' SD	0[w]	0[w]	0	0	0.0	0.0	--	--
6 weeks' SD	14[w]	29[w]	37	4	1.1	1.3	--	--
56-d vernalization								
0 weeks' SD	0[w]	0[w]	0	0	0.0	0.0	--	--
3 weeks' SD	14[w]	0[w]	9	0	1.0	0.0	53	--
6 weeks' SD	43[w]	0[w]	45	0	1.1	0.0	52	--
5 °C								
23-d vernalization								
0 weeks'SD	0[w]	14[w]	0	4	0.0	1.0	--	--
3 weeks' SD	43[w]	14[w]	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[w]	17[w]	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[w]	54	35	1.4	1.2	51	46
7.5 °C								
23-d vernalization								
0 weeks'SD	29[w]	0[w]	7	0	1.0	0.0	57	--
3 weeks' SD	86	57[w]	29	8	1.5	1.2	51	55
6 weeks' SD	86	71[w]	43	17	1.3	1.2	52	52
56-d vernalization								
0 weeks' SD	86	14[w]	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[w]	39	32	1.2	1.2	49	48
10 °C								
23-d vernalization								
0 weeks'SD	0[w]	0[w]	0	0	0.0	0.0	--	--
3 weeks' SD	100	57[w]	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[w]	29[w]	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								
Cultivar (CV)			*		NS		*	
SD duration (SD)			**		*		*	
Vernalization duration (VD)			*		NS		**	
Temperature (T)[u]			NS		NS		NS	
CV × SD			NS		NS		NS	
CV × VD			NS		NS		*	
SD × VD			NS		NS		NS	
CV × SD × VD × T			NS		NS		*	

[NS, *, **]Non-significant or significant at $P \leq 0.05$ or 0.001, respectively.

[z]Plants were given zero, three, or six weeks of short days (SDs) before vernalization. No plants flowered following 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.

[w]Significantly different from 100% flowering by χ^2 ($\alpha = 0.05$, 1 df).

[v]No flowering plants or flowering took longer than 70 days.

[u]Temperature interactions that are not shown are not significant.

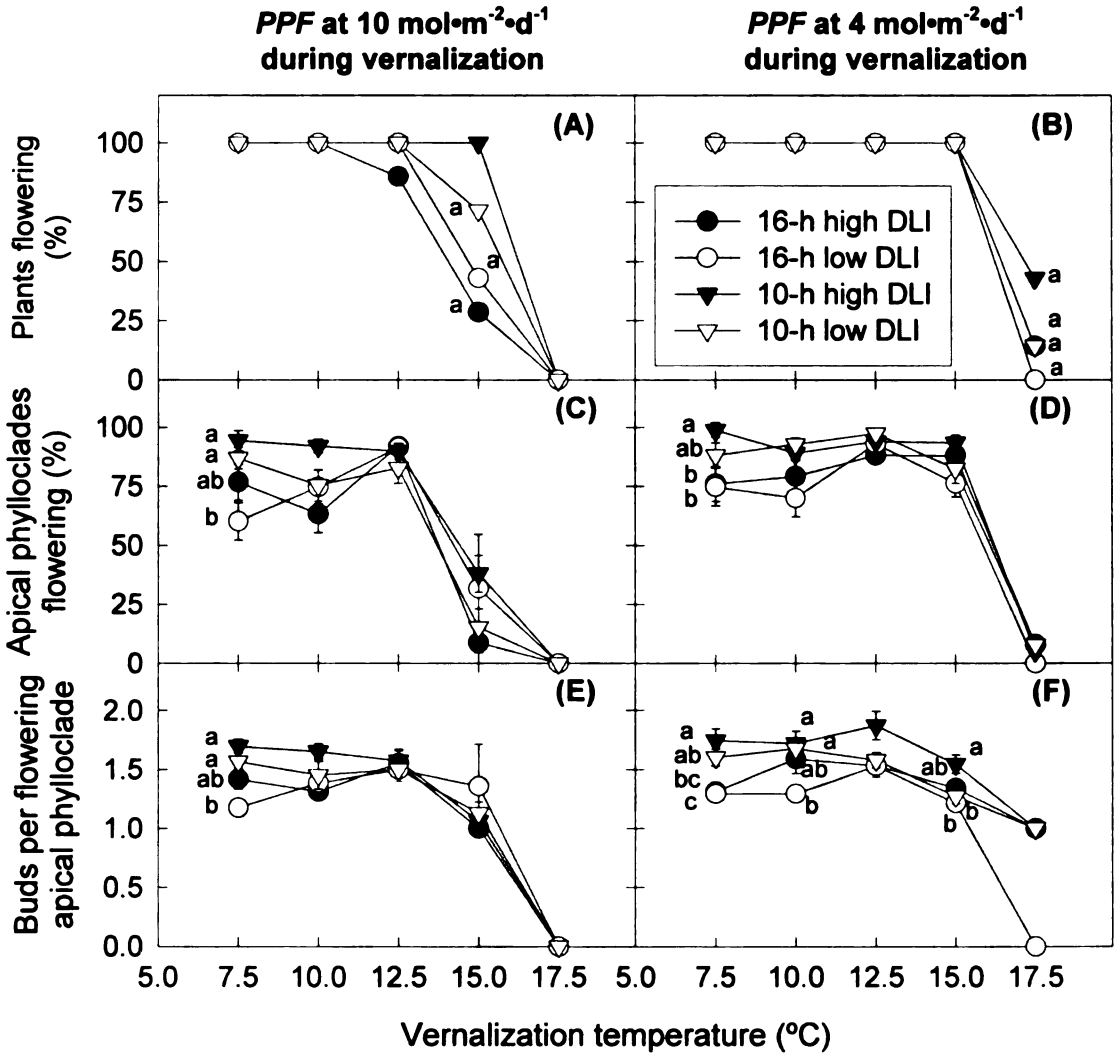

Figure 1. Flowering of *Hatiora gaertneri* 'Jan' given short-day (10-h) or long-day (16-h) treatment at high daily light integral (DLI) [≈12 mol•m^{-2}•d^{-1} photosynthetic photon flux, (PPF)] or low DLI (≈4.5 mol•m^{-2}•d^{-1}) for six weeks followed by vernalization at ≈10 or ≈4 mol•d^{-1} PPF and 7.5, 10, 12.5, 15, or 17.5 °C for eight weeks. Vertical bars represent ±1 SE. Labeled treatments in graphs (**A**) and (**B**) are significantly different from 100% flowering according to single degree-of-freedom χ^2 ($\alpha = 0.05$). Lower case letters near the symbols in graphs (**C**)–(**F**) indicate significant differences within each temperature ($P \leq 0.05$; $n \leq 7$, depending on percentage of plants flowering), and the absence of letters indicates no statistical differences.

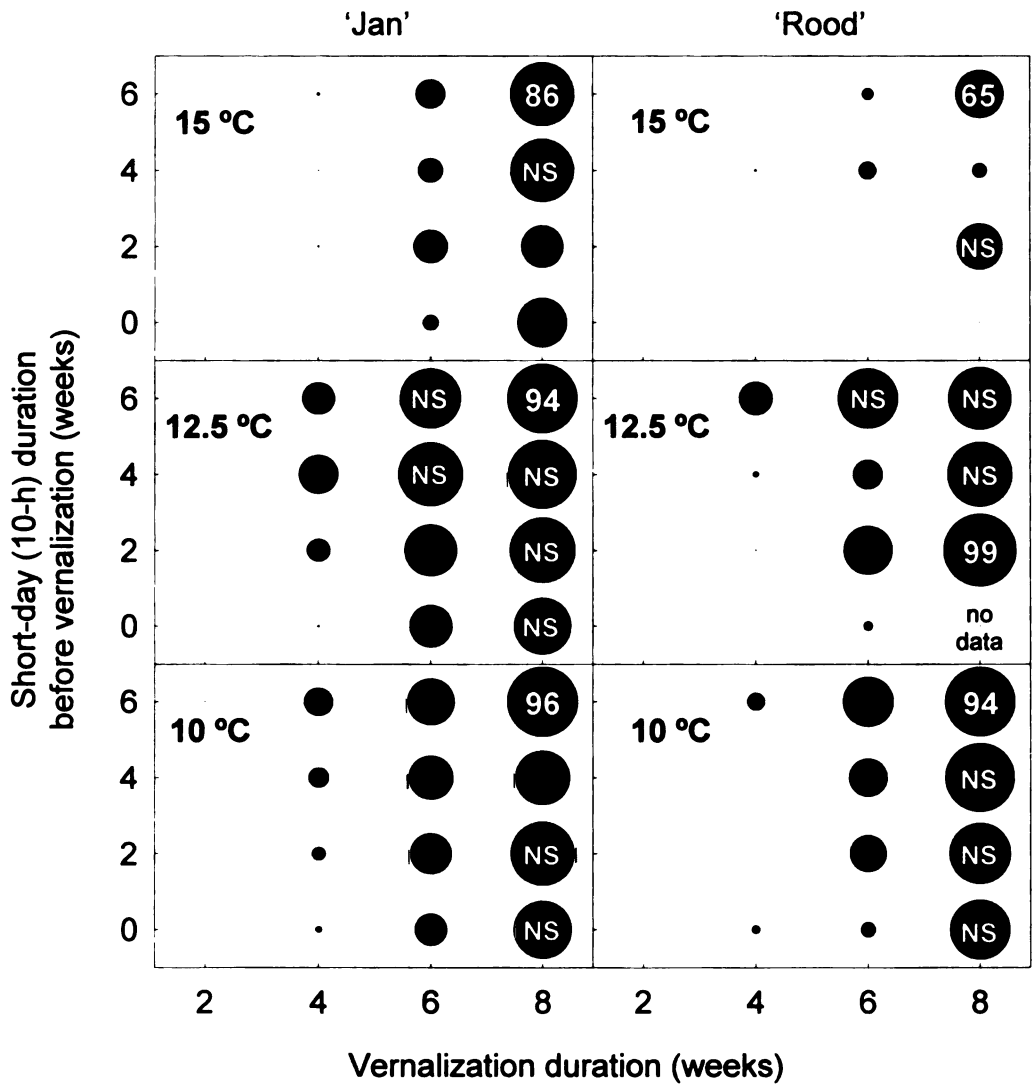

Figure 2. Effects of vernalization duration, temperature, and a 10-h short-day prevernalization treatment on flowering uniformity in *Hatiora gaertneri* 'Jan' and 'Rood'. Bubble size was determined by (percentage of plants flowering) × (proportion of apical phylloclades flowering). NS = not significantly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

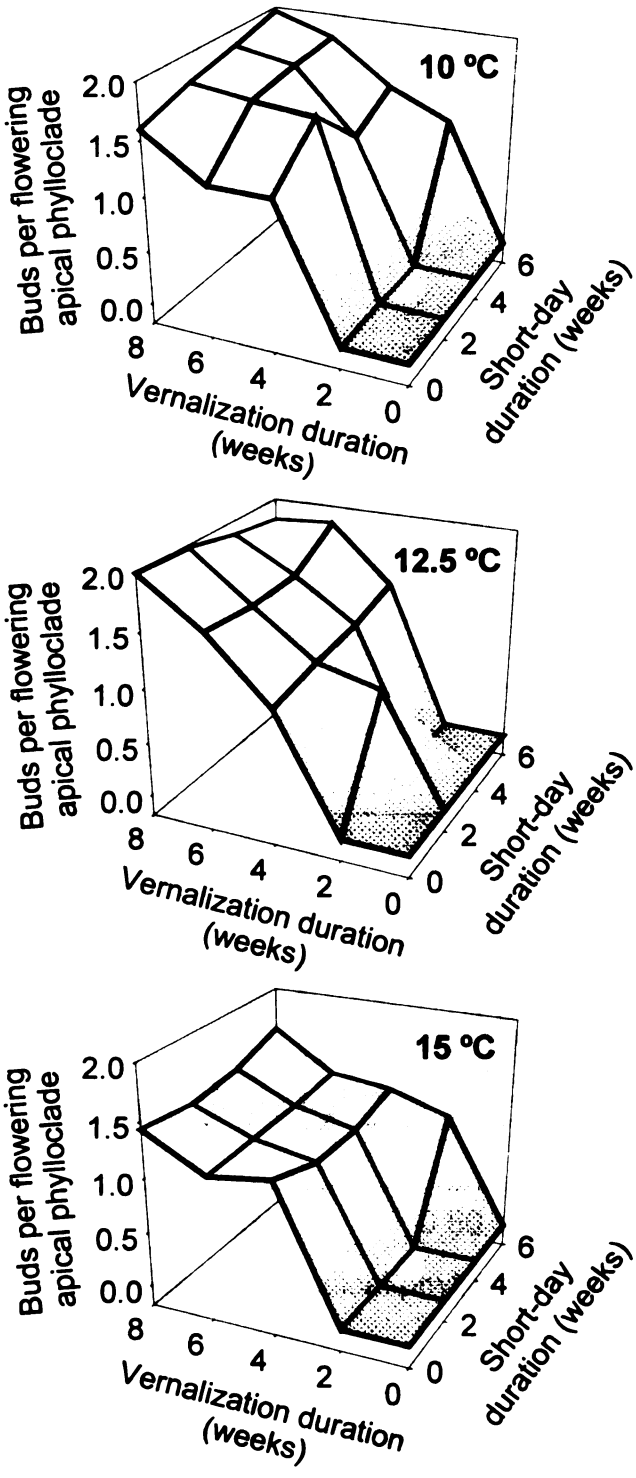

Figure 3. Buds per apical phylloclade on flowering *Hatiora* as a function of short-day (10-hour) duration before vernalization and vernalization duration and temperature. Response is averaged over cultivar (NS at $\alpha = 0.05$).

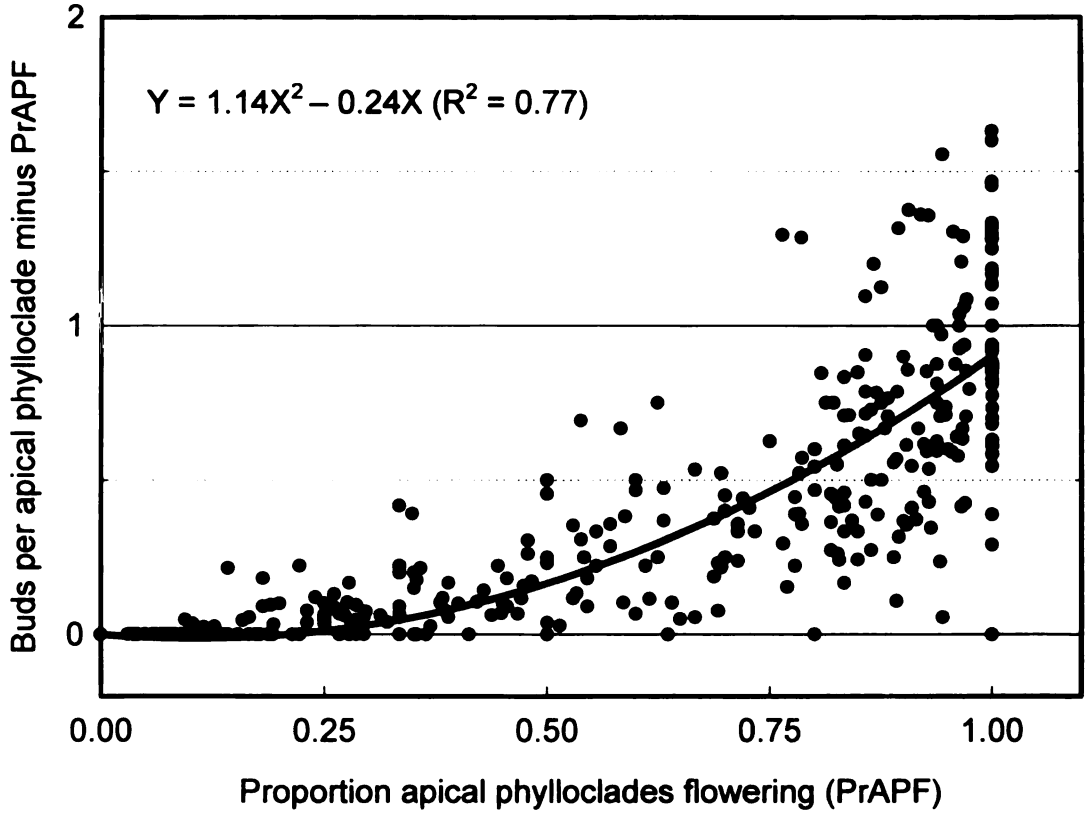

Figure 4. Number of buds per apical phylloclade above the minimum (one per flowering phylloclade) as a function of proportion of flowering phylloclades. All plants (flowering and non-flowering) are included.

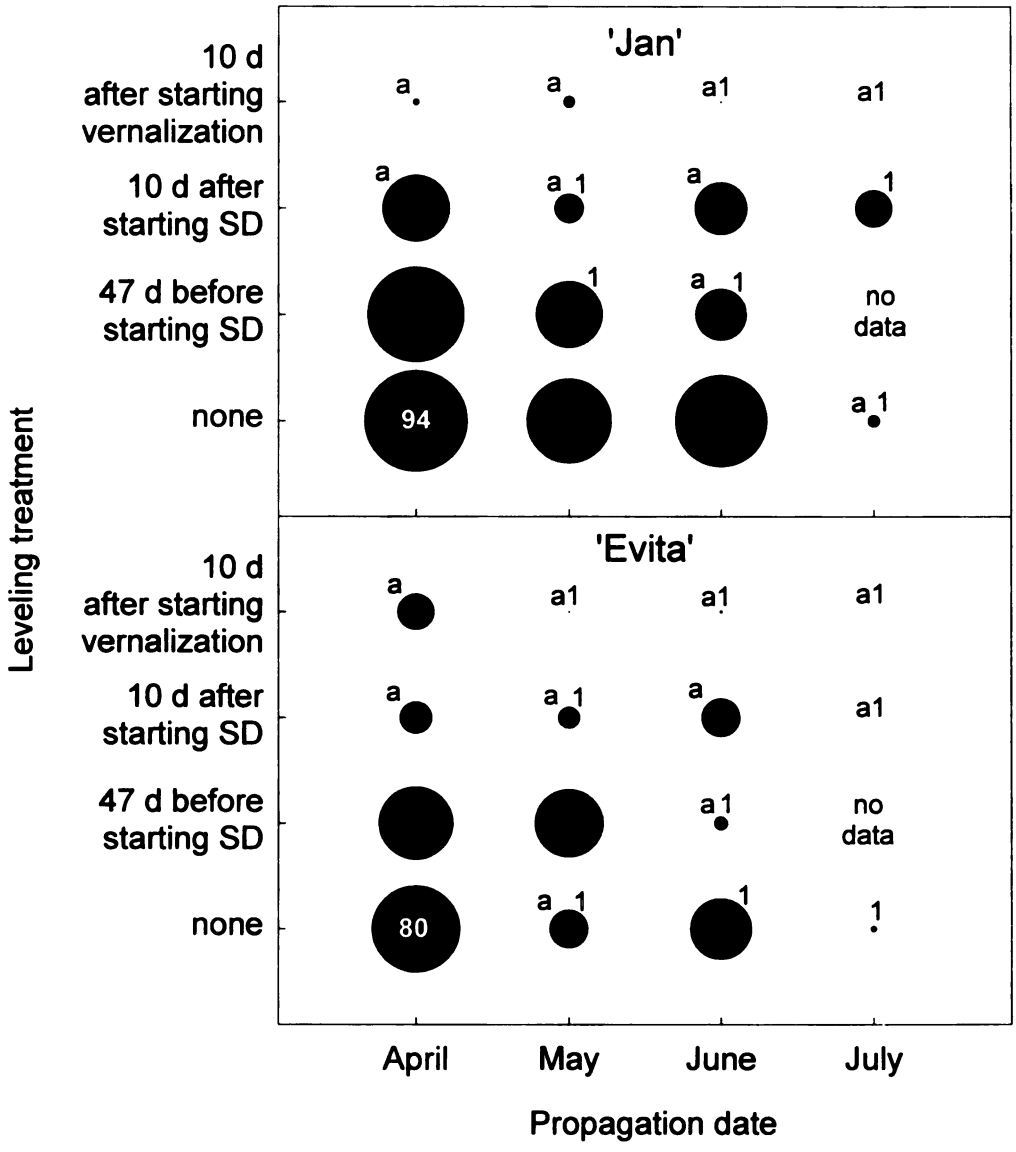

Figure 5. Effect of propagation date and leveling treatment on flowering uniformity in *Hatiora gaertneri* 'Jan' and *H.* ×*graeseri* 'Evita'. Bubble size was determined by (percentage of plants flowering) × (proportion of apical phylloclades flowering). The maximum value in each cultivar is labeled as a reference. SD indicates short days.

[a]Treatment value is significantly different from the maximum value within the cultivar and column (χ^2, $\alpha = 0.05$, 1 df).

[1]Treatment value is significantly different from the maximum value within the cultivar and row (χ^2, $\alpha = 0.05$, 1 df).

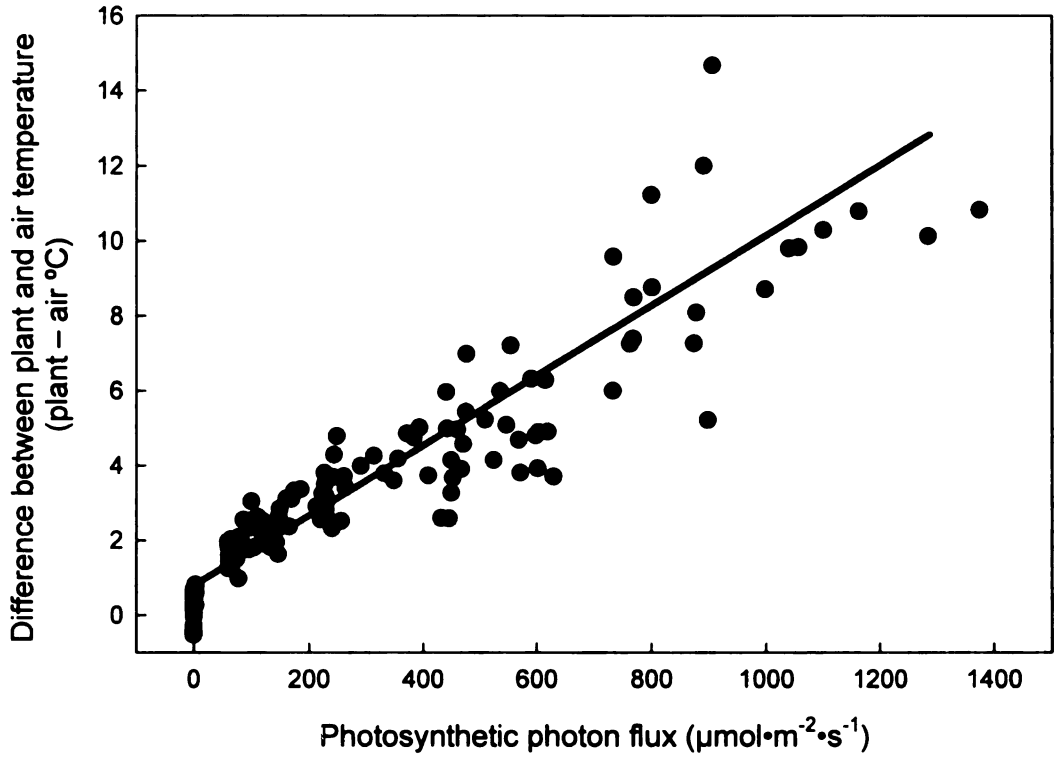

Figure 6. *Hatiora* ×*graeseri* increase in plant temperature above air temperature as a function of photosynthetic photon flux.