Environmental Physiology of Growth and Flowering of Orchids

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Abstract. Flowering potted orchids has become one of the largest segments of floriculture worldwide. Large-scale production of cuts or potted plants exists in China, Germany, Japan, The Netherlands, Taiwan, Thailand, and the United States. Despite the value of the orchids, the flowering physiology of most orchid genera is not well described. Therefore, scheduling flowering crops for specific market dates (such as Easter or Mother’s Day) is not possible for most genera. This paper summarizes world orchid production and reviews how environmental factors regulate growth and flowering of several commercially important orchid genera: Cattleya, Cymbidium, Dendrobium, Miltoniopsis, Phalaenopsis, and Zygopetalum. These genera primarily flower in response to relatively low temperatures, and, for some species and hybrids, flowering is promoted when the plants are also exposed to short photoperiods. Effects of light and temperature on growth and development are summarized for these genera, and implications for controlled production are discussed.

Orchids are marketed globally as cut flowers for corsages, floral arrangements, and bouquets; as potted flowering plants; and as bedding or aerial plants in tropical regions. In 1995, worldwide demand for orchids grown for cut flower and potted plant production was 1.3 billion units of plant stock (Hew and Yong, 1997). The world consumption of orchids (potted plants) was valued at more than $500 million in 2000 (Wang, 2004). Countries with large-scale potted orchid production include China, Germany, Japan, The Netherlands, Taiwan, Thailand, and the United States (Griesbach, 2000). The Dominican Republic, Costa Rica, and India have recently begun to produce orchids for export (Laws, 2004).

Commercial production of potted orchids has increased dramatically throughout the world in the past quarter century. In Japan, the reported value of potted orchids increased 1125% from 1965 to 1991 (Ichihashi, 1997). The most common genera sold in Japan from 1993 to 2002 were Phalaenopsis (30%), Cattleya (15%), Miltoniopsis (20%), Dendrobium (20%), and Cymbidium (15%), and Cattleya (10%) (Hew and Yong, 1997; Laws 2004). In The Netherlands, Phalaenopsis has become the most valuable potted plant sold; from 1983 to 2003, the number of potted orchids sold through flower auctions increased from 50,000 to 18 million pots (Barendse, 2002; Laws, 2004; Wang, 2004).

The U.S. Department of Agriculture (USDA) National Agricultural Statistical Service considered orchids to be a minor crop and did not collect production information until 1997 (USDA, 1998). From 1996 to 2004, U.S. potted orchid production value increased by 170%, and in 2004, its wholesale value was estimated at $128 million (USDA, 1998, 2005). Orchids are presently the second most valuable flowering potted crop in the United States, of which 70% to 90% are Phalaenopsis (Griesbach, 2002; Nash, 2003). In 2004, growers in California, Florida, and Hawaii produced >85% of all the orchids sold in the United States, with wholesale values reported at $50, $47, and $17 million, respectively (USDA, 2005).

Most orchids are grown for the aesthetic beauty of their flowers. However, published research on the flowering physiology of most orchid genera in controlled environments is limited. Therefore, with the exception of a few genera (e.g., Phalaenopsis and some Cattleya), the ability to coordinate the flowering process with specific dates is not possible. Here, we summarize the published, scientific literature on how environmental parameters (primarily, temperature and light) influence the development of some of the most commonly produced orchid genera. In addition, research results from studies performed at Michigan State University are presented.

This summary includes research on selected orchid species and hybrids performed during the past 50 years. Hybridization of orchids is commonplace, and thousands of named cultivars exist. Therefore, because of the genetic diversity of genera and intergeneric hybrids, some hybrids may respond differently than results presented in this summary.

The Juvenile Phase

Similar to that of many other flowering plants, a juvenile phase exists in orchids in which they must reach a certain stage of growth (or maturity) before attaining the capacity to flower. Thus, sexual reproduction is delayed until plants reach a size sufficient to maintain the energetic demands of flowering and seed production. This period of juvenility varies among species and hybrids. Four to seven years are required for many orchids to flower from seed (Goh and Arditti, 1985), but many commercially important hybrids flower within 36 months of germination (Hew and Yong, 1997). Once plants have attained the capacity to flower, environmental or cultural factors can be provided to induce flowering. If conditions are unfavorable, plants may not initiate flowers, or a potential inflorescence may not develop flowers to anthesis. However, if conditions are favorable, flowering usually occurs. For example, the majority of Phalaenopsis are flowering at the end of the southeastern U.S. growing season (October–November), and the majority of Phalaenopsis flowers are observed during the second half of the growing season (November–February) (Goh and Arditti, 1985).

Cattleya

Cattleya is a genus composed of 48 species originating throughout tropical regions of Central and South America (Pridgeon, 2000). The epiphytic plants are found growing atop trees of moist and wet forests from sea level to 1500 m in elevation. Similar to many other tropical orchid genera, growth is more rapid at higher temperature (e.g., >25°C). For example, vegetative growth of Laeliocattleya Culinman’t La Tuilerie’ was greater when plants were grown in a growth chamber at a day/night temperature of 32/29°C compared with that in a 24/20°C greenhouse (Krizek and Lawson, 1974). After 17 weeks, leaf elongation was 4.5 times greater at the warmer temperatures, and after 24 weeks, plants developed two or three lateral shoots compared with just one at the lower temperatures. According to Rotor (1952), 9-h short days stimulated vegetative growth because plants produced two successive shoots during this daylength, but not under long days or natural photoperiods. The maximum recommended light intensity for Cattleya orchids is between 300 and 600 µmol·m–2·s–1 (Dole and Wilkins, 1999).

Cattleya species and hybrids flower at different times throughout the year. Some Cattleya initiate flower buds in response to low temperature and short photoperiods during the spring, but buds do not enlarge and reach anthesis until autumn or winter (Table 1). Thus, environmental conditions for flower bud initiation and flowering can be different (Rotor, 1952). In C. warscewiczi Rchb.f., C. gaskelliana Rchb.f., and C. mossiae Hkr, flower induction occurred under continuous 9-h days at 13°C, whereas few plants flowered under 16-h days at 13°C (Rotor, 1952, 1959). Cattleya warscewiczi apparently requires short days and low temperature as the pseudobulb develops for the most rapid flowering (Rotor, 1952). Flowering was reduced and delayed (by 2 to 3 months) when plants were grown under short days at 18°C compared with plants under short days at 13°C.

In C. labiata Lindley and C. schilleriana Rchb.f., 16-h long days at 18°C prevented flowering (Rotor, 1952, 1959). Cattleyalabiata and C. schilleriana flowered under short days, regardless of the growing temperature, and flowered under long days if the temperature was maintained below 16°C. In a separate study, Cattleya bowringiana Veitch grown under an 8-h photoperiod flowered in 273 d, whereas...
plants grown under a 16-h photoperiod did not flower during the duration of the experiment (Goh and Arditti, 1985).

Goh and Arditti (1985) present a schedule for flowering C. gaskelliana for the Christmas holiday in the northeastern United States. They suggest growing plants under warm conditions (≥16 °C) during the previous November, December, and January, when new pseudobulbs normally begin to develop. Plants should receive short days from February through September, and in the autumn, the night temperature should be reduced to 13 °C. Flowering is expected to occur about 3 to 4 months after flower initiation.

Cymbidium

Cymbidium is a genus of approximately 44 species native from the Himalayas to tropical regions of southeast Asia to Australia (Pridgeon, 2000). The terrestrial, epiphytic, lithophytic, and semiepiphytic species require long days and high night temperatures of 30/25 °C for rapid growth and pseudobulb maturity (Ichihashi, 1997; Pridgeon, 2000) (Table 1). During the warm summer in Japan, several orchid genera (including Cymbidium) are commonly transported from production areas in the lowlands to higher elevations. This strategy helps prevent high-temperature stress during vegetative growth and exposes plants to cooler temperatures and higher light for flower initiation (Ichihashi, 1997).

Due to the large geographic distribution of Cymbidium, they are often divided into three horticultural groups based on their temperature tolerance: cool, intermediate, and warm. Most large-flowered Cymbidium species from the Himalayas and China are induced to flower by a pronounced cool period in which night temperature is kept at about 10 to 14 °C (Pridgeon, 2000; Rotor, 1952, Went, 1957). Went (1957) found that Cymbidium giganteum var. longianum Rchb. f. did not flower when grown for 1 to 3 months at 26/14 °C or 23/14 °C; some inflorescences developed at 26/7 °C or 26/10 °C, and the greatest floral production occurred at 20/10 °C and 20/14 °C. Thus, the day and night temperature likely have an effect on flower induction, not the night temperature alone. Cymbidium grows in California provide relatively high light intensities (up to full sun in winter) and night temperatures of 10 to 13 °C for flower bud initiation (Goh and Arditti, 1985). In Japan, the temperature commonly used for flower induction is between 10 and 16 °C, and the cumulative temperature required for flower bud differentiation is 34,000 °C-hours calculated by multiplying the hours of exposure to 10 to 16 °C by the temperature, e.g., 118 d at 12 °C (Ichihashi, 1997).

Many temperate Cymbidium hybrids derived from the “Asiatic Cymbidium Belt” are reported to flower in response to warm days and cool nights, with a diurnal temperature fluctuation of 10 to 14 °C. Powell et al. (1988) reported that Cymbidium Astrum exposed to day/night temperatures of 26/12 °C and a 14-h photoperiod produced an average of 5.9 inflorescences per plant. At 20/12 °C or 26/18 °C, only 0.8 and 1.7 inflorescences per plant developed, respectively. Temperature ≥25 °C can cause flower bud blasting (abortion) in the early stages of development in many intermediate- and miniature-sized Cymbidium orchids such as Cymbidium pumilum and Cymbidium Sazanami ‘Haru-no-umi’ (Ichihashi, 1997; Ohno, 1991).

Cymbidium orchids originating from warm regions such as Taiwan and Southern China normally flower in the summer (Lee and Lee, 1993). Pseudobulb development and flower formation in Cymbidium ensifolium var. misericors were accelerated at warm day/night temperatures of 30/25 and 25/20 °C, and were deterred at 20/15 °C. At 30/25, 25/20 and 20/15 °C, plants with 2 to 3 year mature pseudobulbs produced 2.3, 1.6, and 1.1 inflorescences, respectively (Lee and Lee, 1993). To our knowledge, no studies have reported photoperiod to have an effect on flower induction (Goh and Arditti, 1985; Goh et al., 1992; Went, 1957).

In vitro flowering of Cymbidium niv-o-marginatum Lindl. has been achieved with a combined treatment of cytokinin (6-benzylamino purine), restricted nitrogen, enriched phosphorus, and root excision (pruning) (Kostenyuk, et al., 1999). In vivo, C. niv-o-marginatum requires 4 to 7 years before it can flower. However, this flower-stimulating technique has limited or no commercial application.

Dendrobium

Dendrobium (the spray orchid) is the second largest genera of the orchid family, with >1,200 epiphytic species that are native to tropical and subtropical Asia, Australia, and various Pacific Islands (Eigeldinger and Murphy, 1972; Baker and Baker, 1996). For most Dendrobium orchids, rapid vegetative growth occurs at temperatures between 24 and 30 °C (Leonhardt, 2000) (Table 1). Dendrobium phalaenopsis Fitz var. statterianum Hort. ex Sander grown at 13 or 18 °C produced one pseudobulb per year; however, those at 13 °C were short and spindly (Rotor, 1952). The development of vegetative shoots was also delayed by 2 months at 13 °C (Rotor, 1952).

Temperatures below 10 °C may cause leaf drop or abscission in some species (American Orchid Society, 2002). Most Dendrobium species and hybrids can tolerate higher light intensities than other orchid genera reviewed in this article (Dole and Wilkins, 1999).

The recommended temperature for flower induction differs among Dendrobium hybrids and species. Dendrobium noble Lindley plants exposed to 13 °C produced flowers regardless of the photoperiod, whereas plants held at 18 °C remained vegetative (Goh and Arditti, 1985; Rotor, 1952). Buds on immature Dendrobium noble pseudobulbs remain dormant and do not respond to low temperature for flowering. Flower induction in D. Snowflake ‘Red Star’ was achieved by providing 25/10 °C (day/night) for 40 to 60 d. Lower day temperature can cause floral induction (Goh and Arditti, 1985), whereas plants held at and reduced growth rates; higher temperature can delay flower bud development (Ichihashi, 1997). In D. phalaenopsis, short days at 18 °C hastened flower bud development and flowering by about 6 weeks compared with that of plants under long or natural daylengths at 18 °C (Rotor, 1952). At 13 °C, this same tendency was observed, but flower bud development was slow because of the low temperature (Rotor, 1952).

Goh and Arditti (1985) postulated that photoperiod and low temperature modify

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Table 1. Summary of the temperature and light environments that promote vegetative growth (inhibit flowering) or stimulate flowering for several orchid genera and their horticultural groups. Some species and hybrids within a genus may have different flower induction responses.

| Genus       | Temp (°C) | Max light intensity (µmol·m−2·s−1) | Flower initiaiton |
|-------------|----------|-----------------------------------|------------------|
| Cattleya    | 24–29 night | 300–600 | 12–16 | 18 | Short days |
| Cymbidium   | 25–30 | No response | 360–600 | 20−26 day/10–14 night (cool) | Short days |
| Dendrobium  | 24–30 | No response | 480–720 | 10–13 | 18 | Short days |
| D. phalaenopsis | 20–23 | 150–300 | 11–14 | Short days |
| Miltoniopsis| 27–30 | No response | 240–400 | 15–25 | No response |
| Phalaenopsis| 22–26 | Long days | 300–500 | 11–14 | Short days |

* Cymbidium is often divided into three horticultural groups based on their temperature tolerance: cool, intermediate, and warm.
concentrations of endogenous growth regulators. Low temperature and short days could change the concentrations of endogenous growth regulators leading to induction of flowering in sympodial orchids. Sakai et al. (2000) reported that the injection of 100 mM 6-benzyladenine (BA) into first-year leaved stems of *Dendrobium* Jaquelyn Thomas ‘Uniwai Princess’ significantly increased the number of inflorescences (8.9) compared with that of untreated plants (0.5). Injecting 10 or 100 mM BA into the center of the stem below the top 2 top-most vegetative buds of leafless, 2-year-old pseudobulbs increased floral spray production (4.0 and 6.3 in untreated plants, 0.5). Injecting 10 or 100 mM BA into the center of the stem below the top 2 top-most vegetative buds of leafless, 2-year-old pseudobulbs increased floral spray production (4.0 and 6.3 in untreated plants, 0.5). Injecting 10 or 100 mM BA into the center of the stem below the top 2 top-most vegetative buds of leafless, 2-year-old pseudobulbs increased floral spray production (4.0 and 6.3 in untreated plants, 0.5). Injecting 10 or 100 mM BA into the center of the stem below the top 2 top-most vegetative buds of leafless, 2-year-old pseudobulbs increased floral spray production (4.0 and 6.3 in untreated plants, 0.5). Injecting 10 or 100 mM BA into the center of the stem below the top 2 top-most vegetative buds of leafless, 2-year-old pseudobulbs increased floral spray production (4.0 and 6.3 in untreated plants, 0.5).

**Miltoniopsis**

*Miltoniopsis* is an epiphytic or lithophytic genus of six species distributed from the wet cloud forest regions (610 to 2100 m) of Costa Rica to Peru (Baker and Baker, 1993; Pridgeon, 2000). Their distribution extends from southern India to Australia, including China, Taiwan, and the Philippines.

*Miltoniopsis* orchids remain vegetative above about 27 to 29 °C (Sakanishi et al., 1980) and can tolerate temperatures as high as 32 to 35 °C for short periods before exhibiting signs of heat stress (Baker and Baker, 1991). The calculated base temperature for *Phalaenopsis* is 10.8 to 11.2 °C for all developmental stages (Robinson, 2002). *Phalaenopsis* exposed to temperatures of 2, 4, or 7 °C for 1, 2, 4 and 8 hours developed chilling injury symptoms, including sunken, yellow, water-soaked spots on upper leaf surfaces (McConnell and Scheehan, 1978).

**Phalaenopsis**

*Phalaenopsis* contains >50 species originating from tropical and subtropical areas of the South Pacific Islands and Asia (Pridgeon, 2000). Their distribution extends from southern India to Australia, including China, Taiwan, and the Philippines.

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*Phalaenopsis* requires a period of exposure to relatively moderate temperature (≤26 °C) to trigger the initiation of the inflorescence, or spiking (Lee and Lin, 1984, 1987; Sakanishi et al., 1980; Wang, 1995b; Yoneda et al., 1992). The inflorescence usually emerges from the third and often the forth node below the apical leaf (Sakanishi et al., 1980). Flower bud initiation occurs after the spike has reached about 5 cm in length if environmental conditions are favorable. Lee and Lin (1984) showed that uniform spiking can be achieved when plants are grown at day/night temperatures of 25/20 °C or 20/15 °C for 4 to 5 weeks. Recent research indicates that constant temperatures of 20, 23, or 25 °C can initiate flowering in a variety of...
Phalaenopsis (Blanchard and Runkle, 2004; Y.-T. Wang, unpublished data).

Once the flowering spike has initiated, time to the first open flower is a function of the average daily temperature. However, if a plant with an inflorescence <10 cm is subsequently grown at 28 °C or higher for extended periods, a spike can form a vegetative air plantlet referred to as a “kink” instead of flower buds, buds may abort, or the stem may elongate indefinitely without open flowers (Sakanishi et al., 1980; Wang, 1995b). Temperature has little or no effect on spike height or flower size (Robinson, 2002; Sakanishi et al., 1980).

In 2002, Robinson conducted experiments to quantify the effects of temperature (from 14 to 29 °C) on time from spike emergence to flowering and on plant quality. The rate of flower development for all three hybrids of Phalaenopsis studied increased linearly as temperature increased from 14 to 26 °C. For example, as temperature increased from 20 to 23 °C, days from visible flower bud to first flower appeared decreased from 50 to 35 days.

A few studies reported that short days enhance spiking and spike length, and long days promote vegetative growth and the development of aerial plantlets (De Vries, 1953; Griesbach, 1985; Rotor, 1952; Yoneda et al., 1991). For example, Yoneda et al. (1991) found that flowering percentages were 50% and 70% when 6-year-old seedlings were grown under natural days and 8-h SD, respectively, at 22 or 23 °C. However, time to spike emergence was not significantly different. The short-day promotion of flowering could be a result of the extension of cool night temperatures and not daylength itself (Sakanishi et al., 1980). Robinson (2002) reported that time to visible inflorescence was reduced from 300 to 10 days when plants were exposed to long days (14 h LD, 10 h SD) and then cooled at 11 to 14 °C for about 8 weeks (Lopez et al., 2003). A population of Zygopetalum plants exposed to long days before cooling had a lower flowering percentage (<50%), compared to 80% for plants exposed to short days. When plants were cooled at 17 or 20 °C, the flowering percentage was also reduced (<50%). Therefore, a short photoperiod followed by cool temperature (11 to 14 °C) stimulates the flowering process. After the cooling period, time to visible inflorescence was relative rapidly at 23 °C (about 3 weeks). Average time from visible inflorescence at 14, 17, 20, 23, and 26 °C was 64, 49, 40, 34, 30, respectively (Lopez and Runkle, 2004).

The inflorescence of Zygopetalum generally arises out of young, developing pseudobulbs. In our research, we have observed that for a cooling period to induce flowering, it must be delivered when new pseudobulbs are immature (<8 cm in length) at the onset of the cooling period. If shoots are more mature (e.g., 12 cm or longer) at the beginning of cooling, then flower initiation does not usually occur. Thus, Zygopetalum initiates flowers on emerging pseudobulbs, whereas Miltoniopsis initiates flowers on relatively mature pseudobulbs.

**Summary**

Flowering of many of the most commonly grown orchid genera is influenced by temperature and light. In particular, a relatively low temperature induces flowering, while a high temperature inhibits it. For many of these genera, an inductive temperature is about 12 °C, but it is much higher (≤25 °C) for Phalaenopsis (Table 1). For some species and hybrids of Cattleya, Dendrobium, Miltoniopsis, and Zygopetalum, the combination of short photoperiod and low temperature induces flowering in the most complete, rapid, and uniform manner. With this information, it may be possible for greenhouse growers to induce a variety of orchid genera into flowering using a common cool environment (about 12 °C). However, for many orchids, the delivery of a cool temperature treatment must coincide with a developmental stage in which plants are sensitive to an inductive low temperature treatment. Once flower buds have initiated, flower development time is dependent upon genotype and temperature.

Zygopetalum, or the ladybird orchid, is a sympodial, terrestrial, and epiphytic South American genus composed of about 20 species. They are native to neotropical mid-elevation mountains (1300 to 1700 m) of Brazil, Guiana, Venezuela, and Peru (Rose, 1993). Vegetative growth is rapid at 26 °C, but at temperatures of 23 °C is suggested to balance growth rate with desirable growth characteristics (e.g., long leaves) (Lopez, 2003) (Table 1). Black necrotic lesions can form when light intensity exceeds about 500 µmol·m⁻²·s⁻¹ (R. Lopez and E. Runkle, unpublished data).

The most rapid, complete, and uniform flowering of Zygopetalum Redvale ‘Fire Kiss’ occurred when plants were grown under short days and then cooled at 11 to 14 °C for about 8 weeks (Lopez et al., 2003). A population of Zygopetalum plants exposed to long days before cooling had a lower flowering percentage (<50%), compared to 80% for plants exposed to short days. When plants were cooled at 17 or 20 °C, the flowering percentage was also reduced (<50%). Therefore, a short photoperiod followed by cool temperature (11 to 14 °C) stimulates the flowering process. After the cooling period, time to visible inflorescence was relative rapidly at 23 °C (about 3 weeks). Average time from visible inflorescence at 14, 17, 20, 23, and 26 °C was 64, 49, 40, 34, 30, respectively (Lopez and Runkle, 2004).

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Potted flowering orchids is a promising crop category that offers greenhouse growers a profitable alternative to other floriculture crops currently grown in the United States. With the increasing popularity and production of orchids throughout the world, further research is needed to determine the cultural and flower inductive requirements of other orchid hybrids. Addition, more information is needed on orchid genera currently grown because the specific inductive requirements can vary from one hybrid to another. This information will enable growers to produce more diverse flowering orchid plants for specific market dates and give consumers alternatives to traditional crops such as poinsettias for Christmas or Easter lilies for Easter.

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