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EFFECTS OF TEMPERATURE ON FLOWER DEVELOPMENT RATE AND MORPHOLOGY OF *PHALAENOPSIS*.

BY

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ABSTRACT

EFFECTS OF TEMPERATURE ON FLOWER DEVELOPMENT RATE AND MORPHOLOGY OF *PHALAENOPSIS*.

By

Kari Ann Robinson

Although *Phalaenopsis* orchids are now the second most valuable flowering potted plant according to 2001 USDA statistics, little specific quantitative information is available on the plant relating plant development to the environment. The objective of this investigation was to quantify the effects of temperature on time from spike emergence to flowering. Vegetative *Phalaenopsis* BL. were induced to flower then were placed into growth compartments at different constant temperatures. An initial calibration experiment was performed with *P.* Taisuco Smile, followed by validation experiments using several cultivars. Flower, node, and bud development rate were modeled as a linear function of development rate. Average time to flower increased from 10 to 26 weeks as temperature decreased from 26 to 14 °C. At any constant temperature for any given cultivar, time to visible bud was about 60% of the total time from spiking to flower. Plants grown at 29 °C failed to develop to anthesis, and most buds aborted soon after they were visible. The thermal time from appearance of the flower spike to anthesis was 769 degree days with, a calculated base temperature of 10.8 °C. Node and bud development rates also increased linearly as temperatures increased. Temperatures from 17 to 26 °C did not affect the number of nodes and flowers, spike height, or flower size.

DEDICATION

To the two most important people in my life, my Mother, Carol Ann Robinson and my Fiancé, Robert James Mazzaferro.

Without you, none of this would have been possible.

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And to Robert, thank you for just being there.

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LITERATURE REVIEW

Introduction

Because of improved cultural practices, reliable and uniform hybrids, and heightened consumer interest, *Phalaenopsis* BL. are quickly becoming an important economic crop, despite lack of a specific market date. In the United States, orchids are the second most valuable potted crop and are valued at over $99 million wholesale (USDA, 2002). *Phalaenopsis* are currently the most valuable pottted crop in Holland (Barendse, 2002). In the Netherlands, *Phalaenopsis* sales have risen from 3 million pots sold in 1984 to over 9 million pots sold in 2001 (Griesbach, 2000; Vakblad voor de Bloemisterij, 2002). The Netherlands and Taiwan account for a large portion of potted *Phalaenopsis* production, as do China, Germany, Japan, and the United States (Griesbach, 2000). In 1993, the Japanese market for potted orchids was estimated to be $261 million, with the Netherlands accounting for $62 million and ASEAN (Association of the South East Asian Nations) accounting for $53.7 million (Hew and Young, 1997). It is feasible that the production of *Phalaenopsis* will continue to increase and, with the development of decision support tools, have great economic potential.

Producing flowering plants for a specific market date requires knowledge of the relationship between temperature and flower development rate. For example, Easter lilies, which are the fourth most valuable potted crop, are grown for a specific date, Easter. The day after Easter, plants are worthless (Larson, 1992), so controlling this crop's time to flower is important. Research on Easter lily

flowering is extensive (Fisher et al., 1997a, b; Holcomb and Berghage, 2001; Karlsson et al., 1988; Wang, 1996a; Wilkins, 1988a, b; Wilkins and Grueber, 1990), as is work on poinsettias and chrysanthemums (Karlsson et al., 1989; Larson, 1992), valuable potted crops with specific market dates.

Although orchids are now the second largest potted crop in the United States, little specific quantitative information is available relating plant development rate to temperature from the time of visible spiking to flower. The lack of complete production information is in part *Phalaenopsis* having no specific market date. *Phalaenopsis* can be grown and sold year-round (Ichihashi, 1997), and strict scheduling of these plants has not been needed. Also, research done on *Phalaenopsis* generally has been done outside the United States, mostly in Asian countries. The published results of these studies are not always readily available to growers, and most of them have not been translated into English (Ichihashi, 1997). Also, these studies often show conflicting results and can be difficult to interpret. The objectives of this investigation were to quantify the effects of temperature on time from spike emergence to flowering and develop a cohesive growing protocol for potted orchid production.

Orchids

Background

Distribution. Orchids belong to Orchidaceae, which are distributed worldwide. An estimated 1000 genera and 25,000 species exist (Jones and Luchsinger, 1986). Orchids are found largely in the tropics but also grow in regions of the Arctic, semidesert areas of Australia, and throughout the United States (Pridgeon, 2000).

History. The word *orchid* is derived from the Greek word *orchis*, meaning testis (Reinikka, 1972). In Greek culture, orchids were used as an herbal remedy for infertility according to the teaching of the doctrine of signatures: plants could be used to treat human ailments successfully if plant parts resembled the affected area in color or shape. Orchids were also thought to grow from dropped animal semen, a belief that was upheld for hundreds of years because orchid seeds are no more than dustlike particles and virtually invisible. Orchids were largely banished by Western Europe because of their association with Greek culture and sexual connotations (Berliocchi, 1996). Although the early history of orchids is normally associated with Greek culture, orchids were first recorded as early as 800 b.c. in paintings and literature in the Orient. The Chinese word for orchid is *lan*, a term used in ancient writing in reference to the *Cymbidium* orchid (Berliocchi, 1996; Reinikka, 1972).

An increasing number of orchids were discovered during the 1600s as exploration expanded and travel between continents became possible. Orchids became noted more for their beauty than their healing qualities. The most valuable orchids were *Vanilla* species that were used for making perfumes and flavorings. In the early 1800s, orchid collecting became a fashionable hobby among the wealthy. During this time, the first *Cattleya* and *Dendrobium* orchids were introduced. Prices for orchids then began to skyrocket. Payments of $500 for a single plant and $2000 for a true "investment" were not uncommon (Logan and Cosper, 1953).

Despite the orchid craze, the culture of orchids still remained a mystery. All orchids were thought to need tropical conditions. They were grown in so called stoves that were made of dense glass and had coal fires and brick flues. The bricks were drenched with water to create steam and maintain high humidity. These structures had no movable windows and hence were unventilated. In 1817, Joseph Hooker described the English cultivation technique as the "grave of tropical orchids". Using work by John Lindley (1799–1865), the father of modern orchidology, Sir Joseph Paxton changed orchid culture when he abandoned the stoves entirely and opened up the windows of his greenhouses, keeping them relatively cooler (Reinikka, 1972). The plants thrived in the new environment, and soon other growers abandoned stoves and used more practical, successful methods to grow orchids.

During the mid-1800s, the first orchid crosses were made; yet despite single orchid pods containing between 500,000 and 1 million seeds, new hybrids were difficult to develop because a successful way to germinate seeds still eluded growers (Larson, 1992). The first breakthroughs for forcing germination were made independently by Hans Bergeff in Germany and Noel Bernard in France between 1899 and 1909. They used a symbiotic method in which seeds were grown in association with mycorrhizae (Reinikka, 1972). *Phalaenopsis* seeds, like all orchids, are incredibly tiny and have no endosperm and only a rudimentary seed coat. The fungus assists germination by supplying the nutrients that the endosperm would supply. Although this method of germination was used successfully, the need for mycorrhizae as a reserve for the seeds was questioned. In a classic article, Lewis Knudson (1922) of Cornell University refuted symbiotic germination; he had developed an asymbiotic method by using a sugar medium in place of the fungus. The medium was a combination of a nutrient solution, fructose or glucose, and agar gel.

The asymbiotic method is still widely used today. It helped the commercial orchid industry expand and made the introduction of more hybrids possible. Since the first hybrid was developed, more than 100,000 hybrids have become available to growers (Pridgeon, 2000).

Plant description

Flowers. Orchids are thought to be the most advanced of all monocotyledons (Pridgeon, 2000). They differ from all other flowering plants in that their stamens and pistils are fused into a structure called the column (gynandrium). Like most other plants in the Liliidae subclass, flowers have three sepals and three petals; however, the sepals can be colored or green, and one of the three petals is usually modified into a lip structure called the labellum. The flowers are zygomorphic, meaning bilaterally symmetrical (Jones and Luchsinger, 1986).

Growth habit. Orchid root habit depends on whether these perennial herbs are terrestrial or epiphytic. Epiphytic roots are usually covered with a silvery-gray velamen, which helps the plant adhere to surfaces and absorb water and nutrients. Healthy root tips are green and able to photosynthesize (Elliott, 1998). Terrestrial orchids have hairier roots that normally have no green tip. Orchid roots have the same basic function that all other plant roots have: to anchor the plant on and in the medium and absorb water and nutrients.

Phalaenopsis

Background

Distribution. Most *Phalaenopsis* originate from tropical and subtropical areas of the South Pacific Islands and Asia (Baker and Baker, 1991; Noble, 1971). In the South Pacific, they range from Sri Lanka to southern India and westward to Papua New Guinea and Australia. In Asia, *Phalaenopsis* is found in China, Taiwan, and the Philippines (Christenson, 2001). Approximately 40 *Phalaenopsis* species are known today (Baker and Baker, 1991).

History. Compared with other orchids such as *Cymbidium* and *Vanilla*, *Phalaenopsis* is a relatively new genus in terms of its discovery. Though first described in the mid-1750s, however, Karl Ludwig was the first to classify them as *Phalaenopsis* in 1825 (Noble, 1971). *Phalaenopsis* stems from the Greek words *phalaina*, meaning moth, and *opsis*, a suffix denoting resemblance (Coombes, 1985). The common name for *Phalaenopsis* is the moth orchid.

Phalaenopsis was introduced in Europe during the height of the orchid craze in the early 19th century (Christenson, 2001). However, cultural requirements of the genus were unknown, and most plants succumbed to bacterial crown rot. *Phalaenopsis* production greatly benefited from the seed germination work of Lewis Knudson (Christenson, 2001). In the 1940s, the first tetraploid *Phalaenopsis* Doris was established (Christenson, 2001). Tetraploid flowers have flowers greater longevity and substance, creating more demand for *Phalaenopsis* as a cut flower and potted plant. *Phalaenopsis* are currently

propagated from seed or, more commonly, by tissue culture (Christenson, 2001). Tissue culture has become less expensive and also results in more uniform plants.

Plant Description

Growth habit. In the wild, *Phalaenopsis* are epiphytic or lithophytic, with their main axis growing somewhat horizontally away from the tree so that water drains down the midrib of the leaves. The main axis consists of a short stem with alternating leaves whose leaf color ranges from light green to purplish-green. Each leaf is associated with two auxiliary buds from which an inflorescence can form (Figure 1). Normally only the top bud elongates; the bottom bud remains dormant unless the other bud is damaged. The inflorescence, most commonly called a spike, grows at a right angle to the vertical host stem (Christenson, 2001). Each inflorescence has four to eight nodes below the buds, and each of these nodes can develop into a lateral branch, that can in turn also branch, creating a raceme. The spike normally emerges from the third to fifth node below the top leaf (Sakanishi et al. 1980; Yonda 1985). Spike emergence from the first or second nodes below the top leaf is uncommon. The root tips are normally green and are able to photosynthesize. Roots are unbranched, unless they have been damaged or are aging. The leaves of *Phalaenopsis* are thick and fleshy and usually persistent.

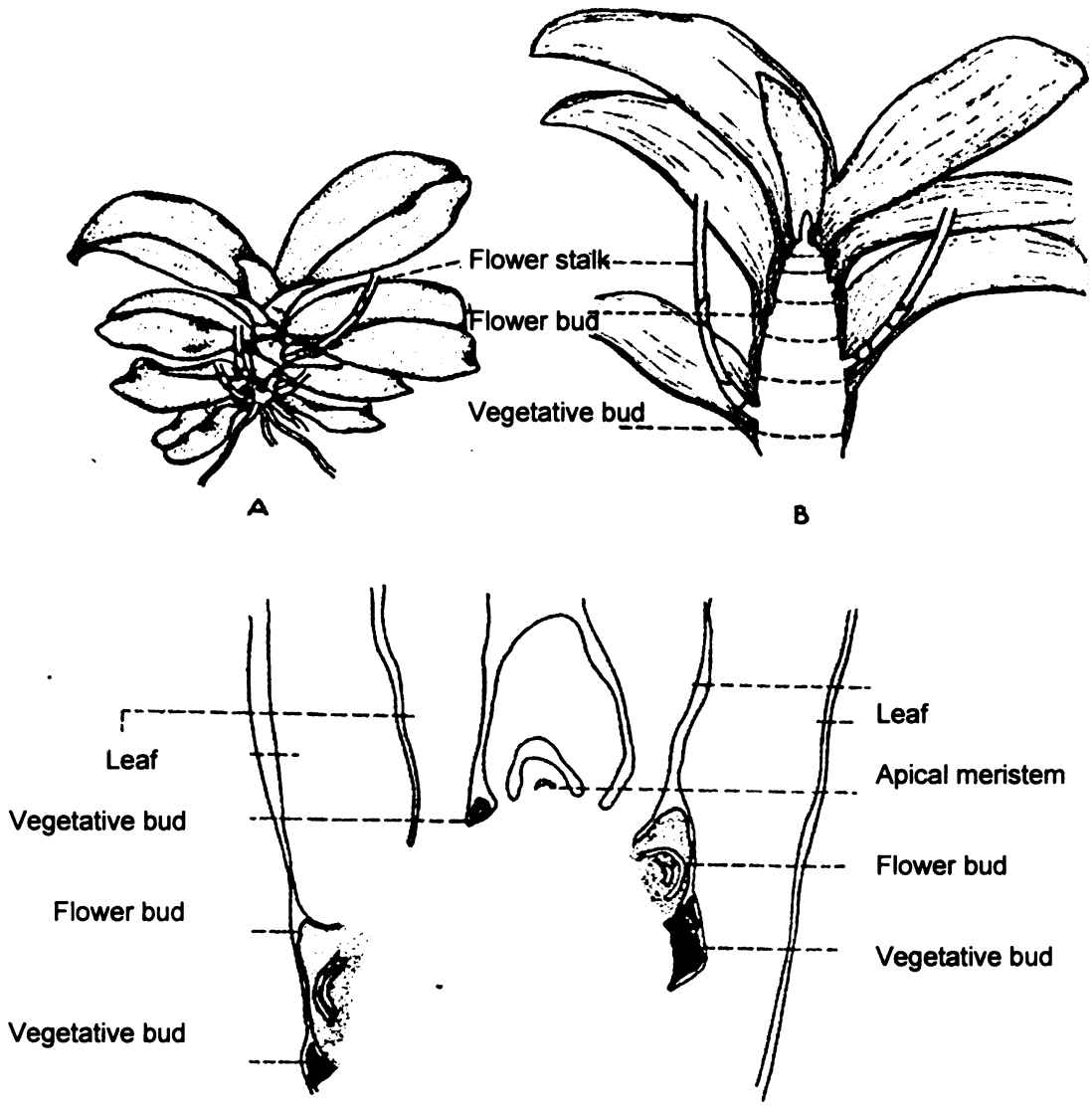

Figure 1. Growth habit of *Phalaenopsis* (Rotor, 1952)

Flowers. Like those of most orchids, the flowers of *Phalaenopsis* have three sepals and three petals. The sepals form a triangle and are often the same color as the petals but may be spotted or resemble the lip color. Two of the petals are mirror images, set opposite each other, giving *Phalaenopsis* its moth-like appearance. The third petal forms the lip, which has two tendrils, characteristic of *Phalaenopsis* (Figure 2). The majority of *Phalaenopsis* are pink or white;

however, with hybridization, yellow and bicolored flowers have become more common. Flowers often last from 2 to 5 months (Baker and Baker, 1991; Wang and Lee, 1994a). Recently, purple hybrids have become available and are popular.

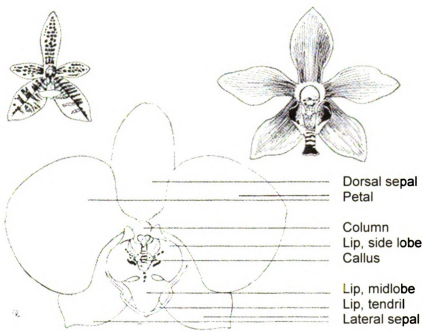

Figure 2. *Phalaenopsis* flower morphology and types (Noble, 1971)

Commercial Production

Standards. There is a consensus among growers of what a marketable plant should look like; however, there are no official standards regarding physical specifications for commercial orchids. Most plants sold have a flower width of 7.6 cm (Wang and Lee, 1994a). *Phalaenopsis* with multiple and well-branched spikes can be sold at a higher price than plants with only one spike and no lateral branches.

Growing protocol. Phalaenopsis can be grown from seeds or as mericlones in tissue culture; however, both methods require aseptic conditions with exact nutrients and environmental conditions (Dole and Wilkins, 1999). However, *Phalaenopsis* quickly mature and flower compared to many other orchids, with most taking approximately 24 months from seed to flower (Wang, 1994a). Most commercially produced *Phalaenopsis* in the United States are flowered from bare-root plants with a leaf span between 20 and 30 cm and four to five mature leaves. Plants of this size can be spiked and flowered in about four to six months. Larger, prespiked plants can also be purchased wholesale to flower but at a higher cost to the grower.

Plant height is not normally controlled with growth regulators, but studies by Wang and Hsu (1994) have shown that paclobutrazol (50, 100, 200, or 400 $mg \cdot L^{1}$) and uniconazole (25, 50, 100, or 200 $mg \cdot L^{-1}$) used as either a 5-sec dip or a foliar spray resulted in shorter spikes. Plants treated with a 5-sec dip showed more uniform results but had a longer flowering delay the following year than those treated with the foliar spray. The growth regulators did not affect flower size or count but did delay flowering as concentration increased. Daminozide produced no effects when applied as a dip or to foliage, at 2500, 5000, or 7500 $mg \cdot L^{-1}$.

Greenhouse Environment

Medium and Nutrition. Although used only since the 1950s, fir bark-based medium is the primary medium used to grow orchids, including *Phalaenopsis,* in North America and the Netherlands (McLellan, 1956). Before bark-based medium, osmunda fiber was used but was scarce and expensive. Despite the mass use of fir bark, it has drawbacks such as quick decomposition, lack of uniformity, inability to hold nutrients, and general lack of practicality for large-scale potted plant production. For these reasons, other materials that provide better water and nutrient retention, such as pure sphagnum and peat-based medium, commonly referred to as a mud mix by orchid growers, are increasing in popularity (Brenneise and Halgren, 2000; Ichihashi, 1997). Peat-based medium can be mixed with various percentages of fir bark, perlite, coconut fiber, and other materials. Peat-based media have been shown to improve *Phalaenopsis* leaf growth, flower size, and number because of more lateral inflorescences (Wang 1995b; Wang and Gregg, 1994). Medium type did not affect time to flower (Wang, 1995b; 1996b; Wang and Gregg, 1994).

When a peat-based medium is used, a balanced water-soluble fertilizer at 1 $g \cdot L^{-1}$ per irrigation is recommended for *Phalaenopsis* (Wang, 1996b; Wang and Gregg, 1994). Increasing fertilizer rate from 0.25 to 1 $g \cdot L^{-1}$ per irrigation did not change the time to flowering during a short-term commercial forcing schedule, but did reduced time to flower during a second force (Wang and Gregg, 1994). A 20-20-20 water-soluble fertilizer with N at 100 mg L^{-1} was recommended for

Phalaenopsis Toyland at each irrigation when the hybrid is grown in a bark-based medium (Griesbach, 1985). Maintaining high N concentrations (100 $mg \cdot L^{-1}$) before and after spiking is important for obtaining high flower counts. In experiments in which N was reduced or stopped during spike development, flower counts were reduced (Wang, 2000).

Irrigating *Phalaenopsis* before and after flower development by using a fertilizer that has a high P ratio reportedly results in superior flowers (Gordon, 1990). However, in other studies, increasing P resulted in fewer flowers; it may actually reduce flowering longevity (Wang, 2000). Also, flower development was not affected by P concentration (Gomi et al., 1980; Wang, 2000).

Irradiance. Phalaenopsis require relatively low light levels compared with most plants. Light levels for *Phalaenopsis* range from 200 to 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with a maximum tolerance of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Baker and Baker, 1991). Baker and Baker (1991) suggest that high light levels may initiate blooming in some species; however, very high irradiance levels can severely burn the thick fleshy leaves of *Phalaenopsis* and, in severe cases, kill the plant.

Plants receiving very low light levels (8 or 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) do not respond to induction temperatures and remain vegetative at any temperature if kept under low light. Plants receiving at least 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 12 h perceived induction treatments and flowered normally (Wang, 1995a). Additional studies have shown

that the suppression of spiking during low light levels is not due to low levels of endogenous gibberellin (Satoshi et al., 1996). Growing plants at low light levels can be an alternative to heating greenhouses to maintain vegetative plants and reduce heating costs.

Temperature. *Phalaenopsis* are tropical and subtropical plants that require warm temperatures to grow vegetatively. Plants remain vegetative above 27 to 29 °C (Sakanishi et al., 1980) and can tolerate temperatures as high as 35 °C (Baker and Baker, 1991). Baker and Baker (1991) suggest that minimum growing temperatures of 17 to 18 °C and 21 to 30 °C are ideal growing conditions, but at higher temperatures *Phalaenopsis* will not flower.

Temperature management is important during spike development. Although temperatures below 25 °C initiate spiking in *Phalaenopsis*, they do not initiate flowering (De Vries, 1950; Sakanishi et al., 1980). Table 1 shows the floret developmental stages (I to VII) of a given spike lenght, and Table 2 shows the effect of high temperature at these spike lenghts.

De Vries (1950) described six stages of flower development, from spike emergence (stage I) to stamen recognition (stage VI). At stage V, the spike had developed for 6 weeks and was 1.6 to 11.8 mm long. When the spike is less than 5 cm, florets 3 through 6 have not initiated the primordia of the floret (stage I), and the spike can remain vegetative at high temperatures. A keiki, a vegetative

Table 1. Developmental stages of florets in relation to flower-stalk elongation (Sakanishi et al. 1980)

Length of Flower stalk (cm)	Order of florets on flower stalk	Developmental stages of Florets						
		I	II	III	IV	V	VI	VII
1-5	1,2		8	1	1			
	3,4	5	5					
	5,6	10						
6-10	1,2		1	1	6	2		
	3,4	1	5	3	1			
	5,6	8	2					
11-20	1,2		1	1	2	6		
	3,4		4	1	5			
	5,6	7	2	1				
21-30	1,2				2	6	2	
	3,4				2	7	1	
	5,6		3	4	2	1		
	7,8	6	3	1				
31-40	1,2					1	1	8
	3,4					1	3	6
	5,6				1	2	6	1
	7,8			2	2	5	1	
41-50	1,2						1	9
	3,4						3	7
	5,6					4	5	1
	7,8				3	5	2	

Five Flower-stalks of each length were used for the observation.

*: Showing the respective stage of floret development as follows,

- I : Primordia of floret not appeared,
- II : Primordia of floret initiated,
- III : Sepals differentiated,
- IV : Petals differentiated,
- V : Gynostermium differentiated,
- VI : Anthers differentiated,
- VII : Pollen formed.

Table 2. Effect of high temperature above 28 °C during elongation of flower-stalks on flowering (Sakanishi et al., 1980)

Length of flower- stalk at start of high temp.	Percent-age of aborted stalks	Mean days from flower-stalk emergence to flowering	Length of flower stalk	Number of florets per stalk
Control *	0.0%	103 ± 8 S.E.	61.8 cm	7.5
< 5 cm	15.4	59 ± 5	36.0	4.1
10 cm	0.0	59 ± 5	47.2	6.8
21 – 30 cm	0.0	65 ± 5	48.4	5.7
41 – 50 cm	0.0	73 ± 5	59.1	6.8

*: Plants were grown continually in the greenhouse

air plantlet, may form instead of buds, or buds may be aborted altogether (De Vries, 1950; Sakanishi et al., 1980). Abortion of buds can be avoided if the temperature around the plant can be kept below 28 °C untill the spike has reached 5 cm in height, after which the spike will develop at most temperatures because the floret primordium is already initiated and beginning to differentiate (Table 2).

When plants were kept at 28 °C for 6 h per day or fewer, the percentage of spiking was unaffected, but as time at 28 °C increased to 12 h per day, spike emergence was repressed. Plants kept at 28 °C for 24 h never spiked (Sakanishi et al., 1980). De Vries (1950) reported that plants spiked at any temperature between 11 and 25 °C, with the optimum temperatures for spiking being 15 to 20 °C. Although spikes grown at an average daily temperature (ADT) of 28 °C had

delayed flowering, there was little effect on size of flowers or spike height (Lee and Lin, 1984; Sakanishi et al. 1980).

The exact reason *Phalaenopsis* spike below 27 °C is open to speculation (Chou et al., 2000; De Vries, 1950; Ota et al., 1991). Many of the theories relate to CO_2 fixation by the plants. *Phalaenopsis* are crassulacean acid metabolism (CAM) plants that fix CO_2 most readily at night and under relatively cool growing conditions (Ota et al., 1991). Chou et al. (2000) demonstrated that plants grown at a day/night temperature of 30/25 °C for 20 consecutive days showed higher concentrations of inactive glucoside cytokinins than plants grown at 25/20 °C. These results suggest that cytokinins may promote bud development at low temperatures. In studies by Wang et al. (2002), *Phalaenopsis hybrida* Bl. spiking was retarded when exogenous abscisic acid (ABA) was applied at 0.1 and 1.0 μg per plant.

Most *Phalaenopsis* can be uniformly spiked when induced at 25/20 °C day/night (Lee and Lin, 1987). However, plant maturity can introduce varying results for percentage and time to flower once plants have spiked (Yonda et al., 1992); in that study, independent of temperature, six year old plants spiked two weeks before the three year old plants. Six year old plants spiked at 100% versus 3-year-old plants that spiked from only 13 to 80% under various temperatures for different lengths of time (Yonda et al., 1992). Younger plants can be spiked uniformly if given lower temperatures or longer durations at a given temperature.

Temperature also affects time from spiking to flowering. However, this phase of development has not been well described. A number of studies (Lee and Lin, 1984; Sakanishi et al., 1980; 1987; Yoneda, 1985; Yoneda et at., 1991, 1992) report the dates of spike emergence and flowering date but not ADTs that are needed to properly determine a temperature effect on flower development. Instead, only the minimum and maximum temperature for a given month, the temperature settings for the greenhouse, or just the temperature the plants were spiked at are given.

Phalaenopsis have been reported to show leaf pitting between 10 and 0 °C (McConnell and Sheehan, 1978). This chilling injury becomes a problem when *Phalaenopsis* are grown with other orchids that require cooler growing temperatures or during shipping.

Phalaenopsis are not reported to be photoperiodic (Sakanishi et al., 1980). However, there are a few studies that report that short days enhance spiking (De Vries, 1950; Griesbach, 1985; Roter, 1952; Yonda et al., 1991) though this short-day enhancement was not observed in other studies (Sakanishi et al. 1980) and is thought to be a result of cool night temperatures resulting from the extended night (Sakanishi et al., 1980).

Miltoniopsis

Background

Distribution. *Miltoniopsis* are native to wet forest regions of Costa Rica and Peru (Berliocchi, 1996). *Miltoniopsis* species are found from 610 m to 2100 m above sea level (Baker and Baker, 1993b). The average minimum and maximum temperatures range from a low of 10 °C to a high of 29 °C .

History. *Miltoniopsis* are named for orchid enthusiast Lord Fitz-William Milton (1786-1857) by John Lindley (Berliocchi, 1996). In 1889, Godefroy-Lebeuf separated *Miltonia* into two groups, *Miltonia* and *Miltoniopsis*. However, this distinction was not officially recognized until the 1970s (Rentoul, 1982), and in some literature the two groups are still treated as one genus. These genera can be distinguished by *Miltonia*'s two-leaved pseudobulb, and *Miltoniopsis*'s has a one–leafed pseudobulb. *Miltoniopsis* also have the classic pansy-shaped flower that led to the common name of pansy orchid. Both of these genera have other distinguishing features, such as rhizome type and column and lip characteristics. *Miltonia* are native to Brazil, while *Miltoniopsis* are native to Colombia. Five or six species of *Miltoniopsis* and 20 species of *Miltonia* have been named (Baker and Baker,1993b; Berliocchi, 1996; Sterwart and Griffiths, 1995). Most modern hybrids are a complex of three species: *Miltoniopsis vexillaria (Rcgb. F.)* Godef-Leb. , *M. roezii* (Rcgb. F.) Godef-Leb. , and *M. phalaenopsis* (Lind. & Rchb. F.) Garay & Dunsterv. (Baker and Baker, 1993b; Nash, 1989).

Plant Description

Growth habit. Miltoniopsis are epiphytes or lithophytes in the wild and have a sympodial growth habit. Like all sympodial orchids, *Miltoniopsis* grow from a pseudobulb. The pseudobulb is an enlarged stem from which flowers arise can have one (homoblastic) or many (heteroblastic) nodes (Hew and Young, 1997). *Miltoniopsis* have homoblastic pseudobulbs. The main function of the pseudobulbs is to store food and water; they will often outlive roots and leaves (Ng and Hew, 2000).

The pseudobulb is capable of flowering only when it is mature. If the mature pseudobulb develops new plantlets instead of flowering spikes, it will not be able to flower (Rittershausen and Rittershausen, 1985). The inflorescence is a raceme with one to several flowers (Berliocchi, 1996; Stewart and Griffiths, 1995). The flowers are large, showy, and flat with a range of colors excluding blue. Flowers can last four to eight weeks (Baker and Baker, 1993a).

The root habit is fine and similar to that of *Odontoglossum,* and leaves are long and narrow, sheathing the pseudobulb (Rentoul, 1982).

Commercial Production

Miltoniopsis are the fourth most valuable potted orchid in the Netherlands, with 797,000 pots sold in 2001 (Vakblad voor de Bloemisterij, 2002); however, there has not been any documented work to develop a growing protocol for these

plants. The only information available on *Miltoniopsis* is a handful of hobbyist-type articles that contain similar cultivation instructions (Baker and Baker, 1993a, b; Ortho, 1999; Rentoul, 1982; Sweet, 1978). The recommendations for growing *Miltoniopsis* are to keep plants evenly moist, and light levels from 900 to 2000 foot-candles. If the leaf edges turn pink, then the plants are receiving too much light (Baker and Baker, 1993a; Ortho 1999; 1993a). Recommended daytime average temperatures range from 27 to 29 °C; night-time temperatures average from 16 to 18°C (Baker and Baker, 1993a; Ortho, 1999;). Temperatures of 17 to 20 °C produce abundant flowering, but whether this is a constant ADT or an induction treatment is not indicated (Baker and Baker, 1993a; Tran Than Van, 1974). In several articles, *Miltoniopsis* are not reported to be among the easier orchids to grow (Baker and Baker, 1993a, b; Rentoul, 1982). *Miltoniopsis* have a greenhouse growth habit and cycle similar to that of *Oncidium* (Hew and Young, 1997).

Paphiopedilum

Background

Distribution. Paphiopedilum are native to tropical and subtropical southeast Asia and islands of the South Pacific (Berliocchi, 1996; Cribb, 1987; Dole and Wilkins 1999) and 60 species have been described (Cribb, 1987).

History. Paphiopedilum were previously classified into the much broader *Cypripedium* until the late 1960s (Berliocchi, 1996; Rentoul, 1980). Although given the common name lady slipper, *Paphiopedilum* literally means Aphrodite's slipper.

Paphiopedilum was discovered in India in the early 1800s (Rentoul, 1980) and has been in cultivation since 1819, when the first plant flowered under glass in the Liverpool Botanic Garden (Hennessy and Hedge, 1989). By 1900, 475 *Paphiopedilum* hybrids were registered and 40 of the 60 species were known despite primitive germination techniques and the lack of knowledge of cultural needs (Hennessy and Hedge, 1989).

Paphiopedilum have been used for cytology studies because of their large chromosome size and affinity for chromosome stains. *Paphiopedilum* are also thought to be one of the most ancestral of all the orchids (Cribb, 1987).

Plant Description

Growth habit. Paphiopedilum are considered terrestrial (Cribb, 1987), semi-terrestrial, lithophytic, or epiphytic herbs (Hennessy and Hedge, 1989). They can be found growing on the forest floor or low in trees.

Paphiopedilum have a sympodial growth habit and, like *Phalaenopsis,* have no pseudobulb. The stems of the plant are relatively short, an inch long or shorter in most cases, and are covered by overlapping leaves that form a fan shape. Leaves can be mottled or entirely green. New plantlets arise from the main plant. The older growth is thought to act like a pseudobulb by supplying nutrients to the developing shoots (Rittershausen and Rittershausen, 1985).

The roots of *Paphiopedilum* are always moist and have a less-developed root system (Ortho, 1999). Roots have a multiseriate velamen and large brown root hairs.

Flowers. Paphiopedilum differ from most other orchids because they have many vegetative buds but have only one reproductive bud primordium, the most apical, that develops into a flower (Rotor, 1952). The apical meristem will elongate while the bud is developing. Individual flowers can last 30 to 120 days (Goh and Arditti, 1985). The bud emerges from the center of the growth. Once the plant flowers, it will not flower again until a vegetative shoot arises.

Although all orchids have unique flowers, *Paphiopedilum* flowers are particularly unusual. The most obvious feature is the upper dorsal sepal, which is usually brightly colored and often used to identify a species. The two lateral sepals are fused and called the synseplaum (Berliocchi, 1996). The flower also bears a dominant saccate lip, which is normally the same color as the two lateral petals.

Commercial Production

Although *Paphiopedilum* are a popular potted plant, with over 500,000 sold in the Netherlands during 2001, almost no published data exist describing their commercial production. Most orchid articles and books give general recommended cultivation for *Paphiopedilum* (Hennessy and Hedge, 1989; Rentoul, 1980; Ortho, 1999; Stewart and Griffiths; 1995). Rotor (1950) reported that *Paphiopedilum insigne* (Wallich ex Lindl.) Pfitz. remained vegetative above 18 °C, but when temperatures were dropped to 13 °C, flower buds initiated two to three weeks later, and plants flowered 6 months later when maintained at 13 °C. *Paphiopedilum barbatum* (Lindl.) Pfitz. remained vegetative at temperatures above 23 °C, but flowered when temperatures were dropped to 16 to 21°C (Goh and Arditti, 1985). These two species were not found to be photoperiodic (Rotor, 1952). Plants are use to low light tolerating 140 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Dole and Wilkins, 1999), and leaves will become yellow with too much light.

Paphiopedilum charlesworthii have a reputation for not being easily cultivated (Hennessy and Hedge, 1989). It is intolerant of constant high temperatures and has a slow growth rate. *Paphiopedilum charlesworthii* are reported to flower better under cool night temperatures of 10 °C, with at least a 5 °C increase for the daytime temperature (Cribb, 1987).

Modeling Plant Development

Modeling plant development is a crucial part of cropping plants for a specific market date and has been used for a wide range of agronomical crops and horticultural crops. The most critical factor in developing a model for plant development is temperature. Although environmental factors such as cool temperatures, photoperiod, and plant size can induce a plant to enter a different phenophase, it is temperature alone that determines the rate of development throughout that phase. This is in contrast to growth, which is a nonreversible process and includes gains in height, weight, or volume.

For any developmental process such as time to flower or number of leaves grown in a given period, the reciprocal can be taken to give a linear function over a given temperature range where the rate (1/days) is equal to the slope plus the product of the intercept temperature:

$$1/\text{Days} = b_0 + b_1 * T \qquad [1]$$

For plants, the rate is linear only between the base temperature (T_b) and the optimum temperate (T_{opt}), otherwise known as the cardinal temperatures (Figure 3). T_b can be determined by

$$T_b = -b_0/b_1 \qquad [2]$$

T_b is the point at which the linear rate crosses the x-axis and development is halted. Development about Ti decreases as temperatures increase. Cardinal temperatures differ among crops or developmental stages of the same crop.

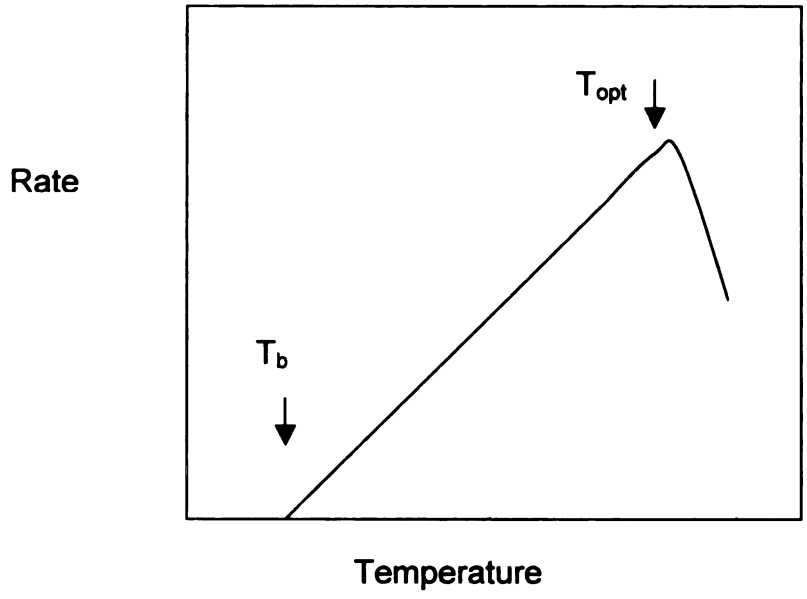

Figure 3 . A degree-day model relating rate of development as a linear function of temperature

In the early 1700s, a French physicist, Rene A. F. de Reaumur, introduced the now widely used concept of growing degree-days (Wegulo and Gleason, 2001). Degree-days is a linear function of temperature and is computed by subtracting T_b from the ADT. Growing degree-days are computed only for days when the ADT is higher than base temperature:

$$°Days = 1/b_1 \qquad [3]$$

Although this model has been widely used to predict development in plants, it has weaknesses (Wang, 1960). The model assumes that the development rate is a linear function; however, outside T_b and $T_{opt,}$ the response becomes curvilinear. Three equations can be used to represent the relationship when the rate of development is calculated below T_b, above T_{opt} , and between T_b and T_{opt} (Steininger et al., 2002).

$$\begin{aligned} &\text{Degree-days} = 0 && \text{when } T_j \leq T_b \\ &\text{Degree-day} = a_0 + b_0 * T_j && \text{when } T_b < T_j \leq T_{opt} \\ &\text{Degree-days} = a_1 + b_1 * T_j && \text{when } Tj > T_{opt} \end{aligned} \qquad [4]$$

Literature Cited

Baker, M.L. and C. Baker. 1991. Orchid species culture. Timber Press, Portland, Ore.

Baker, M.L. and C. Baker. 1993a. *Miltoniopsis*. Amer. Orchid Soc. Bul. 62: 794–799.

Baker, M.L. and C. Baker. 1993b. Miltoniopsis II. Amer. Orchid Soc. Bul. 62: 901–908.

Barendse, M. 2002. De sierteclt-toppers van 2001. Vakblad voor de Bloemisterij. 24–26.

Berliocchi, L. 1996. The orchid in legend and lore. Timber Press, Portland, Ore.

Brenneise, H.R. and R.G. Halgren. 2000. Growing orchids in mud. Orchids. 65:500

Chen, W.S., H.W. Chang, W.H. Chen, Y.S. Lin. 1997. Gibberellic acid and cytokinin affect Phalaenopsis flower morphology at high temperatures. HortScience 32:1069–1073.

Christenson, E.A. 2001. Phalaenopsis: a monograph. Timber Press, Portland, Ore.

Chou, C.C., W.S. Chen, K.L. Huang, H.C. and Yu, L.J. Liao. 2000. Changes in cytokinin levels of *Phalaenopsis* levels at high temperatures. Plant Physiol. Biochem. 38:309–314.

Coombes A.J. 1985. Timber Press dictionary of plant names. Timber Press, Portland, Ore.

Cribb, P. 1987. The genus *Paphiopedilum*. Timber Press, Portland, Ore.

De Vries, J.T. 1950. On the flowering of *Phalaenopsis schilleriana* Rchb f. Ann. Bogerienses. 1:61–76.

Dole J.M. and H. F. Wilkins. 1999. Ochidaceae: floriculture principles and species. Prentice Hall, Englewood Cliffs, N.J.

Elliot, J. ed. 1998. Orchid growing in the tropic orchid society of south east asia (Singapore). Times Editions, Singapore.

Fisher, P., R.D. Heins, and N. Ehler, N. 1997a. A decision-support system for real-time management of Easter lily (*Lilium longiflorum* Thunb.) scheduling and height: I. System description. Agr. Systems. 54:23–37.

Fisher, P., R.D. Heins, and N. Ehler, N. 1997a. A decision-support system for real-time management of Easter lily (*Lilium longiflorum* Thunb.) scheduling and height: II. System description. Agr. Systems. 54:39–55.

Goh, C.J. and J. Arditti. 1985. Orchidaceae: handbook of flowering. CRC Press, inc. Bocariaton, FL.

Gordon, B. 1990. Culture of the *Phalaenopsis.* Laid-back Publications, Rialto, Calif.

Greisbach. R.J. 1985. *Phalaenopsis* as potential potted plants. HortScience 20:624.

Greisbach, R.J. 2000. Potted *Phalaenopsis* orchid production: history, present status, and challenges for the future. HortTechnology. 10:429.

Hennessy, E.F. and T.A. Hedge. 1989. The slipper orchids. Acorn Books, Randsburg, Kansas City, MO.

Hew, C.S. and J.W.H. Young. 1997. The physiology of tropical orchids in relation to the industry. World Scientific. Singapore.

Holcomb, E.J. and R. Berghage. 2001. Photoperiod, chilling, and light quality during daylight extension affect growth and flowering of tissue-cultured Easter lily plants. HortScience 36:53–55.

Ichihashi, S. 1997. Orchid production and research in Japan, p. 171–212 In: J. Arditti (ed). Orchid production and research in Japan. Orchid Biology: reviews and perspectives VII: 171–212. Comstock Pub, Ithaca, N.Y.

Jones, S.B., and A.E. Luchsinger. 1986. Plant Systematics. McGraw-Hill. NY, NY.

Karlsson, M.G., R.D. Heins, and J.E. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113: 70–74.

Karlsson, M.G. R.D. Heins, J.E. Erwin, and R.D. Berghage. 1989. Development rate during four phases of chrysanthemum growth as determined by preceding and prevailing temperatures. J. Amer. Soc. Hort. Sci..114:234–240.

Knudson, L. 1922. Nonsymbiotic germination of orchid seeds. Botanical Gaz. 73 : 1–25.

Lee, N. and G.M. Lin. 1984. Effect of temperature on growth and flowering of *Phalaenopsis* white hybrid. Chinese Soc. Hort. Sci.: 30:223–231.

Lee, N. and G.M. Lin. 1987. Controlling the flowering of *Phalaenopsis*. Proc. Symp. Forcing Hort.Crop 10:27–44.

Logan, H.B. and L, Cosper. 1950. Orchids are easy to grow. Prentice Hall, New York, New York.

McLellan, R.I. 1956. Fir bark – miracle? Amer. Orchid Soc. Bul. 25:81–83.

McConnell, D.B. and T.J. Sheehan. 1978, Anatomical aspects of chilling injury to leaves of *Phalaenopsis* Bl. HortScience. 13(6):705–706.

Nash, N. 1989. *Miltoniopsis* in the late 1980s. Amer. Orchid Soc. Bul. 58: 1040–1094.

Ng, C.K.Y, and C.S. Hew. 2000. Orchid pseudobulbs--'false' bulbs with a genuine importance in orchid growth and survival! Scientia Horticulturae 83: 165–172.

Noble. 1971. You can grow *Phalaenopsis* orchids. McQuerry Orchid Books, Jacksonville, Fl.

Ortho. 1999. All about orchids. Merideth Publishing Group, Des Moines, IA.

Ota, K., K. Morioki, and Y.Yamaoto. 1991. Effects of leaf age, inflorescence, temperature, light intensity, and moisture conditions on CAM photosynthesis in *Phalaenopsis*. J. Jpn. Soc. Hort. Sci. 60: 125–132.

Pridgeon, A. 2000. Illustrated encyclopedia of orchids. Timber Press, Portland, Ore.

Reinikka, M.A. 1972. A history of orchids. University of Miami Press, FLa.

Rentoul, J.N. 1982. Growing orchids. Timber Press, Portland, Oregon.

Rittershausen B., and W. Rittershausen. 1985. Orchid growing illustrated. Blandford Press; New York, N.Y.

Rotor, G.B., Jr. 1952. Daylength and temperature in relation to growth and flowering of orchids. Cornell Univ. Agr. Expt. Sta. Bul. 885:1–46.

Sakanishi, Y.H., G. Imanishi, and Ishida. 1980. Effect of temperature on growth of *Phalaenopsis abamibilis*. Bull. Okaka Press Ser. 32: 1– 9.

Satoshi, K., T. Hisamatsu, K. Ichimura, and M. Koshioka. 1996. Effect of light conditions and GA3 application on development of axillary buds during cooling treatment in *Phalaenopsis*. J. Jpn. Soc. Hort. Sci.

Sheehan, T.J. 1992. Orchids, p. 115 –141.In: R. Larson (ed). Introduction to floriculture. Academic Press, San Diego, Calif.

Steininger, J., C.C. Pasian. 2002. Extension of a thermal unit model to represent nonlinearrities in temperature responses of miniature rose development. J. Amer. Soc. Hort. Sci. 127: 349–354.

Stewart, J. and M. Griffiths. 1995. Manual of orchids. Timber Press, Portland, Ore.

Sweet. 1978. The *Miltoniopsis* complex in horticulture. Amer. Orchid Soc. Bul. 47: 917–925.

Tran Than Van, M. 1974. Methods of acceleration of growth and flowering in a few species of orchids. Amer. Orchid Soc. Bul. 43:699–707.

Vakblad voor de Bloemisterij, 2002. June 7 (23a): p88–89.

Wang, J.Y. 1960. A critique of the heat unit approach to plant response studies. Ecology. 41:785–789.

Wang, Y.T. 1995a. *Phalaenopsis* orchid light requirements during the induction of spiking. HortScience. 30: 59–61.

Wang, Y.T. 1995b. Medium and fertilization affect performance of potted *Dendobium* and *Phalaenopsis.* Hortechnology 5: 234–237.

Wang, Y.T. 1996a. Cytokinin and light intensity regulate flowering of Easter lily. HortScience. 31:976–977.

Wang, Y.T., 1996b. Effects of six fertilizers on vegetative growth and flowering of

Phalaenopsis orchids. Scientia Hort. 65: 191–197.

Wang, Y.T., 2000. Impact of a high phosphorus fertilizer and timing of termination of fertilization on flowering of a hybrid moth orchid. HortScience 35(1): 60-62.

Wang, Y.T. and N. Lee. 1994a. A new Look for an Old Crop: Potted Blooming Orchids Part 1. Greenhouse Grower. Jan.

Wang, Y.T and N. Lee. 1994b. Another Look at an Old Crop: Potted Blooming Orchids – Part 2. Greenhouse Grower. Jan.

Wang, Y.T. and L. L. Gregg. 1994. Medium and fertilizer affect the performance of *Phalaenopsis* orchids during two flowering cycles. HortScience 29: 269–271.

Wang, Y.T. and T.S. Hsu. 1994. Flowering and growth of *Phalaenopsis* orchids following growth retardant application. HortScience 29:285-288.

Wang, W., W. Chen, W. Chen, L. Hung, P. Chang. 2002. Influences of abscisic acid of flowering in *Phalaenopsis hybrida*. Plant Physiol. Biochem. 40: 97–100.

Wegulo, S. and M. Gleason. 2001. Degree-days. P. 302-303. O.C. Maloy, T. D. Murray In: Encyclopedia of plant pathology. John Wiley & Sons, New York, N.Y.

Wilkins, H.F. 1988a. Leaf unfolding rate of the Easter lily is temperature dependent. Minnesota State Florists Bulletin. 36: 4–6.

Wilkins, H.F. 1988b. Flower bud development rate for the Easter lily is temperature dependent Minnesota State Florists Bulletin. 36:6–7.

Wilkins, H.F. and K.L.Grueber. 1990. Easter lily height control. Minnesota State Florists Bulletin. 39:26–30.

Yonda, K. 1985. Effects of plant age and time of transfer to highland during summer on *Phalaenopsis*. J. Jpn. Soc. Hort. Sci. 54:101–108.

Yonda, K., H. Momose, S. Kubota. 1991. Effects of daylength and temperature of flowering in juvenile and adult Phalaenopsis plants. J. Jpn. Soc. Hort. Sci. 60(3): 651–657.

Yonda, K., H. Momose, S. Kubota. 1992. Comparison of flowering behavior between mature and premature plants of Phalaenopsis under different temperature conditions. 36(3): 207–210.

United States Department of Agriculture (USDA). 2002. Floriculture crops 2001 summary. National Agricultural Statistics Service.

SECTION 1: EFFECTS OF TEMPERATURE ON *PHALAENOPSIS* FROM SPIKE EMERGENCE TO FLOWERING

Effects of Temperature on *Phalaenopsis* from Spike Emergence to Flowering

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Introduction

Because of improved cultural practices, reliable and uniform hybrids, and heightened consumer interest, *Phalaenopsis* Bl. is quickly becoming an important economic crop, despite lack of a specific market date. In the United States, orchids are the second most valuable potted crop, at over $99 million wholesale (USDA, 2002). *Phalaenopsis* are currently the most valuable pottted crop in Holland (Barendse, 2002). In the Netherlands, *Phalaenopsis* sales have risen from 3 million pots sold in 1984 to over 9 million pots sold in 2001 (Griesbach, 2000; Vakblad voor de Bloemisterij, 2002). The Netherlands and Taiwan account for a large portion of potted *Phalaenopsis* production, as do China, Germany, Japan, and the United States (Griesbach, 2000). In 1993 the Japanese market for potted orchids was estimated to be $261 million, with the Netherlands accounting for $62 million and ASEAN (Association of the South East Asian Nations) accounting for $53.7 million (Hew and Young, 1997). It is probable that the production of *Phalaenopsis* will continue to increase, and with the development of decision support tools, they have even greater economic potential.

Producing flowering plants for a specific market date requires knowledge of the relationship between temperature and flower development rate. For example, Easter lilies, which are the fourth most valuable potted crop, are grown for a specific date, Easter. The day after Easter, plants are worthless (Sheehan, 1992), so controlling this crop's time to flower is important. Research on Easter

lily flowering is extensive (Fisher et al., 1997a, b; Holcomb and Berghage, 2001; Karlsson et al., 1988; Wang, 1996; Wilkins, 1988a, b; Wilkins and Grueber, 1990), as is work on poinsettias and chrysanthemums (Karlsson et al., 1989; Sheehan, 1992), valuable potted crops with specific market dates. Although orchids are now the second largest potted crop in the United States, little specific quantitative information is available relating plant development rate to temperature from the time of visible spiking to flower.

Phalaenopsis are tropical and subtropical plants, originating from areas of the South Pacific Islands and Asia (Baker and Baker, 1991; Noble, 1971), and have unique requirements for the induction of spiking and subsequential flower development. Plants are known to remain vegetative above 27 to 29 °C (Sakanishi et al., 1980) and can tolerate temperatures as high as 32 to 35 °C (Baker and Baker, 1991). Although temperatures below 26 °C initiate spiking in *Phalaenopsis*, plants do not initiate flowers until the spike is more than 5 cm long. When spikes shorter than 5 cm are exposed to temperatures above 26 °C, the shoot remains vegetative and forms a keiki, a vegetative plantlet, instead of flower buds, or the flower buds abort (Sakanishi et al., 1980).

Plants will initiate flowers at any temperature between 11 and 25 °C; however, optimum temperatures for spiking are reported to be between 15 and 20 °C (Sakanishi et al., 1980). *Phalaenopsis* can be uniformly spiked when placed at 25/20 °C day/night (Lee and Lin, 1987). However, plant maturity can influence

percentage of a population that flowers and time to flower after spiking (Yoneda et al., 1992). Young plants can be spiked uniformly if given lower temperatures or longer durations at a given temperature.

A number of studies (Lee and Lin, 1984; 1987; Sakanishi et al., 1980; Yoneda, 1985; Yoneda et at., 1991,1992) have reported the dates of spike emergence and flowering but not average daily temperatures (ADT) that are needed to properly determine a temperature effect on flower development. Instead, only the minimum and maximum temperature for a given month or the set point temperature of the greenhouse were given in the reports.

Phalaenopsis generally are not reported to be photoperiodic (Sakanishi et al., 1980). However, a few studies report that short days enhance spiking (De Vries, 1950; Griesbach, 1985; Rotor, 1952; Yoneda, 1991), but this short-day enhancement is thought to be a result not of the daylength itself but of the extension of cool night temperatures resulting from the extended night (Sakanishi et al., 1980).

The objective of this investigation was to quantify the effects of temperature on time from spike emergence to flowering and determine the effects of temperature on plant quality.

Materials and Methods

Plant Culture. Plants were fertilized at every irrigation with a nutrient solution of well water acidified with H_2SO_4 to a titratable alkalinity of 130 mg $CaCO_3$ L^{-1} and water-soluble fertilizer [125-12-125 N-P-K mg L^{-1} plus 1.0-0.5-0.5-0.5-0.1-0.1 (Fe, Mn, Zn, Cu, B, Mo) mg L^{-1} (MSU Special, Greencare Fertilizers, Chicago, Ill.)]. Vapor pressure deficit was maintained around 0.7 kPa by the injection of water vapor as needed.

Temperature Control. Greenhouse temperatures were controlled by a greenhouse climate-control computer (Priva, Model CD750, De Lier, Holland). Air temperatures on each bench were monitored with 36-gauge (0.127-mm-diameter) type E thermocouples connected to CR10 dataloggers (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 s and recorded the average hourly temperature. For each experiment, actual ADTs of air from the beginning of visible spiking until the average date of flowering for every treatment were calculated and used in data analyses.

Model Theory. Development rate of a *Phalaenopsis* spike from first emergence through a leaf blade to visible bud and flowering can be described as a linear function of average temperature:

$$1/\,DTF = b_0 + b_1 * T \qquad [1]$$

where days to flower (DTF) equals the intercept (b_0) plus the product of the slope (b_1) and temperature (T). The base temperature (T_b) and degree-days to maturity (°days) can be calculated from this linear relationship as

$$T_b = -b_0/b_1 \quad [2]$$

and

$$^{o}days = 1/b_1 \quad [3]$$

Node development rate can also be described by the same linear relationship as that in Eq. [1], where DTF becomes nodes per day.

Bud development was modeled by methods used by Fisher et al. (1996) for Easter lily. They described bud development of Easter lilygrown at a constant temperature with an exponential growth function in the form

$$B = B_0 e^{k(t-to)} \quad [4]$$

where B is flower-bud length, B_0 is initial bud length, t is time, t_0 is time zero, and k is a rate constant that changes with temperature. When k in Eq. [4] is substituted by $f(T)$ to incorporate a function of temperature, and when the maximum bud length (Bf) and number of days (D) to first open flower are known, Eq. [1], for any value of B, becomes

$$B_f = Be^{f(t)D} \quad [5]$$

D can then be estimated by

$$D = \ln(B_f / B) / f(T) \quad [6]$$

Experimental Design: Calibration. One hundred *Phalaenopsis* Taisuco Smile (*Phalaenopsis* Taisuco Bright × *P. equestris*) plants were received from Taiwan on 8 Sept. 2000. Plants were artificial hybrids, or grexes, raised from seedlings. When bare-root plants had a leaf-span diameter of approximately 25 cm, four to six mature leaves were potted into 30-cm pots with a medium composed of 60% (grade 3) perlite and 40% (Sure Mix Perlite, Michigan Grower Products; Galesburg, Mich.) peat-based medium. Plants were then held in the Michigan State University (MSU) research greenhouses at 25 °C (day) for 12 h and 20 °C (night) for 12 h for four weeks to initiate flower spikes (Lee and Lin, 1984). Plants were shaded to maintain an irradiance of no more than 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Once spikes were visible without dissection but had not grown to more than 2 cm, 20 plants were placed in one of five natural-photoperiod greenhouse compartments with constant temperature set points of 14, 17, 20, 23, or 26 °C. The actual ADTs were 14.5, 17.7, 19.9, 23.3, or 25.7 °C from 8 Oct. 1999 to average time of first open flower, when data collection stopped.

Validation Experiment 1. Phalaenopsis Taisuco Smile plants arrived from Taiwan on 8 Mar. 2001 and were potted into bark-based medium composed of 35% medium bark, 35% small bark, 10% coarse charcoal, 10% perlite (#3), and

10% parts fine peat (Porter's Orchids; Grand Ledge, Mich.) and spiked as in the calibration experiment. Once flower spikes were visible, 20 plants per treatment were placed at temperature set points of 17, 20, 23, or 26 °C. The actual ADTs were 18.4, 21.1, 23.0, or 25.9 °C.

Validation Experiment 2. Sixty *Phalaenopsis* hybrids (*P.* Taisuco Moonriver × *P. equestris* 'Alba' (hybrid ID H88-145) plants with a 25-cm leaf span were received from Taiwan on 19 Apr. 2001, potted into bark-based medium (Porter's Orchids), and then held at 28 °C until 11 May 2001, when the greenhouse temperature was set to 25/20 °C day/night for four weeks to initiate flower spikes. Once flowering spikes were visible, groups of 10 plants were placed into one of six long-day growth chambers with constant temperature set points of 14, 17, 20, 23, 26, or 29 °C. Actual ADTs were 14.3, 16.9, 19.5, 22.2, 25.5, and 28.6 °C. Once plants finished flowering in each growth chamber, they were transferred to a greenhouse set at 28 °C for additional vegetative development. The validation experiment was repeated one year later with the same plants. Plants were spiked in two to three weeks in the MSU greenhouses with a temperature set point of 23 °C to initiate flower spikes. Upon spike emergence, plants were transferred to long-day growth chambers at constant temperature set points of 20, 23, or 26 °C once spikes were visible. The ADTs were 19.5, 22.5, 19.5 °C. Plants had produced two or more additional leaves during the previous year, and all had a leaf span greater than 32 cm.

On 30 Oct. 2001, 180 additional plants of two hybrids arrived from Taiwan (*P.* Asian Elegance × P. Taisuco Shen, hybrid ID H88-36, and *Doritaenopsis* Sogo Smith × *D.* Sinica Sunday, hybrid ID H89314). Twenty plants of each cultivar were spiked in the MSU greenhouses at a temperature set point of 23 °C until spikes emerged; plants were then moved into growth chambers similar to those used in the calibration experiment. The ADTs were 19.5, 22.2, and 25.6 °C.

Data Collection and Analysis. Date of spiking, visible bud (VB), and flowering (FLW) were recorded; days from spiking to VB and FLW and from VB to FLW were calculated for each spike of all hybrids, converted to rates, and modeled as a linear function of actual air temperature. Data were analyzed by using SAS procedures (SAS Institute, Cary, N.C., Version 8). Regression analyses were performed by SigmaPlot (SPSS, Inc., Chicago, Ill.). There was no interaction between different spikes on a single plant, so all spikes in a given treatment were treated individually and pooled for analysis.

Time to appearance of each node on the inflorescence was also recorded every three to four days to determine the rate of node development at a constant temperature. Linear regression was performed individually for node count versus time for each spike, and the slopes of the regression lines were plotted against each temperature to determine the node development rate versus time. *Phalaenopsis* Taisuco Smile (validation experiment 1) was used as the

calibration data set, since the node development data from the original calibration set was not complete enough to model.

To model bud development, *P.* Taisuco Smile from validation experiment 1 were used as a calibration data set. Five plants from each treatment were randomly selected, and bud diameter for the first visible flower bud was recorded every two to three days by measuring the maximum distance between the outside edges of the true petals. The constant *k* was estimated for each temperature, and f(T) was formulated according to *k* as in Fisher et al. (1996) by using PROC NLIN in SAS .

Morphological response to temperature was determined by measuring number of nodes, flowers on the main and lateral inflorescence, final inflorescence length, flower diameter, and number of lateral branches on the main spike at first open flower. For each spike, the final inflorescence length was measured from the point of spike emergence to the top of the spike, and the diameter of the first open flower was recorded. Observations ended for each plant when the first flower opened. The levels of significance for linear and quadratic relationships between 0.05 and 0.001 were tested with PROC GLM in SAS. To compare data between cultivars, a common set point temperature of 23 °C (actual temperature, 22.7 °C ± 0.4 °C) was selected, and a means separation test was performed with PROC GLM by using least significant differences (LSD) in SAS.

Modeling flower development rate

Calibration: Phalaenopsis *Taisuco Smile.* Days to VB, days from VB to FLW, and days to FLW decreased as the ADT increased (Fig. 1A-C). Increasing the temperature 3.4 °C from 19.9 to 23.3 °C accelerated flowering more then increasing temperature 2.4 °C from 23.3 to 25.7 °C. For example, days to FLW decreased from an average of 50 to 35 d (15 d, or 4.4 d per degree) as temperature increased from 19.9 to 23.3 °C but decreased only an additional 3 d (35 to 33, or 1.25 d per degree) as temperature increased from 23.3 to 25.7 °C.

The relationship between temperature and the rate of progress toward VB, from VB to FLW, and to FLW was linear (Fig. 1D-F). Regression parameters for the *Phalaenopsis* Taisuco Smile calibration data set are given in Table 1. The reciprocal of the linear regression model closely fit the original data (Fig. 1A-C), indicating a linear regression relating rate of progress to FLW and can be used to predict the time to FLW.

The base temperature was similar for all growth stages of the calibration data set and ranged from 10.8 to 11.2 °C (Table 1). The thermal time to FLW was similar when the model relating time from spiking to FLW was used (769 degree-days; T_b=10.8) or when the two models predicting 1) days to VB or 2) VB to FLW (787 degree-days, T_b=11.2 and 11.0 °C) were used.

Validation: Phalaenopsis Taisuco Smile. Plants in the validation set responded like plants in the calibration experiment. The slope and intercept of the regression lines were not significantly different. The deviation between predicted and observed days to FLW of the validation set was generally within 10 d, except for a few observations that varied by as many as 20 d, according to the parameters for the linear equation of the calibration data set in Table 1 (Fig. 2).

Validation: Additional cultivars. Additional cultivars of *Phalaenopsis* responded to temperature as *P.* Taisuco Smile did, decreasing in time to FLW as temperature increased. The regression parameters were not significantly different with the exception of the intercept for H88-145 (1) ($P \leq 0.05$) and H89314 ($P \leq 0.05$) (Table 1). *Phalaenopsis.* H88-145 (1) grown at 28.6 °C were above T_{opt}, developing slower than those at 25.5 °C. For this reason,plants grown 28.6 °C were excluded from the linear regression analysis.

The parameters of Eq.[1] for all cultivars are given in Table 1, as are the parameters for individual regression lines of each hybrid. The thermal time to flower was similar when the model relating time from spiking to FLW was used (892 degree-days; $T_b = 11.8$) or when the two models predicting first days to VB and then VB to FLW were used (827 degree-days; $T_b = 9.9$ and 10.1 °C). The deviation between predicted and observed days to FLW was generally within ± 10 d according to the parameters for the linear equation of the calibration data

set in Table 1 (Fig. 2). The exception was H88-145(1), which deviated as much as 64 days from the predictive model in days to FLW at 14 °C.

Modeling node development rate

Calibration: Phalaenopsis *Taisuco Smile.* Appearance of nodes on the inflorescence spike increased linearly in the 14.5 to 25.7 °C temperature range (Fig. 3), and the base temperature was 9.9 °C (Table 2). Each 1 °C increase in temperature from 14.5 to 25.7 °C increased the node development rate by an average of 0.016 nodes/d. Regression parameters for the *Phalaenopsis* Taisuco Smile calibration data set are given in Table 2.

Validation: Phalaenopsis. Additional hybrids of *Phalaenopsis* responded similarly to temperature as *P.* Taisuco Smile did, increasing node development as temperature increased, and the slope and intercept of the regression parameters were not significantly different from the calibration experiment slope and intercept (Table 2). The parameters of the regression equation plotted for Taisuco Smile and H88-145 are given in Table 2, as are the parameters for individual regression lines of each hybrid. Node development data for H8836 and H89314 were incomplete and were not used as a validation for the calibration experiment.

Modeling bud development rate

Calibration: Phalaenopsis *Taisuco Smile.* Bud elongation and development rates and the estimated constant *k* increased linearly for buds up to 15 mm long as temperature increased from 18.4 to 25.7 °C (Fig. 4). A linear function ($k = c_1 + c_2{}^{x}T$), statistically significant at $P \leq 0.05$, was fit to the estimated *k* so that Eq. [4] became

$$B = B_0^{(c1 + c2 * T)(t-to)} \qquad [7]$$

where c_1 (d^{-1}) and c_2 ($C^{-1}\ d^{-1}$) are constants. When Eq. [7] was fit to the entire data set simultaneously, c_1 and c_2 were estimated to be 0.0113 ± 0.00389 d^{-1} and 0.0189 ± 0.00177 $C^{-1}\ d^{-1}$, respectively. The model closely fit the bud width data (Fig. 5). The model generally predicted the bud diameter for any given day within 2 to 3 d. (Fig. 6). Table 3 represents the bud development model when in the form of Eq [6].

Morphological data

Phalaenopsis *Taisuco Smile.* Temperature also affected the number of lateral branches on the primary flowering axis (Fig. 7 A-D). Over half of the plants grown at an ADT of 25.7 or 14.5 °C had no lateral branching (Fig. 7 A). When the plants were grown at 23.3 or 19.4°C, they were almost twice as likely to form one to two lateral flowering branches than those grown at 25.7 or 14.5 °C (Fig. 7 B). Plants grown at 17.7 °C also had a high percentage (40%) of plants producing one or two lateral branches (Fig. 7B). Although few plants developed

three or four flowering lateral branches, the percentage decreased from 36% to 6% when plants were grown at an ADT increased from 17.7 to 23.3 °C. No plants in the calibration data set produced more than four lateral branches.

Lateral branching for both replications of *Phalaenopsis* Taisuco Smile was similar (Figure 7 A-D). *Phalaenopsis*. Taisuco Smile replication one had less lateral branch overall compared with replication two, regardless of temperature. Many of the plants in repetition two (49%) produced three to four lateral branches and, in some cases, five to seven lateral flowering inflorescences. In comparison, only 17% of the plants produced three or more spikes, regardless of temperature in replication two (Figure 7 C). Plants producing one or two lateral branches seemed to do so irrespective of temperature.

Temperature had little or no impact on *Phalaenopsis* Taisuco Smile's number of nodes and flowers, height, or flower size (Table 4). The number of nodes on the inflorescence spike was consistently seven from 17.7 to 25.7 °C for *Phalaenopsis* Taisuco Smile. Plants at 14.5 °C averaged about one less node. Main axis flower count per plant increased from 14.5 to 19.9 °C and decreased from 19.9 to 25.7 °C, which resulted in a quadratic trend at $P < 0.05$ for replication 1, but no trend was detected in replication 2. Total flowers per plant varied greatly, depending on the magnitude of lateral branching. Total spike height was shorter for plants grown at 14.5 °C compared with warmer temperatures; however, there

was no significant trend. Temperature had an inconsistent effect on flower width from 16 to 26 °C.

Additional hybrids. Later branching in the additional cultivars occurred infrequently. For 17 to 26 °C, 70% or more of *P.* H88-145 did not produce any lateral branches (Fig. 8A). Of the plants that produced one or two lateral branches, as temperature decreased from 26 to 23 °C the percentage of branching increased for both repetitions of *P.* H88-145. Sixty-five percent of plants grown at 14 °C produced at least one flowering lateral branch (Fig. 8A-C). *Phalaenopsis* 88366 and *P.* 89314 did not produce any lateral branches at any of the temperature treatments.

Temperature did not affect the average number of nodes, flowers, final height, or final flower width for the other cultivars (Table 4). Only the flower width of *P.* Taisuco Smile was linear at $P \leq 0.05$. Morphological traits also differed greatly between repetitions of the same hybrids when temperature set points were compared at 23 °C. Neither repetition of Taisuco Smile differed significantly at $P \leq 0.05$, except for the total number of flowers. Repetition 2 of *P.* Taisuco Smile had an average of 28.7 flowers compared with repetition 1, which had 18.4 flowers. Similarly, *P.* H88-145 repetitions responded similarly, except for flower count and final spike height. Morphological traits differed at $P \leq 0.05$ and between hybrids when temperature set points at 23 °C were compared (Table 4).

Discussion

Phalaenopsis can be flowered and scheduled for a specific market date by controlling greenhouse temperature. Flower, node, and bud development were modeled as a function of temperature and were found to accurately predict the developmental times of these factors.

The optimum temperature for *Phalaenopsis* appears to be 26 °C; the base temperature for a given phenophase, between 8 and 12 °C (Table 1). The rate of flower, node, and bud development for all cultivars of *Phalaenopsis* used in this study increased linearly to increasing temperatures from 14 to 26 °C. Validation experiments using *Phalaenopsis* H88-1454 had an additional treatment of 28 °C, which appears to be above the optimum temperature for that hybrid from spiking to VB being the rate of development was slower at 28 °C than at 26 °C. However, from VB to FLW, the rate of development continued to increase from 26 to 28 °C. When these plants were placed into the growth chambers at 28 °C, all had spikes measuring from 0.5 to 1.0 cm long; however, only three developed buds, and of those, only one flowered, producing one flower on the main axis. The remaining plants grown at 28 °C returned to a vegetative state by either aborting the spike, or in a few cases, forming vegetative keikis on the spikes instead of buds. These findings are consistent with these of Sakanishi et al. (1991), who reported that plants grown above 27 to 29 °C remained vegetative.

For this study, plants above the optimum temperature and outside the linear response range were not included in the regression.

Comparing *Phalaenopsis* flowering rates to other reports in literature is difficult because the actual growing temperatures, or the length of the time at the described day/night temperatures, are not given. For example, Lee and Lin (1987) reported that plants being grown at day/night temperatures of 20/15 °C, 25/20 °C, and 30/25 °C required 205, 104, and 67 d, respectively, from spike to FLW. From the model developed from our study, assuming day and night temperature were in 12-h increments, plants should have flowered in 114, 65, and 46 d from spiking if grown at an ADT of 17.5, 22.5, and 27.5 d, respectively. If the days from spike to LFW for the Lee and Lin (1987) were to correspond with our study, the ADTs would have to have been 14.5, 18.2, and 22.3 °C, respectively. Discrepancies in the two data sets may be the result of differing definitions of what visible spiking was, inaccurate temperature monitoring in the Lee and Lin (1987) experiment, or differing plants sizes and hybrids. Sakanishi et al. (1980) also report the time to FLW decreased as temperature increased, but only the minimum and maximum growing temperatures are reported. For experiments performed in this study, *Phalaenopsis* hybrids grown at ADTs of 17.7, 20.0, 22.5, and 27.5 °C required an average of 66, 49, 36, and 30 d, respectively, to reach VB from spiking and 133, 88, 64, and 53 d to FLW from spiking. At any constant temperature for any given cultivar, time to VB was about 60% of the total time from spiking to flower.

Yoneda et al. (1992) reported that plant maturity affected time to spike and subsequent FLW. In validation experiments for our study, two replications using *Phalaenopsis* H88-145 were performed. The second replication included plants that had grown for an additional year after flowering in replication one. *Phalaenopsis* H88-145 replication two did not develop faster from spike to FLW than when these plants were spiked and flowered the previous year. The more mature, larger plants spiked in 14 ± 5 d from the start of cooling compared to plants in the first replicate, which spiked in 28 ± 3 d from the start of cooling, which is consistent with other studies (Yoneda, 1985; Yoneda et al., 1992).

The effects of temperature on node development rate have not been reported in other studies. The regression line fit the calibration set well (Fig. 3) ($r^2 = 0.98$) and estimated a T_b of 9.9 °C (Table 2), which is close to the estimated T_b for flower development (Table 1). Individual data for node development and flower development agreed. For example, when an average node count of seven is used to estimate the time to produce a spike to VB from the node development model at 26 °C, the spike is predicted to take 28 d and 30 d from spiking to VB according to the flower development model.

The model used for relating bud development to temperature performed well in the calibration data set, predicting the bud width within 4 d for a given day and temperature (Fig. 5 and 6). This model is accurate only for buds that are shorter

to 15 mm, or about 3 to 5 d before the bud opens. Bud development beyond 15 mm does not develop according to the same linear function. A validation experiment was not performed, but should be conducted with *P.* Taisuco Smile before being implemented. The parameters of this model are not assumed to be accurate for large flowering hybrids, but it may be possible to use this model on a relative scale for any size flower if the maximum bud size before opening and the days from spiking to VB are known.

Lateral branching was also influenced by temperature (Fig. 7 and 8); however, the potential for *Phalaenopsis* to develop lateral branches was also cultivar dependent. Of the 4 cultivars in this experiment, only *P.* Taisuco Smile and *P.* H88-145 formed lateral branches. Both of these cultivars share a parent, *P. equestris,* which is used for breeding because of its branching habit (D. Garling, personal communication). The reason some cultivars branch and others do not is not understood, but the reason plants branch better from 17 to 23 °C may have a simple answer. Ota et al, (1991) reported that *Phalaenopsis,* which are CAM (Crassulacean Acid Metabolism) plants, have the greatest nocturnal uptake of CO_2 at 20 °C.

Temperatures in the range used for commercial production of *Phalaenopsis*, 17 to 26 °C, did not affect the number of nodes and flowers, spike height, or flower width, but these factors did vary between cultivars. Other studies have reported the effect of temperature on the number of flowers and spike height, but results

are contradictory. Yoneda et al. (1992) reported that *P.* Jimmy Hall x *P.* (Dos Pueblos x Anne) grown at 20 °C had more flowers and shorter spikes than when grown at 25 °C. Lee and Lin (1984) also report that spikes on plants grown at a day/night temperature of 20/15 °C were shorter than those on plants grown at 25/20 °C for *P.* Dos Pueblos x *P.* Juanit, but plants grown at 20/15 °C had fewer flowers than those grown at 25/20 °C.

Temperatures beyond the range of 17 to 26 °C, those approaching T_b and T_{opt}, had negative effects on morphological characteristics. Temperature treatments of 14 °C produced plants that had fewer flowers and nodes than others of the same hybrid. *Phalaenopsis* Taisuco Smile averaged 20 cm shorter than *P.* Taisuco Smile grown at higher temperatures. Conversely, *P.* H88-145 flowered at 14 °C and were 3 to 25 cm taller than those grown at higher temperatures. *Phalaenopsis* H88-145 grown at 28 °C produced a number of nodes similar to those grown at other temperatures; however, of 10 plants, only one progressed to FLW, and that plant had only one flower. *Phalaenopsis* H88-145 grown at 28 °C were also the shortest of all plants in the treatments, at an average of 25.5 cm long. These data reconfirm that 28 °C is above the T_{opt} for growing *Phalaenopsis.*

In summary, *Phalaenopsis* perform best when grown at an ADT of ≈23 °C. Although plants grown at ≈23 °C progressed to VB and FLW approximately seven to 10 d later than those grown at 26 °C, some hybrids grown at an ADT of 23 °C had the additional benefit of forming lateral branches. Also, although our

study included four cultivars of various parentages, other cultivars might be more sensitive to being grown at 26 °C, which may be above their optimum growing temperature. Growing plants at cooler temperatures (from 17 to 20 °C) will not harm them and may enhance lateral branching, although time to FL increases greatly, from 64 to 133 d respectively.

Literature Cited

Baker, M.L. and C. Baker. 1991. Orchid species culture. Timber Press, Portland, Ore.

Barendse, M. 2002. De sierteclt-toppers van 2001. Vakblad voor de Bloemisterij. 24–26.

De Vries, J.T. 1950. On the flowering of *Phalaenopsis schilleriana* Rchb f. Ann. Bogorienses. 1:61–76.

Fisher, P., R.D. Heins, and N. Ehler. 1996. Modeling flower bud elongation in Easter lily (*Lilium longiflorum Thunb.*) in response to temperature. HortScience 31:349–352.

Fisher, P., R.D. Heins, and N. Ehler. 1997a. A decision-support system for real-time management of Easter lily (*Lilium longiflorum* Thunb.) scheduling and height: I. System description. Agr. Systems. 54:23–37.

Fisher, P., R.D. Heins, and N. Ehler. 1997b. A decision-support system for real-time management of Easter lily (*Lilium longiflorum* Thunb.) scheduling and height: II. System description. Agr. Systems 54:39–55.

Greisbach, R.J. 1985. *Phalaenopsis* as potential potted plants. HortScience 20:624.

Greisbach, R.J. 2000. Potted *Phalaenopsis* orchid production: History, present status, and challenges for the future. HortTechnology 10:429.

Hew, C.S. and J.W.H. Young. 1997. The physiology of tropical orchids in relation to the industry. World Scientific,. Singapore.

Holcomb, E.J. and R. Berghage. 2001. Photoperiod, chilling, and light quality during daylight extension affect growth and flowering of tissue-cultured Easter lily plants. HortScience 36:53–55.

Karlsson, M.G., R.D. Heins, and J.E. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113:70–74.

Karlsson, M.G., R.D. Heins, J.E. Erwin, and R.D. Berghage. 1989. Development rate during four phases of chrysanthemum growth as determined by preceding and prevailing temperatures. J. Amer. Soc. Hort. Sci.114:234–240.

Lee, N. and G.M. Lin. 1984. Effect of temperature on growth and flowering of *Phalaenopsis* white hybrid. Chinese Soc. Hort. Sci. 30:223–231.

Lee, N. and G.M. Lin. 1987. Controlling the flowering of *Phalaenopsis*. Proc. Symp. Forcing Hort. Crop 10:27–44.

Ota, K., K. Morioki, and Y.Yamaoto. 1991. Effects of leaf age, inflorescence, temperature, light intensity, and moisture conditions on CAM photosynthesis in *Phalaenopsis*. J. Jpn. Soc. Hort. Sci. 60: 125–132.

Noble, M. 1971. You can grow *Phalaenopsis* orchids. McQuerry Orchid Books, Jacksonville, Fla.

Rotor, G.B., Jr. 1952. Daylength and temperature in relation to growth and flowering of orchids. Cornell Univ. Agr. Expt. Sta. Bul. 885:1–46.

Sakanishi, Y.H., H. Imanishi, and G. Ishida. 1980. Effect of temperature on growth of *Phalaenopsis abamibilis*. Bul. Okaka Press Ser. 32:1– 9.

Sheehan, T.J. 1992. Orchids, p. 115 –141. In: R. Larson (ed.). Introduction to floriculture. Academic Press, San Diego, Calif.

United States Department of Agriculture (USDA). 2002. Floriculture crops 2001 summary. National Agricultural Statistics Service.

Vakblad voor de Bloemisterij, 2002. June 7 (23a): 88–89.

Wang, Y.T. 1996. Cytokinin and light intensity regulate flowering of Easter lily. HortScience 31:976–977.

Wilkins, H.F. 1988a. Leaf unfolding rate of the Easter lily is temperature dependent. Minnesota State Florists' Bul. 36:4–6.

Wilkins, H.F. 1988b. Flower bud development rate for the Easter lily is temperature dependent. Minnesota State Florists' Bul. 36:6–7.

Wilkins, H.F. and K.L. Grueber. 1990. Easter lily height control. Minnesota State Florists' Bul. 39:26–30.

Yoneda, K. 1985. Effects of plant age and time of transfer to highland during summer on *Phalaenopsis*. J. Jpn. Soc. Hort. Sci. 54:101–108.

Yoneda, K., H. Momose, and S. Kubota. 1991. Effects of daylength and temperature of flowering in juvenile and adult *Phalaenopsis* plants. J. Jpn. Soc. Hort. Sci. 60(3):651–657.

Yoneda, K., H. Momose, and S. Kubota. 1992. Comparison of flowering behavior between mature and premature plants of *Phalaenopsis* under different temperature conditions. 36(3):207–210.

Table 1: Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud (VB) and anthesis (FLW) and from VB to FLW in cultivars of *Phalaenopsis*. The intercept and slope were used to calculate the base temperature (T_b) and degree-days. All r^2 significant at $P < 0.0001$. All regression lines were compared to the calibration data set Taisuco Smile for significant differences between the slope and intercept.

Hybrids	Intercept (b_o) (1/d)	Slope (b_1) [(1/d)/°C]	T_b (°C)	Degree-days	r^2
		Spiking to VB			
Taisuco Smile (1)[z]	-0.0248 ± 1.86E-3[x]	-0.0022 ± 8.70E-5	11.2	454	0.84
Taisuco Smile (2)	-0.0264 ± 4.48E-3[NS]	-0.0023 ± 1.93E-4[NS]	11.5	436	0.60
H88-145 (1)	-0.0129 ± 1.89E-3***	-0.0017 ± 8.52E-5[NS]	7.5	578	0.77
H88-145 (2)	-0.0370 ± 4.18E-3[NS]	-0.0029 ± 1.85E-4[NS]	12.8	347	0.80
H8836	-0.0277 ± 7.26E-3[NS]	-0.0023 ± 3.20E-4[NS]	11.9	431	0.78
H89314	-0.0171 ± 1.15E-2[NS]	-0.0021 ± 5.10E-4[NS]	8.3	484	0.48
All hybrids	-0.0219 ± 1.52E-3[NS]	-0.0021 ± 6.93E-3[NS]	9.9	468	0.73
		VB to FLW			
Taisuco Smile (1)	-0.0330 ± 2.80E-3	-0.0030 ± 1.30E-4	11.0	333	0.81
Taisuco Smile (2)	-0.0202 ± 5.69E-3[NS]	-0.0024 ± 2.29E-4[NS]	8.3	409	0.53
H88-145 (1)	-0.0249 ± 4.07E-3[NS]	-0.0027 ± 1.81E-4[NS]	11.0	442	0.64
H88-145 (2)	-0.0487 ± 5.74E-3[NS]	-0.0036 ± 2.55E-4[NS]	13.7	280	0.76
H8836	-0.0406 ± 1.20E-2[NS]	-0.0033 ± 5.28E-4[NS]	12.4	306	0.72
H89314	-0.0452 ± 1.22E-2*	-0.0036 ± 5.50E-4[NS]	12.5	276	0.73
All hybrids	-0.0329 ± 2.04E-3[NS]	-0.0030 ± 9.32E-5[NS]	10.6	353	0.74
		Spiking to FLW			
Taisuco Smile (1)	-0.0141 ± 8.05E-4	-0.0013 ± 3.74E-4	10.8	769	0.90
Taisuco Smile (2)	-0.0152 ± 1.62E-3[NS]	-0.0013 ± 7.20E-5[NS]	11.4	751	0.77
H88-145 (1)	-0.0094 ± 9.54E-4[NS]	-0.0011 ± 4.24E-5[NS]	8.7	933	0.84
H88-145 (2)	-0.0205 ± 1.59E-3[NS]	-0.0016 ± 7.06E-5[NS]	12.8	627	0.89
H8836	-0.0157 ± 2.59E-3[NS]	-0.0013 ± 1.14E-4[NS]	11.9	762	0.90
H89314	-0.0115 ± 3.54E-3[NS]	-0.0012 ± 1.60E-4[NS]	9.5	824	0.78
All hybrids	-0.0132 ± 6.19E-4[NS]	-0.0012 ± 2.81E-5[NS]	11.8	892	0.84

The intercept and slope were used to calculate the base temperature (T_b) and degree-days. All r^2 were significant at $P < 0.0001$. All regression lines were compared to the calibration data set Taisuco Smile for significant differences between the slope and intercept.

[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[z] S.E.

[y] Replication (1) and (2)

Table 2: Parameters of linear regression analysis relating forcing temperature to rate of node development in hybrids of *Phalaenopsis*. The intercept and slope were used to calculate the base temperature (T_b). All r^2 significant at P < 0.0001. All regression lines were compared to the calibration data set Taisuco Smile for significant differences.

Hybrids	Intercept (b_o) (1/d)	Slope (b_1) [(1/d)/°C]	T_b (°C)	r^2
Taisuco Smile (1)[z]	-0.1568 ± 1.53E-2	-0.0158 ± 1.60E-3	9.9	0.97
Taisuco Smile (2)	-0.1585 ± 9.29E-2 [NS]	-0.0114 ± 4.12E-3 [NS]	7.5	0.79
H88-145 (1)	-0.1277 ± 1.36E-2 [NS]	-0.0136 ± 9.21E-4 [NS]	9.4	0.96
H88-145 (2)	-0.1873 ± 1.64E-3 [NS]	-0.0179 ± 7.24E-3 [NS]	10.5	0.86

The intercept and slope were used to calculate the base temperature (T_b). All r^2 were significant at $P < 0.0001$. All regression lines were compared to the calibration data set Taisuco Smile for significant differences.

[NS], *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[z] S.E.

[y] Replication (1) and (2)

Table 3. Bud development computed from Eq. [6] [D = $ln(B_f / B) / f(T)$], where $f(T) = c1 + c2 * T$ (c_1 = 0.0113 ± 0.00389 d^{-1} and c_2 = 0.0189 ± 0.00177 C^{-1} day^{-1}

Bud width	Temperature °C				
(mm)	18	20	22	24	26
1	59.8	55.2	51.2	47.8	44.8
2	44.5	41.0	38.1	35.7	33.3
3	35.5	32.8	30.4	28.4	26.6
4	29.2	26.9	25.0	23.3	21.9
5	24.2	22.4	20.8	19.4	18.2
6	20.2	18.7	17.3	16.2	15.1
7	16.8	15.5	14.4	13.5	12.6
8	13.9	12.8	11.9	11.1	10.4
9	11.3	10.4	9.7	9.0	8.5
10	8.9	8.3	7.7	7.2	6.7
11	6.8	6.3	5.9	5.5	5.1
12	4.9	4.5	4.2	3.9	3.7
13	3.2	2.9	2.7	2.5	2.4
14	1.5	1.4	1.3	1.2	1.1
15	0.0	0.0	0.0	0.0	0.0

Table 4. The effect of temperature on the average number of nodes, total flower count, flowers on the main spike axis, final spike height and flower width for *Phalaenopsis* Taisuco Smile (repetitions 1 and 2), *P.* H88-145 (repetitions 1 and 2), *P.* H88-36, and *P.* H89314.

Hybrid	Treatment temperature	Actual temperature	Number of nodes	Number of flowers	Number of Flowers on main axis	Final spike height (cm)	Flower width (mm)
Taisuco Smile							
Rep 1	14	14.9	5.8	8.9	4.8	27.7	
	17	17.7	7.6	22.4	10.8	51.9	
	20	19.9	7.1	22.8	13.5	55.1	
	23	23.3	7.2 a[z]	18.4 b	12.5 a	53.1 ba	60.0 b
	26	25.7	7.7	16.8	11.5	59.7	64.2
			L*		Q*		
Rep 2	17	20.2	7.2	37.4	13.7	69.6	68.9
	20	21.0	7.3	35.3	14.5	67.5	73.1
	23	22.9	7.5 a	28.7 a	13.3 a	57.7 a	63.7 b
	26	25.6	7.5	18.7	13.3	54.5	63.5
							L*
H88-145							
Rep 1	14	13.5	6.1	25.6	9.8	55.8	M
	17	16.9	6.2	5.3	5.2	47.6	54.3
	20	19.5	6.9	9.4	7.8	52.4	58.0
	23	22.2	6.1 a	7.7 ab	7.3 cb	40.6 c	63.4 b
	26	25.5	6.6	4.6	4.6	37.4	62.3
	29	28.5	6.0	0.2	0.2	25.5	M
Rep 2	20	19.5	6.8	10.8	9.1	48.7	59.0
	23	22.5	7.3 a	9.3 c	7.1 b	49.4 b	65.5 b
	26	25.5	6.2	10.0	9.8	43.1	61.5
H88-36	20	19.5	7.7	7.3	7.3	69.8	92.7
	23	22.5	5.6 bc	7.0 c	7.0 cb	47.8 bc	83.6 a
	26	25.6	5.7	3.8	3.8	49.2	92.0
H89314	20	19.5	4.6	4.5	4.5	39.9	75.5
	23	22.5	4.4 c	3.8 c	3.8 c	35.6 d	82.0 a
	26	25.6	4.3	2.0	2.0	28.0	85.9

* Significant at $P \leq 0.05$. The absence of letters under a cultivar in a column indicates no significance. L and Q indicate a linear or quadratic trend, respectively

Plants grown at a temperature set point of 23 °C were used for hybrid comparisons. Temperatures were started at spike emergence and continue to the first open flower. All parameters were measured when the first flower opened.

[z] Mean separation only within plants grown at 23 °C by Least Significant Difference at $P = 0.05$.

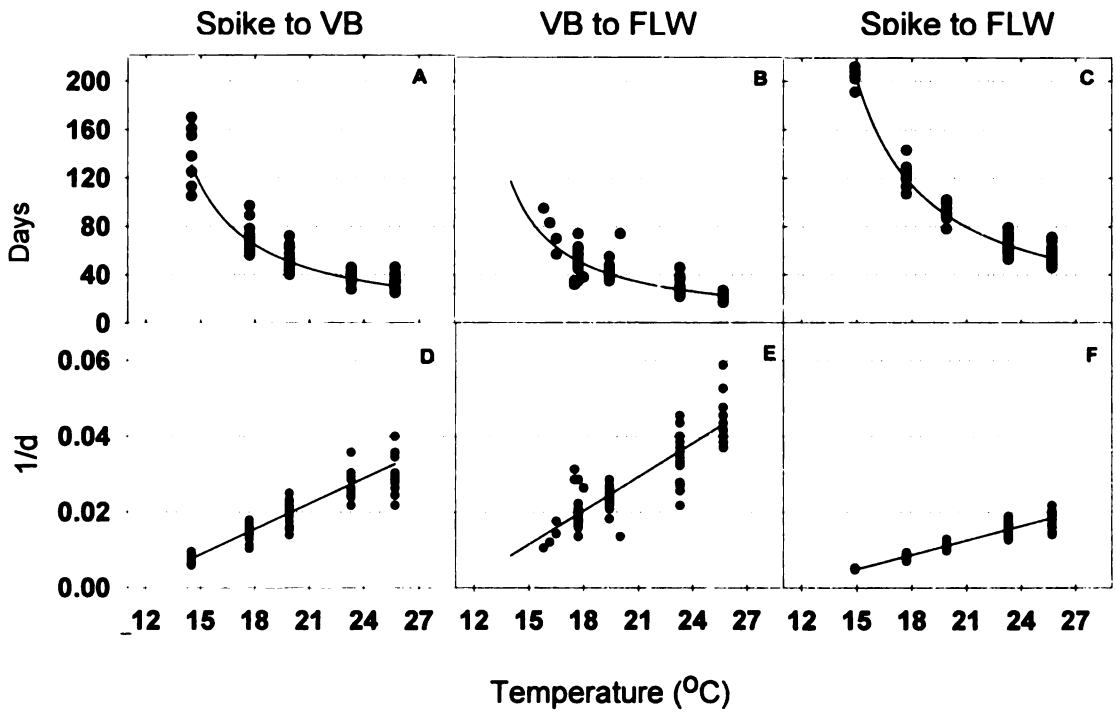

Figure 1. Effects of temperature on time to visible bud (VB) and flower (FLW) (A, B, and C) and rate of progress(D, E, and F) in calibration data set *Phalaenopsis* Taisuco Smile (•). Each symbol (•) represents one spike. The parameters of linear regression lines are presented in Table 1. The quadratic regression lines in A, B, and C are the reciprocal of the linear regression lines in D, E, and F, respectively.

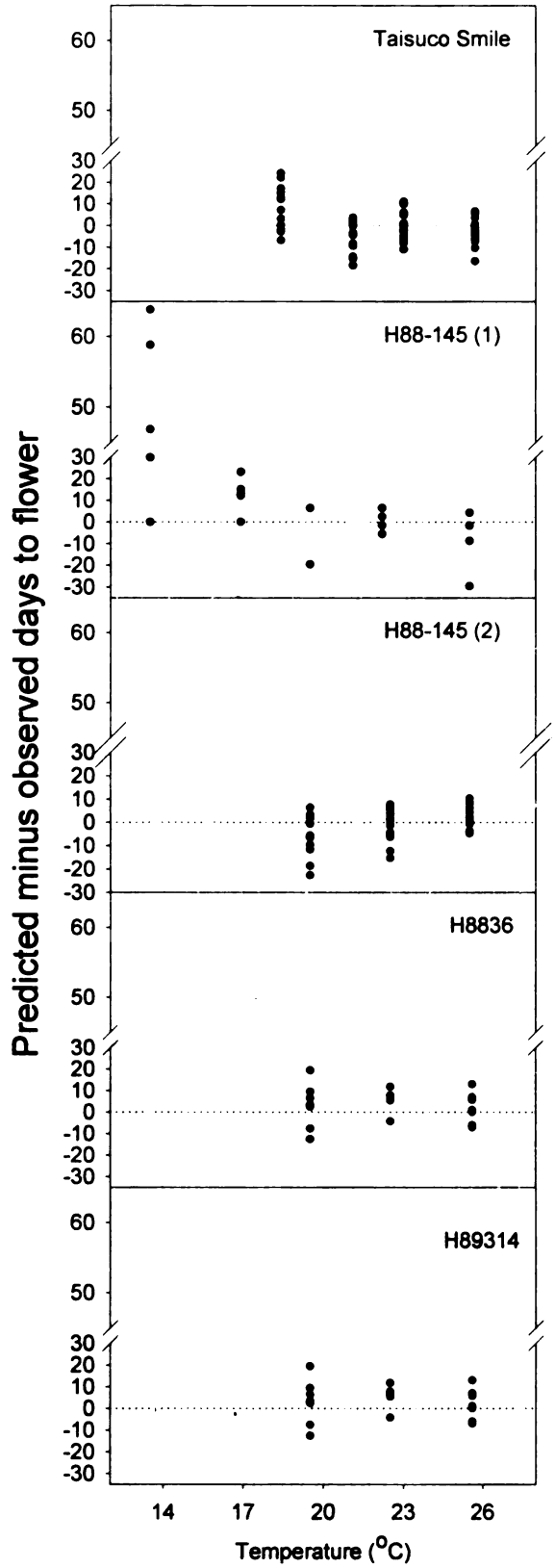

Figure 2. Deviation between predicted and observed days to from spiking to flower for validation data sets of *Phalaenopsis* hybrids.

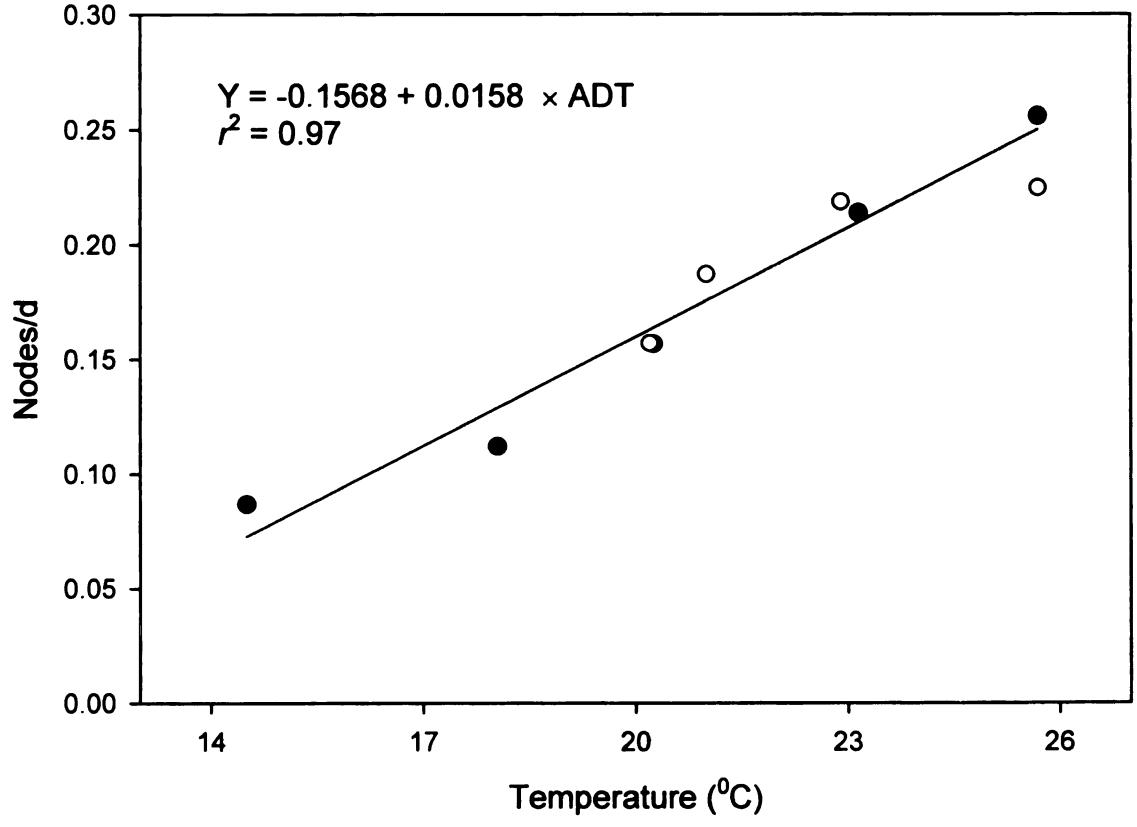

Figure 3. Effects of temperature on inflorescence node development rate of *Phalaenopsis* Taisuco Smile. Data points represent the slope of Eq. [1] calculated for node count versus time for *Phalaenopsis* Taisuco Smile in the calibration data set (●). The validation data set *Phalaenopsis* Taisuco Smile (○) was plotted against the regression line for comparison.

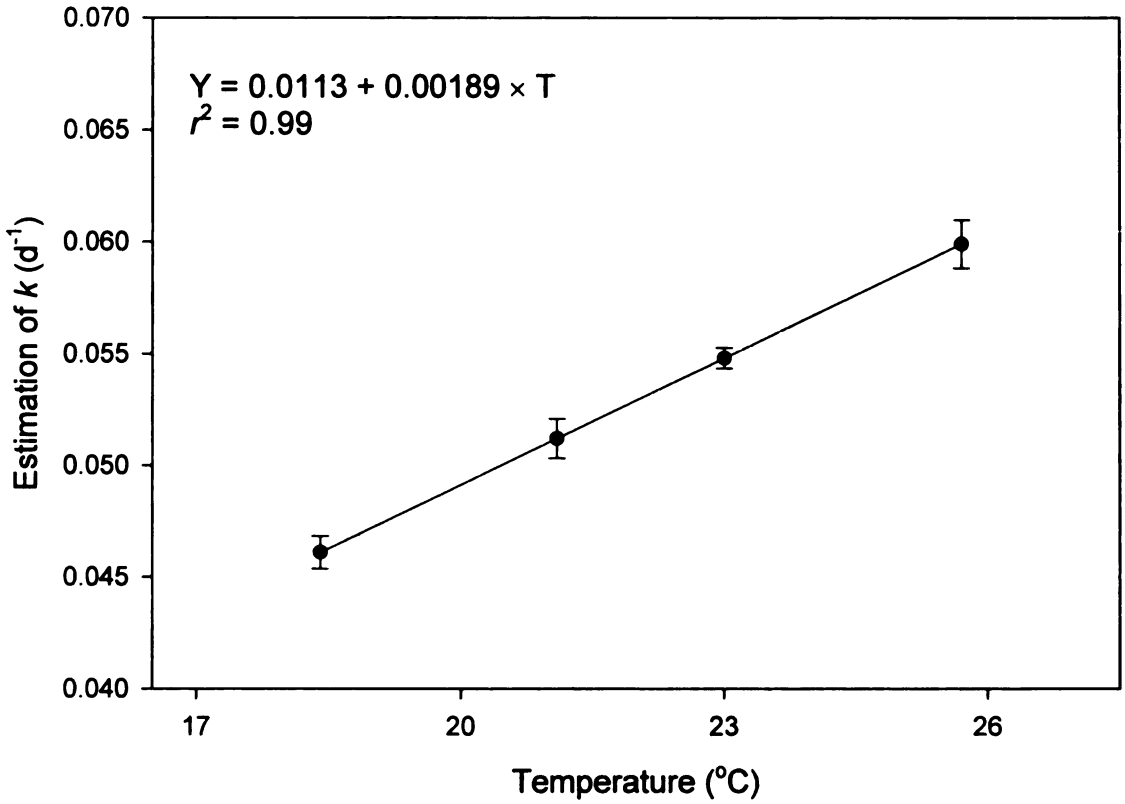

Figure 4. Estimates of *k*, the rate parameter in Eq. [1] for *Phalaenopsis* Taisuco Smile, obtained by using nonlinear regression to fit Eq. [1] separately to data from four temperature treatments in the calibration experiment [(●) symbol ± S.E.] and the linear function *f(T)* (solid line).

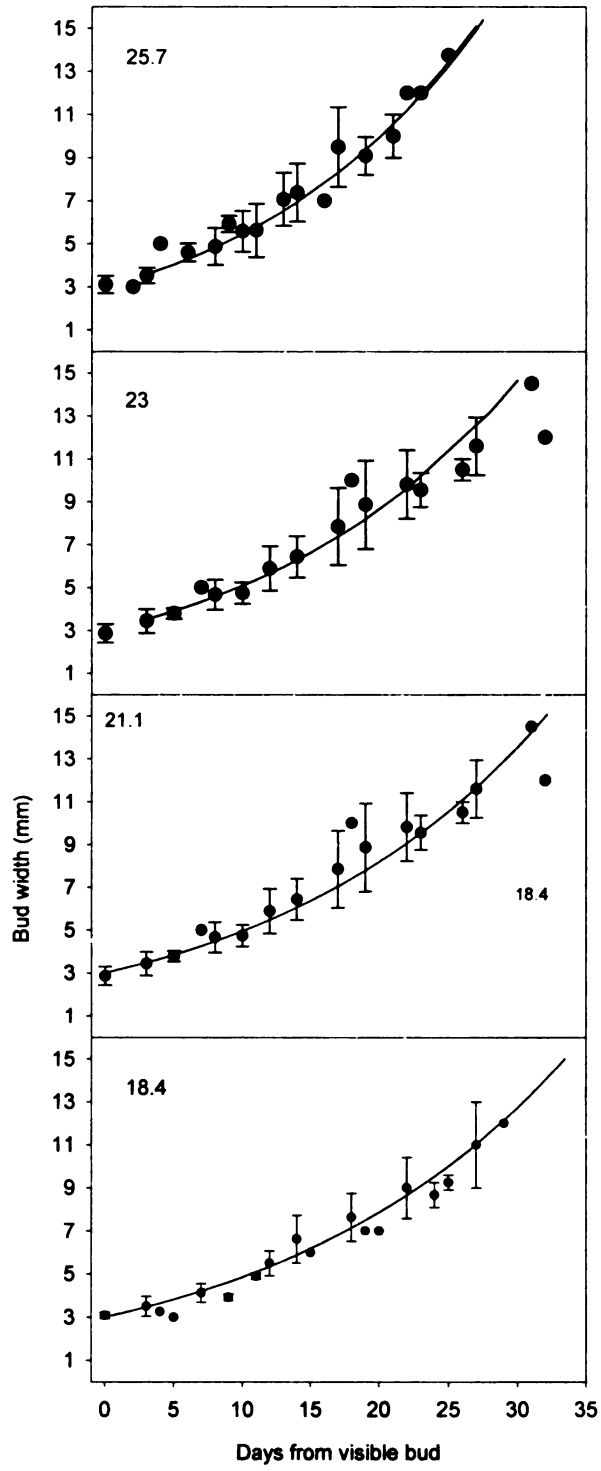

Figure 5. Predicted (solid line) and observed (●, mean ± SE) bud length for each treatment in the calibration experiment of *Phalaenopsis* Taisuco Smile.

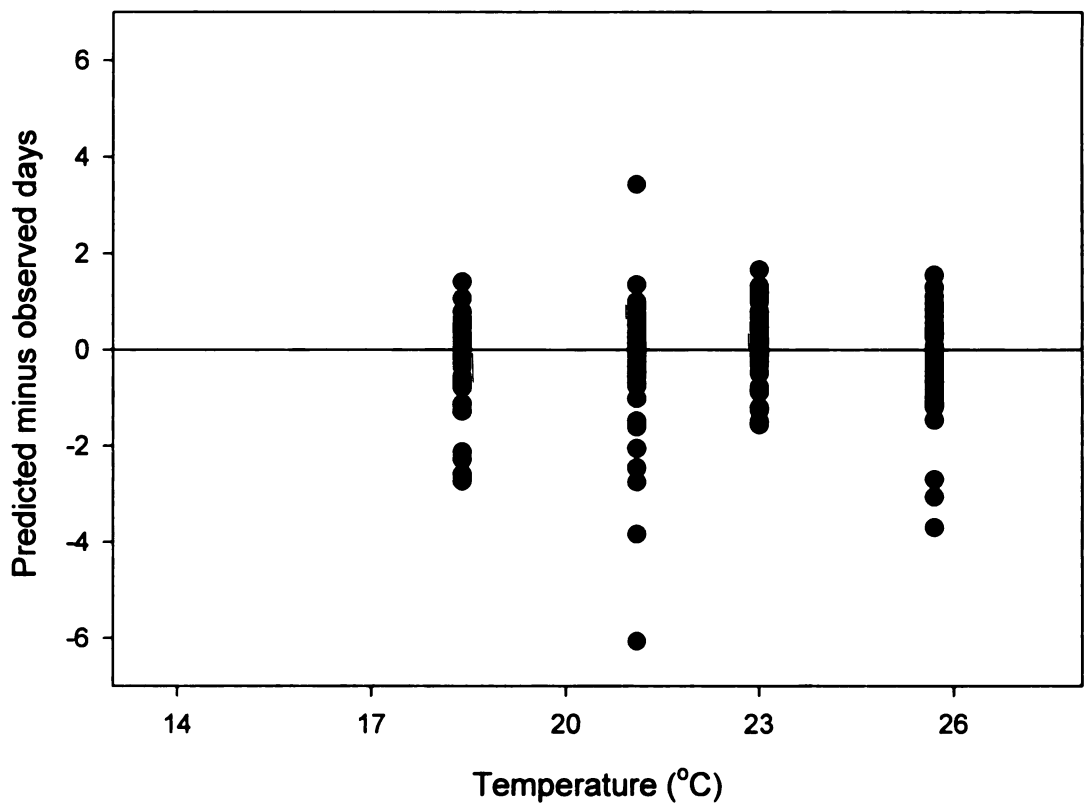

Figure 6. Deviation between predicted and observed days for calibration data set *Phalaenopsis* Taisuco Smile.

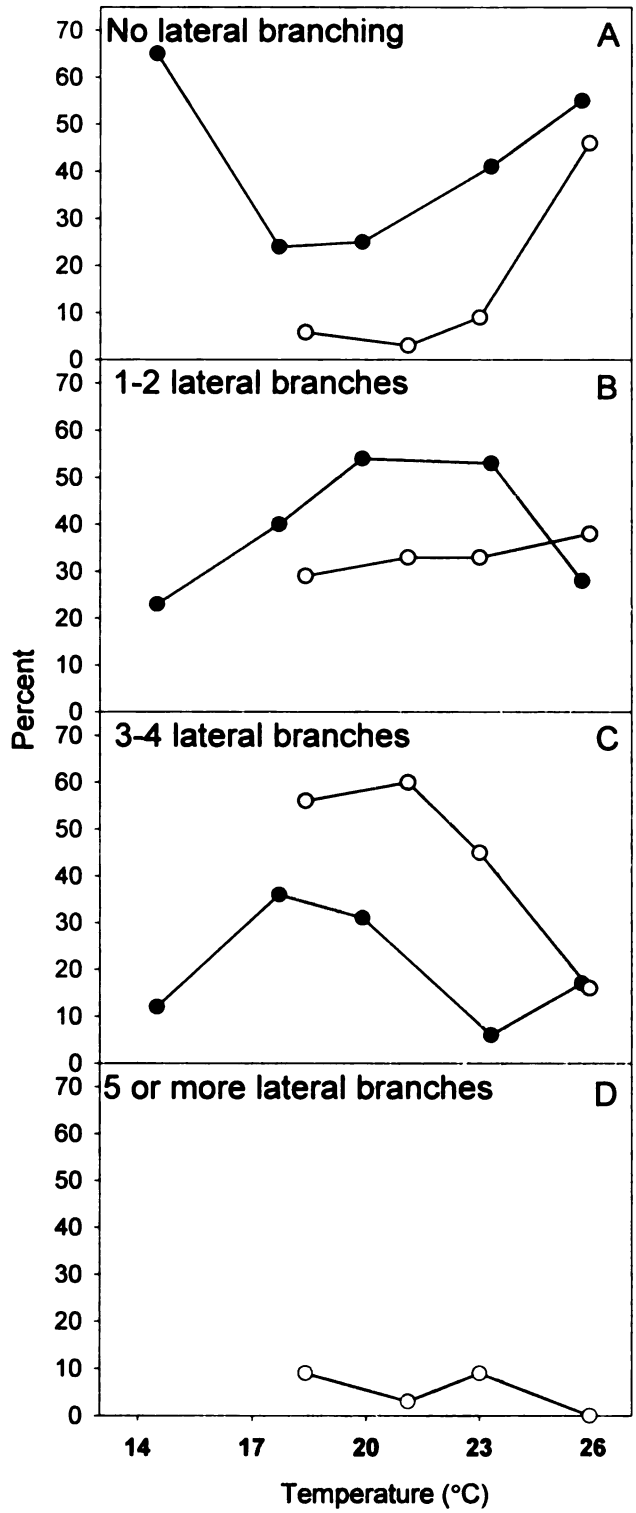

Figure 7. Percentage of plants with a primary inflorescence spike that branched and formed either no flowering lateral branches (A), 1 to 2 (B), 3 to 4 (C), or 5 or more (D) flowering lateral inflorescences as a function of average daily temperature for *Phalaenopsis* Taisuco Smile repetition 1 (●) and 2 (○).

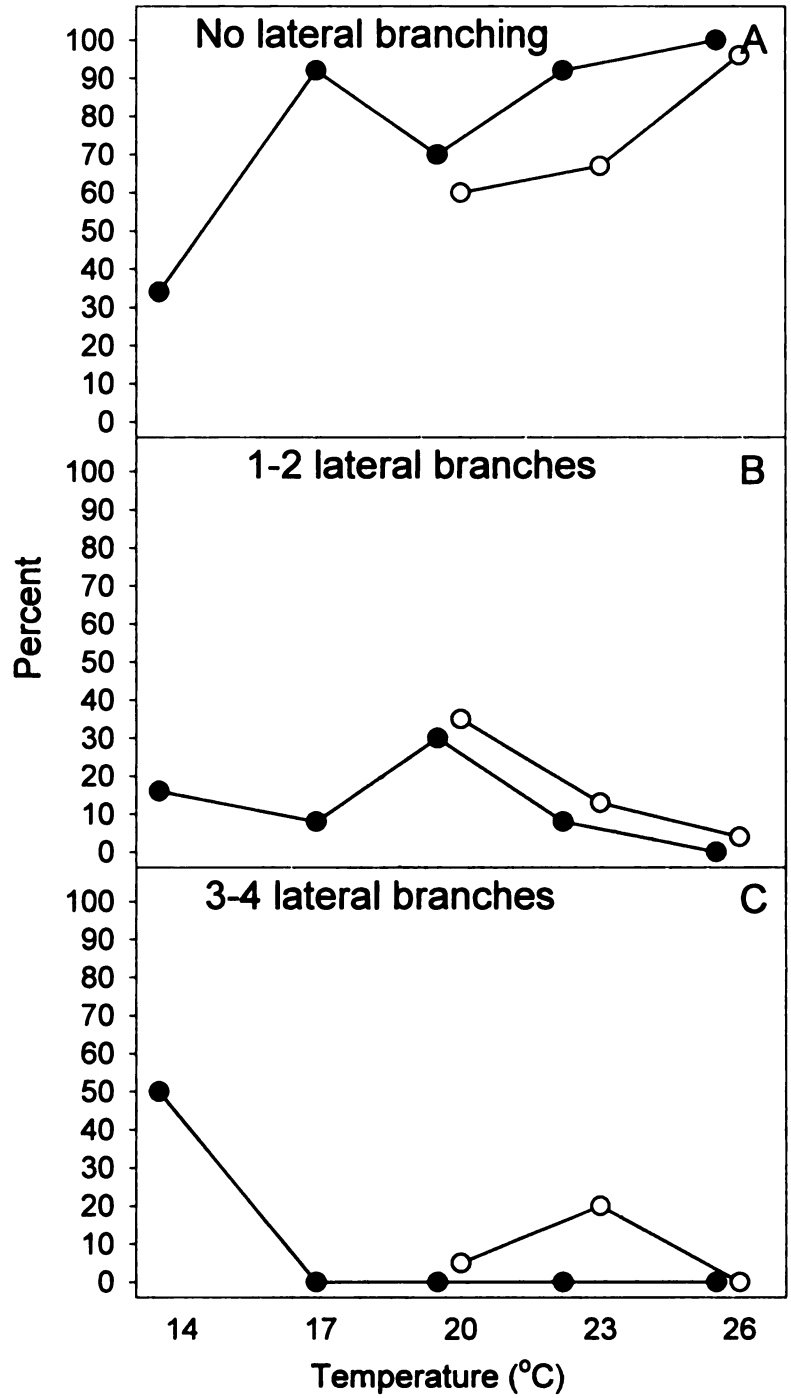

Figure 8. Percentage of plants with a primary inflorescence spike that branched and formed either no flowering lateral branches (A), 1 to 2 (B), 3 to 4 (C), or 5 or more (D) flowering lateral inflorescences as a function of average daily temperature for *Phalaenopsis* H88-145 repetition 1 (•) and 2 (○).

APPENDIX

Introduction

Miltoniopsis, commonly called the pansy orchid, is native to wet forest regions of Costa Rica and Peru (Berliocchi, 1996) and is found from 610 m to 2100 m above sea level (Baker and Baker, 1993a). The average minimum and maximum temperature for their climate is 10 °C to 29 °C, respectively, in more heat-tolerant species.

Miltoniopsis is currently the fourth most valuable potted orchid in the Netherlands, with 797,000 pots sold in 2001 (Vakblad voor de Bloemisterij, 2002). However there has not been any published work to develop a growing protocol for these plants. The only information available on *Miltoniopsis* is a handful of articles that contain similar cultivation instructions (Baker and Baker, 1993a, b; Nash 1989; Ortho, 1999; Rentoul, 1982). The recommendations for growing *Miltoniopsis* are to keep plants evenly moist, and grow them under low light levels. Pink leaf edges are an indication that the plants are receiving too much light (Baker and Baker, 1993a; Ortho, 1999; Nash, 1989). The recommended daytime average temperature ranges from 27 to 29 °C and the night temperature averages from 16 to 18 °C (Baker and Baker, 1993a; Nash, 1989; Ortho, 1999). Temperatures of 17°C to 20 °C, reportedly produce abundant flowering, but there is no indication if this is a constant ADT or an induction treatment (Baker and Baker, 1993a; Tran Than Van, 1974).

Paphiopedilum are native to tropical and subtropical southeast Asia and islands of the South Pacific (Berliocchi, 1996; Cribb, 1987; Dole and Wilkins, 1999), and 60 species are known (Cribb, 1987).

Although *Paphiopedilum* are a popular potted plant, with over 500,000 sold in the Netherlands during 2001, almost no data exist describing their commercial production. Most orchid articles and books give general cultivation for *Paphiopedilum* (Hennessy and Hedge, 1989; Ortho, 1999; Rentoul, 1982; Stewart and Griffiths; 1995). Only one refereed journal article has been published dealing with the cultivation of *Paphiopedilum*. Rotor (1952) reported that *P. insigne* remained vegetative above 18 °C, but when temperatures were dropped to 13 °C, flower buds initiated two to three weeks later and plants flowered six months later when maintained at 13 °C. *Paphiopedilum. barbatum* remained vegetative above 23 °C but flowered when temperatures were dropped to 16 to 21 °C (Goh and Arditti, 1985). Plants were not photoperiodic (Rotor; 1952)

Materials and Methods

Plant culture. Plants were fertilized at every irrigation with a nutrient solution of well water acidified with H_2SO_4 to a titratable alkalinity of 130 mg $CaCO_3$ L^{-1} and water-soluble fertilizer [125-12-125 N-P-K (mg L^{-1}) plus 1.0-0.5-0.5-0.5-0.1-0.1 Fe, Mn, Zn, Cu, B, Mo (mg L^{-1}) (MSU Special, Greencare Fertilizers, Chicago, Ill.)].

Temperature control. Greenhouse and growth chamber temperatures were controlled by a greenhouse climate-control computer (Priva, Model CD750, De Lier, Holland). Air temperatures on each bench were monitored with 36-gauge (0.127-mm-diameter) type E thermocouples connected to CR10 dataloggers (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 s and recorded hourly. Vapor pressure deficit was maintained around 0.7 kPa by the injection of water vapor as needed. For each experiment, actual daily ADTs from the beginning of visible spiking until the average date of flowering for every treatment were calculated and used in data analyses.

Experimental design: flower induction without bulking. On 5 May 2001, 500 *M.* Augres 'Trinity' and *P. laser* x *charlesworthii* prepotted in a bark-based medium arrived from Nurserymen's Exchange in Half Moon Bay, Calif. Plants were held at 23 °C under natural photoperiods until 8 June 2001, when 120 nonflowering *Miltoniopsis* plants with at least one mature and two immature

pseudobulbs were transferred to environmental growth chambers. Also, 120 nonflowering *Paphiopedilum* plants were transferred to growth chambers. Ten plants of each genera were placed in either long days (LD) of 9 h (from 2200 to 0200 HR) with a night interruption from incandescent lamps or short days (SD) of 9 h in one of six chambers with temperature set points of 14, 17, 20, 23, 26, or 29 °C. The ADTs were 13.5, 16.9, 19.6, 22.4, 25.5, and 28.6 °C. Cool-white florescent lights were placed so that irradiance averaged 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. At 31 weeks, observations for *Miltoniopsis* were terminated for plants held at 23, 26, and 29 °C because of lack of response or plant mortality. Observations of *Paphiopedilum* held at 29 °C were also terminated at 31 weeks after the start of treatments because of response or plant fatality.

Experimental design: flower induction following bulking. Plants were held at 23 °C under natural days for nine weeks after arrival. On 1 July 2001, 200 plants were covered with black cloth from 1700 to 0800 HR, incandescent lamps at 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were switched on from 1700 to 2400 HR to create a 16-h LD. Plants were divided into two groups on 1 Sept. 2001; the first group was maintained with a 16-h; the second, a 9-h SD. Both groups were maintained at 23 °C. Eight weeks later on 26 Oct. 2001, each of the two groups was divided again and placed under LDs or SDs into one of five greenhouse compartments with constant temperature set points of 11, 14, 17, 20, or 23 °C, so that each of the 20 treatments had 10 plants. All plants were returned to 23 °C natural days on 21 Dec. 2001.

Data collection and analysis. For all plants in the temperature experiment without bulking, days to visible spiking, spiking to flowering, and days to flower were recorded. Also flower longevity, final flower size, number of flowers, and spike height were noted at the end of the experiment.

For all plants, the length of the flowering spike was measured from the base of the pseudobulb to the tip of the spike once plants began to spike once a week. Date of flowering was recorded when the first flower opened. Flower diameter was measured at the maximum diameter of the true petals.

For *Miltoniopsis* experiments conducted in the greenhouse, days to visible spike, number of visible spikes from 21 Dec. 2001, and number of new shoots and mature bulbs that had formed from 26 Oct. 2001 to 27 June 2002 were recorded. *Paphiopedilum* data included days to visible spiking, days from spiking to flowering, and days to flower. Also flower longevity, number of flowers, and flower size were noted at the end of the experiment.

Results

Flower induction experiments with *M.* Augers *'Trinity'* and *P. laser* x *charlesworthii* did not provide any conclusive results (Tables 1-4).

Miltoniopsis in the flower induction experiments with nine weeks of bulking provided no significant differences in the number of new mature bulbs or reproductive spikes formed (Table 1). At the conclusion of the experiment, plants at the 11 and 14 °C inductive temperature treatments did not spike, but if the experiment had been allowed to continue, these plants probably would have spiked according to results from our experiments without nine weeks of bulking. Plants in the warmer inductive treatments (20 and 17 °C) had spiked, but buds aborted soon after they were visible. Although the reason for bud abortion is unknown it possibly was high light or temperature or a combination of the two. Of plants that did spike, time to visible spiking from the end of inductive temperature and photoperiod treatments was approximately a week shorter for plants in the SD bulking treatments (Table 1).

Miltoniopsis in the flower induction experiment without bulking responded to temperatures and photoperiod (Table 2). Plants at a constant ADT from 23 to 29 °C never spiked under either photoperiod. Plants grown at an ADT of 20 °C spiked and flowered under SD; however, no plants in the 20 °C LD treatment spiked. All plants at 14 and 17 °C spiked, but only treatment at 17°C resulted in

100% spiking and flowering. Time from the start of treatments to visible spike was inconsistent across photoperiods.

Paphiopedilum laser x *charlesworthii* showed no photoperiodic responses and flowered randomly at all temperatures in both experiments (Tables 3–4).

Literature Cited

Berliocchi, L. 1996. The orchid in legend and lore. Timber Press, Portland, Ore.

Baker, M.L. and C. Baker. 1993a. *Miltoniopsis*. Amer. Orchid Soc. Bul. 62: 794–799.

Baker, M.L. and C. Baker. 1993b. Miltoniopsis II. Amer. Orchid Soc. Bul. 62: 901–908.

Cribb, P. 1987. The genus *Paphiopedilum*. Timber Press, Portland, Ore.

Dole J.M. and H. F. Wilkins. 1999. Ochidaceae: floriculture principles and species. Prentice Hall, Englewood Cliffs, N.J.

Goh, C.J. and J. Arditti. 1985. Orchidaceae: handbook of flowering. CRC Press. Boca Raton, Fla.

Hennessy, E.F. and T.A. Hedge. 1989. The slipper orchids. Acorn Books, Randsburg, Kansas City, Mo.

Nash, N. 1989. *Miltoniopsis* in the late 1980s. Amer. Orchid Soc. Bul. 58: 1040–1094.

Ortho. 1999. All about orchids. Merideth Publishing Group, Des Moines, Iowa.

Rentoul, J.N. 1982. Growing orchids. Timber Press, Portland, Ore.

Rotor, G.B., Jr. 1952. Daylength and temperature in relation to growth and flowering of orchids. Cornell Univ. Agr. Expt. Sta. Bul. 885:1–46.

Stewart, J. and M. Griffiths. 1995. Manual of orchids. Timber Press, Portland,

Ore.

Tran Than Van, M. 1974. Methods of acceleration of growth and flowering in a few species of orchids. Amer. Orchid Soc. Bul. 43:699–707.

Vakblad voor de Bloemisterij, 2002. June 7 (23a): 88–89.

Table 1. The effects of temperature and photoperiod on *Miltoniopsis* 'Augres' Trinity with 9 weeks' bulking in a greenhouse.

Bulking Photoperiod[z]	Inductive Temperature (°C)	Inductive Photoperiod	Days to Visible Spike	No. of New Mature Pseudobulbs	No. of New Vegetative Shoots	No. of New Reproductive Spikes
LD	11	LD	...	1.4	1.4	...[x]
LD		SD	...	0.5	0.5	...
SD		LD	...	3.0	1.6	...
SD		SD	...	1.4	1.9	...
LD	14	LD	...	0.5	2.0	...
LD		SD	109	1.5	1.9	2.3
SD		LD	...	2.3	1.9	...
SD		SD	109	1.6	3.0	2.2
LD	17	LD	91	3.3	3.6	2.9
LD		SD	102	2.3	3.3	2.1
SD		LD	83	1.3	2.1	1.7
SD		SD	85	1.9	2.7	2.3
LD	20	LD	105	1.4	5.5	2.6
LD		SD	100	1.4	4.1	2.5
SD		LD	89	1.4	4.0	2.6
SD		SD	91	2.2	3.8	2.2
Significance						
Temperature			NS	NS	NS	NS
Photoperiod			**	NS	NS	NS
Interaction			*	NS	**	NS

NS, *, **, *** Not significant or significant at $P \leq 0.05$ 0.01 0.001, respectively

[z] LD indicates long days; SD indicates short days

[x] treatments in which plants did not flower

Table 2. The effects of temperature and photoperiod (PD) on *Miltoniopsis* 'Augres' Trinity grown in growth chambers. where VS is visible spiking and FLW is flowering

Temperature (°C)	PD trt[z]	VS[y] %	FLW[x] %	Days to VS	Days from VS to FLW	Days to FLW	Flower Longevity (Days)	No. of Flowers	Final FLW Size (mm)	Spike Height (cm)
14	LD	100	71	176	91	262	46	2.8	80	38
	SD	100	90	215	71	284	54	2.5	78	38
17	LD	100	100	202	66	261	45	3.8	81	31
	SD	100	100	176	70	246	54	3.8	89	34
20	LD	0	0	...[w]	...	...	...	...	...	...
	SD	90	90	211	61	273	32	3.8	56.5	31
23	LD	0	0	...	...	...	...	...	...	...
	SD	0	0	...	...	...	...	...	...	...
26	LD	0	0	...	...	...	...	...	...	...
	SD	0	0	...	...	...	...	...	...	...
29	LD	0	0	...	...	...	...	...	...	...
	SD	0	0	...	...	...	...	...	...	...
Significance										
Temperature				NS	**	NS	NS	NS	***	**
Photoperiod				NS	NS	NS	NS	NS	NS	NS
Interaction				**	*	*	NS	NS	NS	NS

NS, *, **, *** Not significant or significant at $P \leq 0.05$ 0.01 0.001, respectively.
[z] LD indicates long days; SD indicates short days
[y] Visible Bud
[x] Flowering
[w] treatments in which plants did not flower

Table 3. The effects of temperature and photoperiod (PD) on *Paphiopedilum laser* x *charlesworthii* .

Temperature (°C)	PD trt[z]	VS[y] %	FLW[x] %	Days to VS	Days from VS to FLW	Days to FLW	No. of Leaves per Flowering Shoot
11	LDLD	50	20	131	206	102	8.1
	LDSD	60	30	170	247	80	8.3
	SDLD	80	40	147	159	53	8.1
	SDSD	80	60	150	206	57	8.4
14	LDLD	70	60	165	218	72	8.9
	LDSD	90	50	179	240	95	8.6
	SDLD	80	40	194	260	79	8.1
	SDSD	100	70	150	264	131	8.1
17	LDLD	70	70	169	227	69	8.1
	LDSD	90	70	155	227	77	8.5
	SDLD	60	60	161	215	54	7.3
	SDSD	100	90	148	216	68	8.0
20	LDLD	80	80	147	221	74	8.2
	LDSD	90	60	142	199	73	8.1
	SDLD	60	60	114	210	97	8.3
	SDSD	80	60	155	210	80	8.1
23	LDLD	90	70	147	212	62	8.4
	LDSD	70	60	124	275	154	8.9
	SDLD	80	70	137	204	70	8.6
	SDSD	60	60	149	217	68	8.1
Significance							
Temperature				*	NS	NS	NS
PD treatment				NS	NS	NS	NS
Interaction				NS	NS	NS	NS

NS, *, **, *** Not significant or significant at $P \leq 0.05$ 0.01 0.001, respectively.

[z] LD indicates long days; SD indicates short days

[y] Visible Bud

[x] Flowering

[w] treatments in which plants did not flower

Table 4. The effects of temperature and photoperiod (PD) on *Paphiopedilum laser* x *charlesworthii* grown in growth Chambers. where VS

Temperature (°C)	PD trt[z]	VS[y] %	FLW[x] %	Days to VS	Days from VS to FLW	Days to FLW	Flower longevity	Final FlW size	No. Flowers Per pot	Spike height
14	LD	60	40	142	80	205	16	78	1	32
	SD	50	20	137	127	214	45	88	2	24
17	LD	20	10	108	57	117	....	97	1	35
	SD	50	30	125	101	208	43	78	1	34
20	LD	70	70	128	71	173	63	100	1	31
	SD	60	40	133	73	209	55	98	1	33
23	LD	50	40	89	70	135	67	106	1	32
	SD	50	30	109	68	139	68	67	1	35
26	LD	60	50	150	82	226	37	90	1	27
	SD	30	30	136	78	196	58	104	1	34
29	LD	0	0	100	...[w]	...	...	...	...	...
	SD	30	0	49	...	...	..	...	...	...
Significance										
Temperature				NS	NS	***	NS	NS	*	NS
PD treatment				NS	NS	NS	NS	NS	*	NS
Interaction				NS	NS	NS	NS	NS	*	*

NS, *, **, *** Not significant or significant at $P \leq 0.05$ 0.01 0.001, respectively.
[z] LD indicates long days; SD indicates short days
[y] Visible Bud
[x] Flowering
[w] treatments in which plants did not flower