



RESEARCH PAPER

Temperature during the day, but not during the night, controls flowering of *Phalaenopsis* orchids

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Abstract

Phalaenopsis orchids are among the most valuable potted flowering crops commercially produced throughout the world because of their long flower life and ease of crop scheduling to meet specific market dates. During commercial production, *Phalaenopsis* are usually grown at an air temperature ≥ 28 °C to inhibit flower initiation, and a cooler night than day temperature regimen (e.g. 25/20 °C day/night) is used to induce flowering. However, the specific effect of day and night temperature on flower initiation has not been well described, and the reported requirement for a diurnal temperature fluctuation to elicit flowering is unclear. Two *Phalaenopsis* clones were grown in glass greenhouse compartments with constant temperature set points of 14, 17, 20, 23, 26, or 29 °C and fluctuating day/night (12 h/12 h) temperatures of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. The photoperiod was 12 h, and the maximum irradiance was controlled to ≤ 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$. After 20 weeks, $\geq 80\%$ of plants of both clones had a visible inflorescence when grown at constant 14, 17, 20, or 23 °C and at fluctuating day/night temperatures of 20/14 °C or 23/17 °C. None of the plants were reproductive within 20 weeks when grown at a constant 29 °C or at 29/17 °C or 29/23 °C day/night temperature regimens. The number of inflorescences per plant and the number of flower buds on the first inflorescence were greatest when the average daily temperature was 14 °C or 17 °C. These results indicate that a day/night fluctuation in temperature is not required for inflorescence initiation in these two *Phalaenopsis* clones. Furthermore, the inhibition of flowering when the day temperature was 29 °C and the night temperature was 17 °C or 23 °C suggests that a warm day temperature inhibits flower initiation in *Phalaenopsis*.

Key words: Average daily temperature, flower initiation, potted plants, temperature fluctuation.

Introduction

The orchid family, Orchidaceae, is among the largest of families of angiosperms, containing >25 000 described species within 859 genera (Cribb and Govaerts, 2005). Orchids are distributed in all regions of the world except Antarctica and are found growing in many different habitats and elevation gradients (Pridgeon, 2000). Despite the diversity of orchids in nature, only a small number of genera are cultivated in large quantities as commercial ornamental crops (e.g. *Cymbidium*, *Dendrobium*, *Oncidium*, and *Phalaenopsis*).

During the past decade, commercial production of orchids as potted flowering plants has increased tremendously throughout the world. In the USA, orchids are the second most valuable potted flowering crop, with a total reported wholesale value of US\$144 million in 2005 (US Department of Agriculture, 2006). Among all orchid genera sold within the USA, *Phalaenopsis* comprises 85–90% of the potted orchid sales (Nash, 2003) because of their ease of scheduling to meet specific market dates, high wholesale value, and long post-harvest life. In The Netherlands, *Phalaenopsis* was the most valuable potted plant at Dutch flower auctions: 29.4 million plants valued at €143.7 million wholesale were sold in 2005 (Vereniging van Bloemenveilingen in Nederland, 2006).

Flower induction in many plant species is controlled by exposure to particular photoperiods or after periods of low temperature. Vernalization is defined as a period of low temperature that promotes flowering when given to imbibed seeds, bulbs, or whole plants (Vince-Prue, 1975). The flowering response of plants to low temperature can

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Abbreviations: ADT, average daily temperature; HPS, high-pressure sodium; PPF, photosynthetic photon flux; VI, visible inflorescence.

be characterized as either a qualitative or a quantitative vernalization response. For example, some spring cultivars of wheat (*Triticum aestivum* L.) have a quantitative response to vernalization in which exposure to optimum temperatures between 3.8 °C and 6.0 °C is not required but rather accelerates flower induction (Baloch *et al.*, 2003). Other species, such as *Phalaenopsis* orchids, have a qualitative vernalization response in which the effective temperature for vernalization is as high as 25 °C (Chen *et al.*, 1994).

Phalaenopsis develop at least two undifferentiated bud primordia at each node that partially develop and then become dormant (Rotor, 1959). Under appropriate environmental and cultural conditions, the upper bud elongates and emerges through the epidermis of the stem and develops into an inflorescence (Wang, 1995). The primary environmental signal that initiates inflorescence development in *Phalaenopsis* is temperature. During commercial production of *Phalaenopsis*, plants are commonly grown at a temperature ≥ 28 °C to inhibit flower initiation and maintain vegetative growth (Sakanishi *et al.*, 1980; Chen *et al.*, 1994). To promote flowering of *Phalaenopsis*, Lee and Lin (1984, 1987) recommend a diurnal temperature fluctuation (e.g. 25/20 °C or 20/15 °C). However, to our knowledge, no data have been published to support the requirement for a diurnal temperature fluctuation for flower initiation in *Phalaenopsis*.

Although many diverse species have a vernalization response for flowering, few plants have been reported to require a diurnal temperature fluctuation to elicit flowering. *Scilla autumnalis* L. and *Urginea maritima* L. Baker remained vegetative when grown at a constant temperature of 10, 15, or 20 °C, whereas plants flowered when grown at 20/10 °C day/night (Halevy, 1990). In *Cymbidium* orchids, a positive diurnal fluctuation of 10–14 °C was suggested as a requirement for flower initiation; *Cymbidium* Astronaut 'Radjah' grown at 20/12, 26/12, or 26/18 °C (14 h day/10 h night) developed an average of 3.3, 11.7, or 6.2 inflorescences per plant, respectively (Powell *et al.*, 1988). However, the requirement for a diurnal temperature fluctuation for flower induction of *Cymbidium* remains unclear because treatments with and without a diurnal temperature fluctuation did not have the same average daily temperature (ADT).

Experiments were performed to resolve whether a diurnal temperature fluctuation is required for flowering of *Phalaenopsis*. In addition, the effects of day and night temperature on inflorescence initiation and flowering of two *Phalaenopsis* clones were determined to describe further this unique flower induction response.

Materials and methods

Plant material

In July 2003, clones of *Phalaenopsis* Brother Goldsmith '720' and *Phalaenopsis* Miva Smartissimo×Canberra '450' were transplanted

into 10 cm pots in medium containing 75% fine-grade Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) bark, 15% medium-grade Perlite, and 10% sphagnum peat (by volume), and grown in a commercial greenhouse in California. Plants were grown at 26 °C under a natural photoperiod (latitude 37 °N) and a maximum photosynthetic photon flux (PPF) of 280 $\mu\text{mol m}^{-2} \text{s}^{-1}$. On 22 September 2003, 240 plants were shipped to East Lansing, MI, and were subsequently grown in a glass-glazed greenhouse at a constant temperature of 29 °C to inhibit flowering. The photoperiod was a constant 16 h (06.00 h to 22.00 h) consisting of natural photoperiods (latitude 42 °N) with day extension lighting provided by high-pressure sodium (HPS) lamps delivering a PPF of 20–25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant height [as measured with a line quantum sensor (Apogee Instruments, Inc., Logan, UT, USA)]. Light transmission was reduced using woven shade curtains (OLS 50, Ludvig Svensson Inc., Charlotte, NC, USA) and whitewash applied to the greenhouse glazing so that the maximum PPF at plant height was 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The average plant leaf span was 24–31 cm at the beginning of the experiment. Leaf span was measured by extending the longest opposing leaves on each plant to a horizontal position and then measuring the length from one leaf tip to the opposite leaf tip. The same plant material was used during replication 2 as in replication 1. The average plant leaf span at the beginning of replication 2 was 31–44 cm. The *Phalaenopsis* clones used in this study were selected based on commercial availability.

Plant culture

Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing (mg l⁻¹): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU Special, GreenCare Fertilizers, Inc., Kankakee, IL, USA). In year 2, all plants were transplanted into 15 cm pots and grown in medium consisting of 33% medium-grade Douglas fir bark (Rexius Forest By-Products Inc., Eugene, OR, USA), 45% medium-grade chopped coconut (*Cocos nucifera* L.) coir (Millenniumsoils Coir, St Catharines, Ontario, Canada), 11% long-fibre Canadian sphagnum peat (Mosser Lee Co., Millston, WI, USA), and 11% coarse-grade Perlite (OFE Intl. Inc., Miami, FL, USA) (by volume).

Temperature treatments

Ten plants of each *Phalaenopsis* clone were placed in each of 12 glass greenhouse sections with constant temperature set points of 14, 17, 20, 23, 26, or 29 °C or fluctuating day/night (12 h/12 h) temperature set points of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. Temperature set points were maintained by an environmental computer that controlled roof vents, exhaust fans, evaporative cooling, and heating as needed. The transition period from the day to night temperature set point was often within 5 min, whereas the transition from the night to day temperature set point was within 30 min. The photoperiod was maintained at 12 h by pulling opaque black cloth from 17.00 h to 08.00 h and extended with light from incandescent lamps (2–3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant height).

The photoperiod and skotoperiod paralleled the day and night temperature set points, respectively. A vapour pressure deficit of 0.9 kPa was maintained in each greenhouse by the injection of steam below the benches. Light transmission through the greenhouse was reduced as previously described. The average daily light integral at plant level per 4 week period during the experiment was between 2.4 and 4.4 mol m⁻² d⁻¹ (Table 1). Air temperature was measured in each greenhouse section by aspirated thermocouples (0.127 mm type E) every 10 s, and hourly averages were recorded by a CR10 data logger (Campbell Scientific, Logan, UT, USA). Temperature control during the experiment was within ± 2.0 °C of the greenhouse temperature set points for all treatments in both years (Table 2).

Table 1. Average daily light integral ($\text{mol m}^{-2} \text{d}^{-1}$) at plant level per 4 week period during the experiment for year 1 (1 December 2003 to 19 April 2004) and year 2 (26 October 2004 to 15 March 2005)

Year	4 week period				
	1	2	3	4	5
1	2.4	2.6	3.5	3.8	4.1
2	2.7	2.5	2.4	3.1	4.4

Table 2. Actual average air temperatures of each temperature treatment in years 1 and 2

The photoperiod and day and night temperature set points were 12 h.

Day/night temperature set point ($^{\circ}\text{C}$)	Actual day/night temperature ($^{\circ}\text{C}$)	
	Year 1	Year 2
14/14	14.5/14.3	14.1/13.5
17/17	17.4/17.4	17.2/16.6
20/20	20.2/20.1	21.0/20.4
23/23	24.5/22.6	23.4/21.8
26/26	25.8/26.1	26.2/26.0
29/29	29.1/29.4	28.8/28.2
20/14	20.0/13.8	19.1/13.5
23/17	21.9/16.3	22.5/16.9
26/14	25.4/14.3	24.9/13.9
26/20	25.8/19.4	25.9/20.2
29/17	27.8/17.1	28.6/17.3
29/23	28.8/22.3	29.0/23.1

The experiment was replicated beginning on 1 December 2003 (year 1) and on 26 October 2004 (year 2). In each year, plants were assigned randomly to each of the temperature treatments and grown for 20 weeks. After completion of the first replication and until the beginning of the second replication, plants were grown in a common glass-glazed greenhouse with a constant temperature set point of 29°C to inhibit flowering. During that period, the photoperiod was a constant 16 h (06.00 h–22.00 h), consisting of natural photoperiods with day extension lighting provided by HPS lamps delivering a PPF of $20\text{--}25 \mu\text{mol m}^{-2} \text{s}^{-1}$ at plant height. The maximum PPF was maintained at $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ by using woven shade curtains and external whitewash, as previously described.

Data collection

The date the first inflorescence was visible without dissection (0.1–0.5 cm) and the date that the first flower opened were recorded for each plant. Days to visible inflorescence (VI), days from VI to flowering, days to flowering, and VI and flowering percentages were calculated for each treatment. The total number of VIs and flower number on the first VI were recorded for each plant. On the date of flowering, inflorescence lengths (from emergence to the first flower and from the first flower to the inflorescence tip) were measured and the total inflorescence length was calculated. Plants without a VI within 20 weeks of the onset of treatments were considered non-reproductive. The duration of the experiment was 20 weeks because an inflorescence usually emerges after 3–5 weeks after exposure to an inductive temperature $<25^{\circ}\text{C}$ (Lee and Lin, 1987).

Statistical analysis

A completely randomized block design was used each year. Data were analysed with the SAS (SAS Institute, Inc., Cary, NC, USA)

mixed-model procedure (PROC MIXED), and pairwise comparisons between treatments were performed using Tukey's honest significant difference test. Arcsine square root transformation was performed on the data percentage before analysis.

Results

Temperature influenced the percentage of plants that initiated a VI and flowered (Fig. 1). After 20 weeks, $\geq 80\%$ of plants of both *Phalaenopsis* clones had a VI when grown at a day/night temperature of 14/14, 17/17, 20/20, 23/23, 20/14, or 23/17 $^{\circ}\text{C}$. None of the plants were reproductive within 20 weeks when grown at temperatures of 29/29, 29/17, or 29/23 $^{\circ}\text{C}$. In *Phalaenopsis* Miva Smartissimo \times Canberra '450', only some plants within the treatments were reproductive when the day temperature was 26°C and the night was 14, 20, or 26°C (55, 75, and 10%, respectively). By contrast, none of the Brother Goldsmith '720' plants had initiated an inflorescence within 20 weeks at temperature treatments of 26/26, 26/14, and 26/20 $^{\circ}\text{C}$. All of the *Phalaenopsis* Miva Smartissimo \times Canberra '450' plants grown at 20/20, 23/23, and 23/17 $^{\circ}\text{C}$ were in flower within 20 weeks, whereas for *Phalaenopsis* Brother Goldsmith '720', 85% and 75% were in flower when grown at 20/20 $^{\circ}\text{C}$ and 23/23 $^{\circ}\text{C}$, respectively (data not shown).

Day and night temperature had different effects on inflorescence initiation of both *Phalaenopsis* clones in the present study: day temperature was highly significant ($P \leq 0.001$), but night temperature was not significant ($P \geq 0.09$). There was a significant difference in VI percentage among some temperature treatments with a similar ADT (Table 3). For example, the VI percentage of *Phalaenopsis* Miva Smartissimo \times Canberra '450' grown at 23/23, 26/20, or 29/17 $^{\circ}\text{C}$ was 100, 75, and 0%, respectively. Similarly, the VI percentage of *Phalaenopsis* Brother Goldsmith '720' at 23/23, 26/20, and 29/17 $^{\circ}\text{C}$ was 90, 0, and 0%, respectively.

Plants of both *Phalaenopsis* clones grown at an ADT of 17°C initiated inflorescences in a similar amount of time for each year, despite delivery technique; time to VI at 17/17 $^{\circ}\text{C}$ or 20/14 $^{\circ}\text{C}$ ranged from 32–45 d. There were no significant differences in time to VI for both clones grown at day/night temperature treatments of 17/17, 20/20, and 23/23 $^{\circ}\text{C}$, and time to VI ranged from 23–39 d (Table 4). Inflorescence initiation of both clones was slower when grown at a constant 14°C and when Miva Smartissimo \times Canberra '450' was grown at 26/14 $^{\circ}\text{C}$ during year 1. Among the treatments that elicited $\geq 30\%$ flowering within 20 weeks, time from VI to anthesis and total time to anthesis for both clones decreased as ADT increased (Table 4). *Phalaenopsis* Miva Smartissimo \times Canberra '450' and Brother Goldsmith '720' plants grown at 23/23 $^{\circ}\text{C}$ had the shortest total time to flower, requiring on average 102 d and 111 d, respectively.

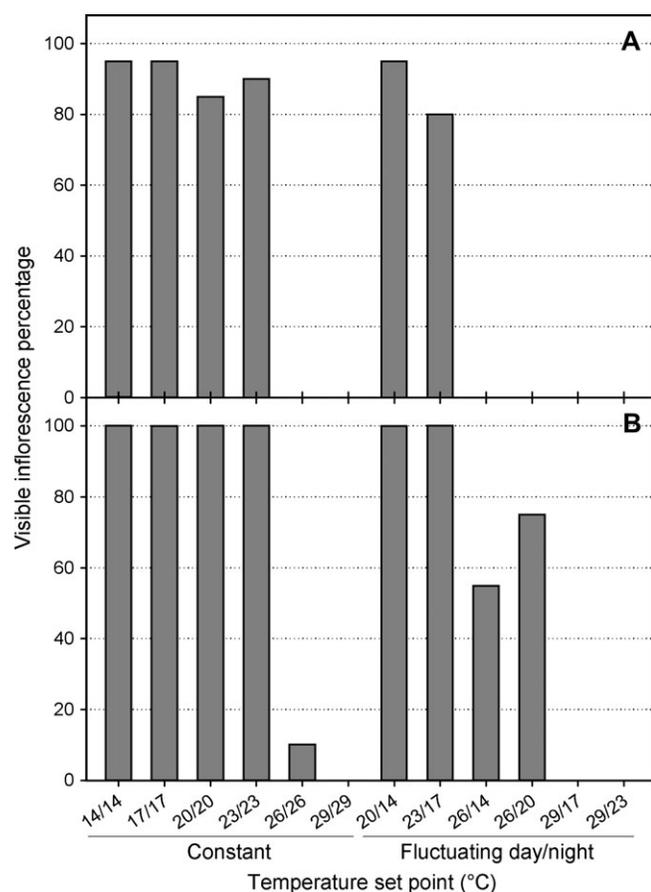


Fig. 1. Percentages of visible inflorescences for *Phalaenopsis* Brother Goldsmith '720' (A) and *Phalaenopsis* Miva Smartissimo×Canberra '450' (B) after 20 weeks at constant temperature set points 14, 17, 20, 23, 26, or 29 °C and fluctuating day/night temperature set points of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. The day and night were 12 h each. Data were pooled for years 1 and 2.

The number of inflorescences per plant in both *Phalaenopsis* clones was greatest at 14 °C and 17 °C (Table 4). In addition, the number of flower buds on the first VI was generally greater at the cooler temperature treatments than at treatments with a higher ADT. For example, average flower bud number of *Phalaenopsis* Miva Smartissimo×Canberra '450' grown at 26/14 °C was 2.2, while plants grown at 14/14 °C had on average 6.2 buds. For *Phalaenopsis* Brother Goldsmith '720', flower bud number was greater (5.7 or 5.8) for plants grown at an ADT of 14 °C or 17 °C compared with that of plants grown at a day temperature of 23 °C. The total inflorescence length at anthesis was not significantly influenced by temperature (Table 4).

Discussion

The present results indicate that *Phalaenopsis* does not require a day/night temperature fluctuation for inflorescence initiation, at least in these two orchid clones. Inflorescence initiation occurred in both clones at constant temperatures of 14, 17, 20, and 23 °C. The inhibition of

Table 3. Comparison of visible inflorescence percentage in treatments with a similar average daily temperature for *Phalaenopsis* Miva Smartissimo×Canberra '450' and Brother Goldsmith '720'

The photoperiod and day and night temperature set points were 12 h. Arcsine square root transformation was performed on the data for years 1 and 2, and the transformed percentages were averaged from each year before analysis. Statistical comparison is within each group and column. NS, non-significant; **, ***, significant at $P \leq 0.01$ or 0.001, respectively.

Day/night temperature set point (°C)	Visible inflorescence (%)	
	Miva Smartissimo×Canberra '450'	Brother Goldsmith '720'
17/17	100	95
20/14	100	95
Significance	NS	NS
20/20	100	85
23/17	100	80
26/14	55	0
Significance	**	***
23/23	100	90
26/20	75	0
29/17	0	0
Significance	***	***
26/26	10	0
29/23	0	0
Significance	NS	NS

inflorescence initiation in plants grown at a constant temperature of 29 °C supports previous results by Sakanishi *et al.* (1980), in which flowering was inhibited when plants were grown at 28 °C. For *Phalaenopsis* Brother Goldsmith '720', none of the temperature treatments induced 100% VI during year 1. It is postulated that this outcome can be at least partially attributed to plant juvenility in year 1 for this clone. Wang and Lee (1994) reported that plants that have not reached sufficient maturity could require cooler temperatures or longer exposure to initiate inflorescences than larger, more mature plants. In year 2, the average plant leaf span of Brother Goldsmith '720' had increased by 5.7 cm, and more complete flowering within a population occurred.

The difference in VI percentage among treatments with a similar ADT indicates that inflorescence initiation in *Phalaenopsis* is inhibited by a high day temperature, regardless of the night temperature. Wang (2004) reported that the 'Lava Glow' clone of the hybrid *Doritaenopsis* (*Phalaenopsis* Buddha's Treasure×*Doritis pulcherrima*) grown for 29–36 weeks at 25/20, 20/25, 25/15, or 15/25 °C (12 h day/12 h night) had flowering percentages of 33, 93, 0, and 100%, respectively. Therefore, a day temperature >26 °C inhibits inflorescence initiation, regardless of the night temperature. However, the night temperature may influence flower initiation when the day temperature is <26 °C. This is supported by the different reproductive percentages in *Phalaenopsis* Miva Smartissimo×Canberra '450' among plants grown at temperature treatments of

Table 4. Days to visible inflorescence (VI), days from VI to flower, total days to flower, number of flower buds on first VI, VI number, and total inflorescence length at flower for *Phalaenopsis Miva Smartissimo*×*Canberra '450'* and *Brother Goldsmith '720'* after 20 weeks in temperature treatments with $\geq 10\%$ VI

Time to flower and inflorescence length data from treatments with $\leq 30\%$ flowering after 20 weeks were not included in the analysis. The photoperiod and day and night temperature set points were 12 h. Means within columns followed by different letters are significantly different by Tukey's honest significant difference test at $P \leq 0.05$.

Day/night temperature set point (°C)	Days to VI		Days from VI to flower		Total days to flower		No. of flower buds on first VI		VI no. ^z	Total inflorescence length (cm) ^z
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2		
<i>Miva Smartissimo</i> × <i>Canberra '450'</i>										
14/14	52 b	63 a	–	–	–	–	6.2 a	5.9 a	1.5 a	–
17/17	39 c,d	32 b,c,d	–	–	–	–	4.0 b,c	6.0 a	1.4 a	–
20/14	45 b,c	38 b,c	–	–	–	–	4.5 b	5.2 a,b,c	1.1 b	–
20/20	34 d	23 d	80 b	89 a	114 b	113 b	4.2 b,c	5.0 a,b,c	1.0 b	40 a
23/17	37 c,d	32 b,c,d	86 a	81 b	123 a	113 b	3.8 b,c	5.4 a,b	1.1 b	41 a
26/14	67 a	38 b,c	–	87 a,b	–	124 a	2.2 d	4.3 b,c	1.0 b	39 a
23/23	34 d	29 c,d	69 d	72 c	103 c	101 c	3.9 b,c	4.5 b,c	1.0 b	38 a
26/20	53 b	40 b	74 c	66 d	127 a	106 b,c	3.2 c,d	4.0 c	1.0 b	41 a
Significance										
Temperature	***	***	***	***	***	***	***	***	***	NS
Year	***		NS		***		***		NS	***
Temperature×year	***		***		***		***		NS	NS
<i>Brother Goldsmith '720'</i>										
14/14	60 a ^z	–	–	–	–	–	5.8 a ^z	–	1.3 a	–
17/17	33 c	–	–	–	–	–	5.8 a	–	1.1 a,b	–
20/14	40 b,c	–	–	–	–	–	5.7 a	–	1.0 b	–
20/20	33 c	–	89 a	96 a	126 a ^z	–	5.2 a,b	–	1.0 b	26 a
23/17	43 b	–	90 a	–	127 a	–	4.5 b	–	1.0 b	30 a
23/23	36 b,c	–	73 b	87 b	111 b	–	4.7 b	–	1.0 b	29 a
Significance										
Temperature	***		***	*	***		*		***	NS
Year	NS		***		***		NS		NS	NS
Temperature×year	*		*		NS		NS		NS	NS

NS, non-significant; *, ***, significant at $P \leq 0.05$ or 0.001 , respectively; ^z, data pooled for analysis; –, not included in the analysis.

26/14, 26/20, and 26/26 °C and the results of Wang (2004).

The requirement for a low temperature for flower initiation in *Phalaenopsis* can be considered as a vernalization process found in many temperate plants. However, the effective temperature range and duration for vernalization vary considerably among species. For example, in *Veronica spicata* L. 'Red Fox', complete flowering occurred after vernalization at -2.5 °C and 0 °C for ≥ 4 weeks, 2.5 °C and 5.0 °C for ≥ 6 weeks, and at 7.5 °C for 8 weeks (Fausey, 2005). In *Odontioda* and *Miltoniopsis* orchids, the most effective vernalization temperature was considerably higher, ~ 14 °C (Blanchard, 2005; Lopez and Runkle, 2006). In *Phalaenopsis*, the maximum effective temperature for vernalization is even higher: ~ 25 °C.

In Easter lily (*Lilium longiflorum* Thunb.), vernalization is a cumulative process in which bulbs must be exposed to temperatures between 2.0 °C and 7.0 °C for 1000 h for uniform shoot emergence and flowering (Lange, 1993). The accumulation of chilling hours in Easter lily bulbs is probably different from the vernalization process in *Phalaenopsis*. If the vernalization process of *Phalaenopsis* were regulated by the accumulation of chilling hours (hours

of exposure to temperature < 25 °C), then 20 weeks should have been sufficient time to observe a reproductive response in plants grown at $29/17$ °C, which is effectively 10 weeks at 17 °C. Alternatively, the inhibition of flowering at $29/17$ °C could be the result of high temperature stress. Further research on the vernalization response of *Phalaenopsis* is needed before a mechanistic model can be proposed.

At temperature treatments of $26/14$ °C and $26/20$ °C, inflorescence initiation occurred in 55% or 75% of *Phalaenopsis Miva Smartissimo*×*Canberra '450'* plants but did not occur in the clone *Brother Goldsmith '720'*. This different response between clones could be attributed to a difference in sensitivity to temperature from their varied genetic backgrounds. The predominant species from which *Phalaenopsis Miva Smartissimo*×*Canberra '450'* have been bred are *Phalaenopsis amabilis* (L.) Blume, *Phalaenopsis aphrodite* Rchb.f., *Phalaenopsis sanderiana* Rchb.f., and *Phalaenopsis schilleriana* Rchb.f., whereas that of *Phalaenopsis Brother Goldsmith '720'* includes *Phalaenopsis stuartiana* Rchb.f. and *Phalaenopsis lueddemanniana* Rchb.f. (Wildcatt Orchids, 2004). The upper temperature limit for inflorescence initiation in *Phalaenopsis Brother Goldsmith '720'* could be lower than that

of Miva Smartissimo×Canberra '450'. For example, the background of Miva Smartissimo×Canberra '450' includes *P. sanderiana*, a species that is native to the Philippines, where the natural flowering period is during the warm summer (Christenson, 2001). As suggested previously, the more mature Miva Smartissimo×Canberra '450' clone may have been less sensitive to temperature than Brother Goldsmith '720'. A juvenility period in which a plant is insensitive to environmental stimuli for flower induction has been reported in several herbaceous plants. For example, *Coreopsis grandiflora* Hogg ex Sweet., *Gaillardia*×*grandiflora* van Houtte, *Heuchera sanguinea* Engelm., and *Rudbeckia fulgida* Ait. responded to vernalization and flowered uniformly when plants had a minimum of eight, 16, 19, and 10 nodes before the cold treatment, respectively (Yuan *et al.*, 1998).

The number of inflorescences per plant and flower buds on the first VI was generally greatest for both clones when they were grown at the coolest temperatures (e.g. 14/14, 17/17, or 20/14 °C). Lee and Lin (1984) observed a similar cool temperature response in *Phalaenopsis* Dos Pueblos×Juanit, in which plants grown at 20/15 °C or 25/20 °C had on average 2.2 and 1.2 inflorescences per plant, respectively. For *Phalaenopsis* Taisuco Moonriver×*P. equestris* 'Alba', the number of flower buds on the main axis of the first VI generally increased from 4.6 to 9.8 as the constant ADT decreased from 25.5 °C to 14.3 °C (Robinson, 2002). However, the low ADT treatments that elicited the greatest flower number also delayed flower development. Temperature had a significant effect on total time to anthesis of *Phalaenopsis* in the present study. Similar results were reported by Robinson (2002), who found that there was a linear relationship between temperature and rate of development toward visible bud and anthesis.

A major economic challenge for the production of *Phalaenopsis* orchids in temperate climates is the high cost of energy for heating a greenhouse to maintain vegetative growth. Energy is typically the second largest greenhouse production cost for growers located in temperate climates (Bartok, 2001). In the present study, inflorescence initiation was inhibited in treatments with a high day temperature set point (e.g. 29 °C), even when the night temperature set point was cool (e.g. 17 °C). Sakanishi *et al.* (1980) investigated the effects of increasing the duration of high temperature exposure when the average night temperature was 20 °C and reported that inflorescence emergence was inhibited when plants were exposed to ≥12 h at a temperature of 28 °C each day. These results suggest that during *Phalaenopsis* production, a cool night temperature set point could be used to inhibit flowering if the day temperature set point was sufficiently warm (≥28 °C). This production strategy could have a significant economic impact for commercial growers because ~80% of the energy for heating a greenhouse is required at night (Bartok, 2001). Further research is necessary to

determine the magnitude of high temperature and minimum daily exposure to high temperature to inhibit flowering.

In year 1, after 11 weeks at the various temperature treatments, symptoms of mesophyll cell collapse (e.g. tan irregular depressions on the adaxial leaf surface) on *Phalaenopsis* Miva Smartissimo×Canberra '450' were observed at day/night temperatures of 20/14, 26/14, 26/20, and 29/17 °C. Mesophyll cell collapse was not observed in treatments with a constant temperature set point or in *Phalaenopsis* Brother Goldsmith '720' at any of the temperature treatments. The symptoms of mesophyll cell collapse could have been chilling injury from a rapid decrease in temperature when the day ended and the night temperature began. At the onset of the skotoperiod, cold air (often ≤0 °C) was actively drawn into the greenhouse sections until the cooler night temperature set point was achieved. The absence of symptoms on *Phalaenopsis* Brother Goldsmith '720' could be attributed to the genetic background of this clone. Mesophyll cell collapse occurred on *Phalaenopsis* after exposure to 2, 4, or 7 °C for 1 h or more in darkness (McConnell and Sheehan, 1978). The collapse of one or more layers of mesophyll cells resulted in the formation of an internal horizontal necrotic layer between the upper and lower epidermal cells (McConnell and Sheehan, 1978). The reported symptoms were dark brown, pitted areas on adaxial leaf surfaces, which were similar to the present observations with Miva Smartissimo×Canberra '450'.

In conclusion, flowering responses of *Phalaenopsis* were different among some treatments with a similar ADT, suggesting that the day and night temperatures have separate effects on inflorescence initiation. These results also indicate that a high day temperature can inhibit inflorescence initiation and flowering, even when the night temperature is otherwise conducive for reproductive development. In addition, a day/night fluctuation in temperature is not required for inflorescence initiation in these two *Phalaenopsis* clones. Although time to flower is shortest at constant 23 °C, the number of inflorescences and flower buds per plant was greater at cooler temperatures.

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References

- Baloch DM, Karow RS, Marx E, Kling JG, Witt MD. 2003. Vernalization studies with Pacific Northwest wheat. *Agronomy Journal* **95**, 1201–1208.

- Bartok Jr JW.** 2001. *Energy conservation for commercial greenhouses*. Ithaca, NY: Natural Resource, Agriculture, and Engineering Service Cooperative Extension.
- Blanchard MG.** 2005. Effects of temperature on growth and flowering of two *Phalaenopsis* and two *Odontioda* orchid hybrids. MS thesis, Michigan State University, USA.
- Chen WS, Liu HY, Yang L, Chen WH.** 1994. Gibberellin and temperature influence carbohydrate content and flowering in *Phalaenopsis*. *Physiologia Plantarum* **90**, 391–395.
- Christenson EA.** 2001. *Phalaenopsis: a monograph*. Portland, OR: Timber Press.
- Cribb P, Govaerts R.** 2005. Just how many orchids are there? In: Raynal-Roques A, Roguenant A, Prat D, eds. *Proceedings of the 18th World Orchid Conference*. Dijon, France, 161–172.
- Fausey BA.** 2005. The effects of light quantity and vernalization on growth and flowering of *Arabidopsis*, *Achillea*, *Gaura*, *Isotoma*, *Lavandula* and *Veronica*. PhD dissertation, Michigan State University, USA.
- Halevy AH.** 1990. Recent advances in control of flowering and growth habit of geophytes. *Acta Horticulturae* **266**, 35–42.
- Lange NE.** 1993. Modeling flower induction in *Lilium longiflorum*. MS thesis, Michigan State University, USA.
- Lee N, Lin GM.** 1984. Effect of temperature on growth and flowering of *Phalaenopsis* white hybrid. *Journal of the Chinese Society for Horticultural Science* **30**, 223–231.
- Lee N, Lin GM.** 1987. Controlling the flowering of *Phalaenopsis*. In: Chang LR, ed. *Proceedings of a symposium on forcing culture of horticulture crops*. Special Publication 10. Changhua, Taiwan, Republic of China: Taichung District Agricultural Improvement Station, 27–44.
- Lopez RL, Runkle ES.** 2006. Temperature and photoperiod regulate flowering of potted *Miltoniopsis* orchids. *HortScience* **41**, 593–597.
- McConnell DB, Sheehan TJ.** 1978. Anatomical aspects of chilling injury to leaves of *Phalaenopsis* Bl. *HortScience* **13**, 705–706.
- Nash N.** 2003. *Phalaenopsis primer: a beginner's guide to growing moth orchids*. *Orchids* **72**, 906–913.
- Powell CL, Caldwell KI, Littler RA, Warrington I.** 1988. Effect of temperature regime and nitrogen fertilizer level on vegetative and reproductive bud development in *Cymbidium* orchids. *Journal of the American Society for Horticultural Science* **113**, 552–556.
- Pridgeon A.** 2000. *The illustrated encyclopedia of orchids*. Portland, OR: Timber Press.
- Robinson KA.** 2002. Effects of temperature on the flower development rate and morphology of *Phalaenopsis* orchid. MS thesis, Michigan State University, USA.
- Rotor GB.** 1959. The photoperiodic and temperature responses of orchids. In: Withner CL, ed. *The orchids: a scientific survey*. NY, USA: Ronald Press, 397–416.
- Sakanishi Y, Imanishi H, Ishida G.** 1980. Effect of temperature on growth and flowering of *Phalaenopsis amabilis*. *Bulletin of the University of Osaka Prefecture, Series B: Agriculture and Biology* **32**, 1–9.
- US Department of Agriculture.** 2006. *Floriculture crops 2005 summary*. Washington, DC: Agricultural Statistics Board.
- Vereniging van Bloemenveilingen in Nederland.** 2006. Annual report 2005. Leiden, The Netherlands: Association of Dutch Flower Auctions.
- Vince-Prue D.** 1975. *Photoperiodism in plants*. London: McGraw Hill.
- Wang YT.** 1995. *Phalaenopsis* orchid light requirement during the induction of spiking. *HortScience* **30**, 59–61.
- Wang YT.** 2004. Effects of reversed day/night temperatures on a *Doritaenopsis* hybrid orchid. *HortScience* **39**, 834.
- Wang YT, Lee N.** 1994. Another look at an old crop: potted blooming orchids, part 2. *Greenhouse Grower* **120**(2), 36–38.
- Wildcatt Orchids.** 2004. *Wildcatt orchids September 2004 database*. Ames, IA: Wildcatt Database Co.
- Yuan M, Carlson WH, Heins RD, Cameron AC.** 1998. Determining the duration of the juvenile phase of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* × *grandiflora* (Van Houtte), *Heuchera sanguinea* (Engelm.) and *Rudbeckia fulgida* (Ait.). *Scientia Horticulturae* **72**, 135–150.