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EFFECTS OF TEMPERATURE ON GROWTH AND FLOWERING OF TWO PHALAENOPSIS AND TWO ODONTIODA ORCHID HYBRIDS

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EFFECTS OF TEMPERATURE ON GROWTH AND FLOWERING OF TWO PHALAENOPSIS AND TWO ODONTIODA ORCHID HYBRIDS

By

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ABSTRACT

EFFECTS OF TEMPERATURE ON GROWTH AND FLOWERING
OF TWO PHALAENOPSIS AND TWO ODONTIODA ORCHID HYBRIDS

By

Matthew George Blanchard

The production value of potted orchids in the United States has increased tremendously in the past decade, and they are now the second-most valuable potted flowering plant. Commercial orchid production has been impeded by the lack of information on flowering requirements of the vast majority of orchid species and hybrids. The objectives of this study were to determine if and how constant and fluctuating day and night temperatures influence flowering of four orchid hybrids. *Phalaenopsis* Miva Smartissimo × Canberra '450', *Phalaenopsis* Brother Goldsmith '720', *Odontioda* George McMahon 'Fortuna', and *Odontioda* Lovely Penguin 'Emperor' were grown at constant temperatures of 14, 17, 20, 23, 26, or 29 °C, and day/night (12 h/12 h) temperatures of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. After 20 weeks, ≥80% of plants of both *Phalaenopsis* hybrids had a visible inflorescence when grown at 14, 17, 20, 23, 20/14, or 23/17 °C. None of the plants were reproductive when grown at temperatures of 29, 29/17, or 29/23 °C. In both *Odontioda* hybrids, ≥90% of plants initiated an inflorescence that did not abort when grown at 14 or 17 °C. Time to flowering data for *Odontioda* were used to develop a thermal-time model relating temperature with inflorescence development. These results indicate that a day/night fluctuation in temperature is not required for inflorescence initiation in these four orchid hybrids. This research information could be used by commercial orchid growers to improve production efficiency and schedule orchids in flower for specific market dates.

DEDICATION

In loving memory of my stepfather, David L. Goff (August 26th, 2004, aged 50) who left this world too early. David loved the outdoors and the beautiful environment around us and he had a special appreciation for plants and my field of study. His smile, humor, and knowledge are sadly missed. Sweet are the memories that never fade.

ACKNOWLEDGMENTS

I would like to first acknowledge my major professor, Dr. Erik Runkle for his encouragement, guidance, and support throughout this project. His advice and insight have been greatly appreciated during the past two years. I look forward in working with him on future projects. I would also like to acknowledge the members of my graduate committee, Drs. Arthur Cameron and Donald Garling for the valuable knowledge, advice, and support they have provided during this project.

Thank you to our floriculture greenhouse technician, Mike Olrich, for his assistance in experimental setup, expertise, and humor. I would also like to thank the rest of the floriculture group and our undergraduate students for their patience and help in opening and closing black-out cloth each day during these experiments. Thank you to my fellow graduate student, Roberto Lopez for his support during my transition into graduate school, assistance in experimental setup, and friendship. To all of my friends and colleagues for making the Department of Horticulture at MSU an enjoyable place to work.

Thank you to my family for all their love, support, and encouragement. Everything you have taught me is reflected in the person that I am today. I would especially like to thank my wonderful wife Laura, for her love, friendship, patience, and support as I work hard to pursue my educational and career goals. You make each day special. I look forward to many more memories as we continue the journey through life together.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

SECTION I

SECTION II

SECTION III

APPENDIX A

APPENDIX B

LIST OF FIGURES

Figure Page

SECTION I

SECTION II

SECTION III

APPENDIX A

APPENDIX B

SECTION I

LITERATURE REVIEW

INTRODUCTION

Orchids are currently the second most valuable potted crop in the United States with a total reported wholesale value of $127.6 million in 2004 (USDA, 2005a) (Fig. 1). Since 1996, when the United States Department of Agriculture (USDA) began collecting data for wholesale value of potted orchids, sales have increased by 172% (USDA, 2005b) (Fig. 2). In 2004, 17.2 million potted orchids were sold at wholesale with an average unit value of $7.41 (USDA, 2005b). In the United States, the largest state producers of potted orchids are California ($50 million), Florida ($47 million), and Hawaii ($17 million) (USDA 2005a). From 1996 to 2004, the number of commercial growers of potted orchids has increased from 175 to 226 and average annual sales per grower increased from $269,000 to $565,000 (USDA, 2005b).

The production of potted orchids for the mass market extends beyond the United States and has global economic importance. The increased worldwide production of orchids is attributed to a rise in consumer demand in Europe, Asia, and the United States; advances in propagation techniques; recognition of large profit potential by growers; improvements in breeding and selection; and a segmentation of the production chain (Britt, 2000). In 2002, the total number of potted orchids produced in China and Japan were 4 million and 28 million, respectively (Wang, 2004). The largest exporting countries of potted orchids by volume include Taiwan, Thailand, the United Kingdom, Italy, Japan, New Zealand and Brazil, while the largest importer of potted orchids is the United States (Laws, 2002). In 2004, 1.4 million kilograms of live orchid plants were imported into the U.S., with a value of $24.7 million (USDA, 2005b). The largest exporting countries of live orchid plants to the United States include Taiwan ($12.2

million), The Netherlands ($3.8 million), and Thailand ($2.8 million). The commercial production of potted orchids in Europe is generally for domestic consumption (Laws, 2002).

The ability for commercial greenhouse growers to produce potted flowering plants for specific dates is economically important. The scheduling of potted flowering plants for periods of high demand allows growers to coordinate marketing and shipping dates, develop and implement a yearly greenhouse production plan, and potentially increase profitability. To schedule a crop for specific market dates, an understanding of the factors that affect plant growth and development is required. Intensive research has been conducted on several economically important floriculture crops such as chrysanthemum, Easter lily, and poinsettia and production schedules have been subsequently developed (Berghage and Heins, 1991; Erwin and Heins, 1990; Fisher et al., 1997; Jacobson and Willits, 1998; Karlsson et al., 1989).

Scientific research on growth and development of orchids has been limited to a few genera and detailed commercial production information is only available for hybrids of the genus *Phalaenopsis*. The primary objective of this research was to quantify the effects of constant and fluctuating temperature on inflorescence initiation and flower development in several orchid hybrids. This information could be used to develop production protocols that can be implemented by commercial greenhouse growers, and improve our understanding of how environmental factors influence the flowering physiology of orchids.

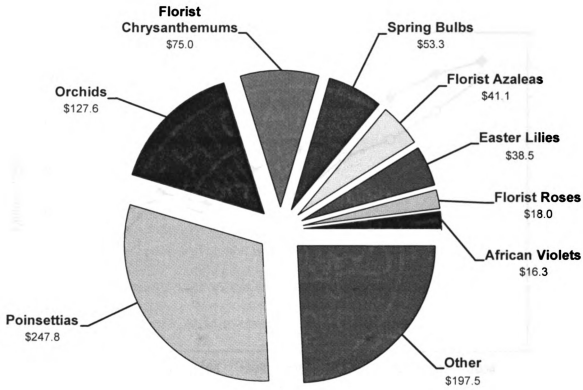

Figure 1. Wholesale value (million USD) of potted flowering plants produced in the United States in 2004 (USDA, 2005a).

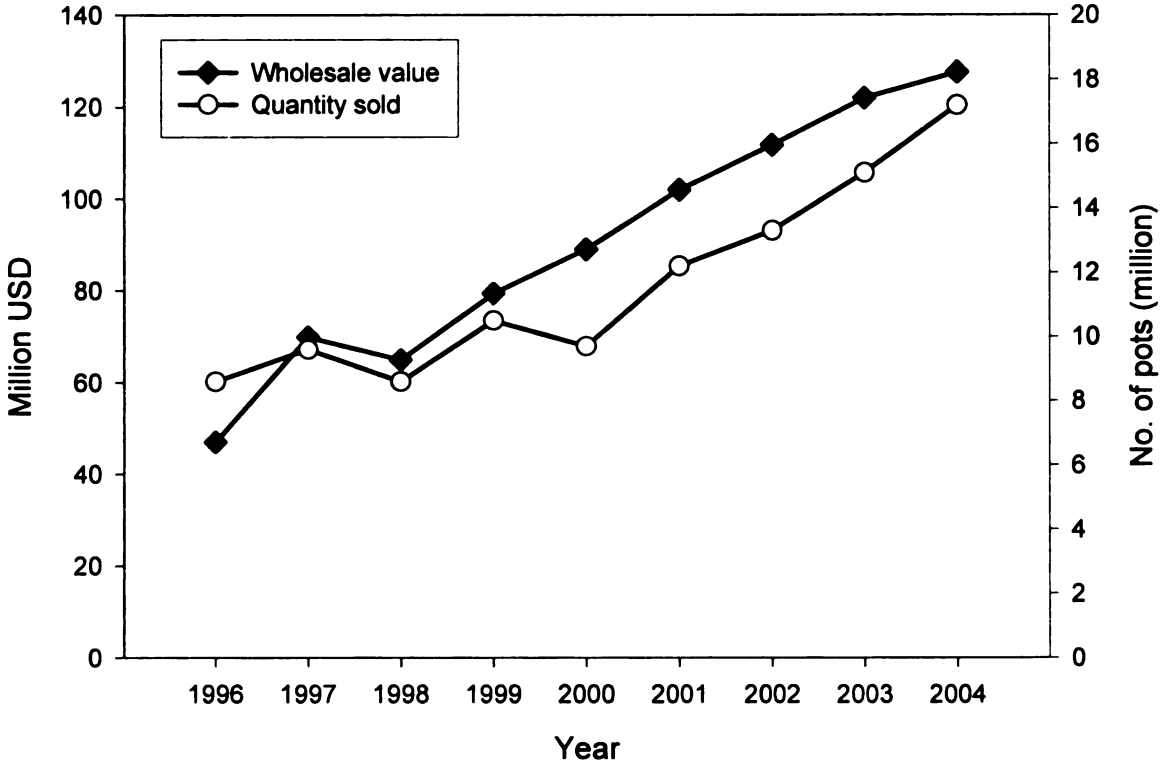

Figure 2. Wholesale value [million USD (♦)] and quantity sold [million (○)] of potted orchids produced in the United States from 1996 to 2004 (USDA, 2005b).

ORCHID BACKGROUND

The orchid family, Orchidaceae, is among the largest of families of angiosperms, containing over 25,000 species within 725 genera (Griesbach, 1985b). Orchids were first classified into two major divisions by Linnaeus in 1740, but between 1830 and 1840, a complete classification was published by botanist John Lindely, known as the father of modern orchidology (Reinikka, 1995). Orchids are distributed in all regions of the world except Antarctica and are found growing in many different habitats and elevation gradients (Pridgeon, 2000). Among all of the orchid genera, the genus *Vanilla* has a major economic value as a food crop. Many of the other orchid genera that are commercially available are selected and grown for aesthetic value or botanical interest (Griesbach, 1985b).

History

The word orchid is derived from the Greek word *orchis*, meaning testis, referring to the testiculate bulbs or tubers that were found on orchid plants from the Mediterranean region (Reinikka, 1995). The first recordings of orchids date back to 500 B.C., when *Cymbidium* orchids were highly desired for their fragrance and Confucius used the word "lan" in reference to all orchids (Rittershausen and Rittershausen, 2003). The earliest Chinese writings on orchids were published in 290 A.D., where they were depicted both in botanical literature and paintings. In the Western hemisphere, orchids were first recognized in 1552 by the Aztecs for the use of *Vanilla* as a perfume and flavoring in foods (Reinikka, 1995).

During the end of the eighteenth century in Europe, greenhouses and conservatories were constructed to grow many of the new plant species that were collected from expeditions around the world (Rittershausen and Rittershausen, 2003). At this time, large orchid collections and nurseries were established, but commerce was limited to the wealthy (Reinikka, 1995). At the beginning of the twentieth century, the popularity of orchids declined as a result of collecting and transportation challenges, inadequate knowledge of propagation and cultivation methods, and expensive greenhouse maintenance (Pridgeon, 2000). Orchid hybridization and commercial propagation became popular after advances in symbiotic seed germination by Noel Bernard and Hans Burgef in 1909, and the development of non-symbiotic germination procedures by Lewis Knudson in 1922 (Griesback, 2002). The procedure to symbiotically germinate orchid seeds involved inoculating a sterilized peat and sand medium with a symbiotic fungus and then sowing seeds on the surface. Non-symbiotic orchid seed germination involved sowing seeds on agar that contained salts and sugars (Griesback, 2002).

After the Second World War, commercial nurseries were established in Europe and the United States, hybridizing and producing orchids for international markets (Rittershausen and Rittershausen, 2003). More than 110,000 hybrids have been registered with the Royal Horticultural Society since the first hybrid was created in 1854 (Royal Horticultural Society, 2004). Approximately 3,000 hybrids are registered each year, most of which are propagated in a laboratory through a process called mericloning (Pridgeon, 2000; Royal Horticultural Society, 2004).

Plant Description

Growth Habit

Orchids have been categorized into two groups according to their habit of growth: monopodial orchids or sympodial orchids. A monopodial growth habit is characterized by having a terminal bud that continues to grow each season, while growth in a sympodial plant occurs through the development of axillary buds. Orchids can also be described based on their growing habitat and substrate: terrestrial, epiphytic, or lithophytic. Terrestrial orchids such as *Cypripedium*, *Dactylorhiza*, and *Orchis*, grow on the surface of the earth and obtain water and minerals from the soil. The majority of tropical orchids are epiphytic and grow naturally on trees, obtaining moisture and minerals from both the air and decomposing organic matter on branches. Lithophytic orchids such as *Phragmipedium besseae* Dodson and Kuhn are found growing in small rocky crevices of harsh environments and acquire water and minerals similar to epiphytic orchids (Rittershausen and Rittershausen, 2003).

Roots

Terrestrial orchids have fleshy and often hairy roots for water absorption and may utilize underground structures, such as corms, rhizomes, or tuberoids for water storage (Elliot, 1998; Rittershausen and Rittershausen, 2003). Sympodial epiphytic orchids store water in structures called pseudobulbs. Pseudobulbs are composed of a fibrous material and species have different shapes and sizes, ranging from as small as a pea to the size of a tennis ball (Rittershausen and Rittershausen, 2003). The aerial roots of epiphytic orchids and some terrestrial orchids are enclosed in a white layer of dead cells called velamen,

which provides mechanical protection and prevents water loss from the root cortex (Dycus and Knudsen, 1957). Lithophytic orchids have smaller, more developed roots with greater surface area to absorb moisture. The roots of lithophytic orchids are also strong enough to attach to rocky cliff faces or crevices (Rittershausen and Rittershausen, 2003).

Leaves

Orchids have simple leaves with varying shapes, such as long and strap-like (e.g. *Cymbidium),* thick and fleshy (e.g. *Phalaenopsis*) or long, rounded, and terete (e.g. *Vanda*) (Elliot, 1998). Epiphytic orchids usually have leaves that are persistent from year to year, while the leaves of non-tropical terrestrial and lithophytic orchids are generally shed seasonally (Pridgeon, 2000).

Flowers

The flowers of orchids are bilaterally symmetrical, termed zygomorphic, and the flower structure is similar to other angiosperms, comprised of four whorls: sepals, petals, stamens, and pistils (Zomlefer, 1994). Orchid flowers can be divided into two forms: Diandrae and Monandrae. Genera such as *Cypripedium*, *Paphiopedilum*, and *Phragmipedium* are grouped into Diandrae and have flowers that consist of two fertile stamens on each side of the staminode, one large colorful dorsal sepal, two small lateral sepals, two elongated lateral petals and an attractive pouch formed by a third petal (Goh and Arditti, 1985) (Fig. 3A). The pouch functions as a trap for insect pollinators, requiring insects to climb out and unintentionally transfer pollen from the anthers to their

abdomen (Rittershausen and Rittershausen, 2003). A majority of genera within the orchid family are grouped into Monandrae, with flowers consisting of stigmas and stamens fused together into a column, one dorsal sepal, two lateral sepals, and three petals (Goh and Arditti, 1985) (Fig. 3B). The third lowermost petal, termed the labelum or lip, is modified into a large and colorful landing platform designed for attracting pollinating insects (Pridgeon, 2000). Orchid flowers may be either solitary on stalks, termed scapes, or arranged in an inflorescence (Pridgeon, 2000) and can range in size from 1 m across (*Phragmipedium grande* Veitch) to as small as the head of a pin (*Stelis* spp.) (Rittershausen and Rittershausen, 2003).

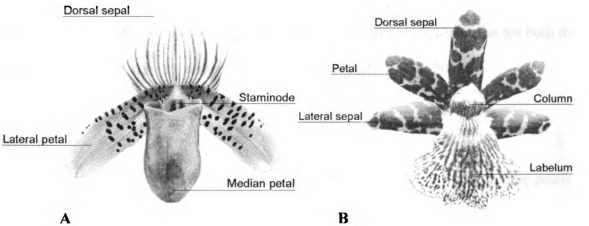

Figure 3. Flower structures of a diandrous orchid, *Paphiopedilum*, with a median petal modified to form a pouch (A), and a monandrous orchid, *Zygopetalum*, with a large and colorful labelum (B).

PHALAENOPSIS

The genus *Phalaenopsis* Blume derives its name from the Greek words *phalaina*, meaning moth, and *opsis*, meaning looking like (Mayr, 1998). The common name moth orchid describes the resemblance of the flowers to night active moth butterflies. The inflorescence, with flowers that are arranged in ranks along a graceful arching stem, has also been compared to the flight of moths (Nash, 2003). The genus consists of approximately 40 species that are native to tropical and subtropical habitats of northern Australia, China, India, Philippines, Tibet, Taiwan, and other countries in Southeast Asia (Baker and Baker, 1991). Sweet (1980) classified the genus *Phalaenopsis* into 10 sections: Amboinenses, Aphyllae, Esmeralda, Fuscatae, Parishianae, Phalaenopsis, Polychilos, Proboscidioides, Stauroglottis, and Zebrinae. *Phalaenopsis* hybrids have been created with all of the known species and breeders have made selections for both the potted plant and cut flower production markets (Griesbach, 1985b, 2002).

History

Phalaenopsis were first found and described by Rumphius in 1750, but the genus was not classified until 1825 by Karl Ludwig Blume (Reinikka, 1995). In the early 1800s, plants were first introduced in Europe and became popular during the Victorian period from 1830 to 1900 (Christenson, 2001; Griesbach, 2002). At this time, *Phalaenopsis* were primarily grown and displayed in European conservatories and greenhouses because of the inadequate environmental conditions in homes. The first artificial *Phalaenopsis* hybrid was created in 1875, but procedures for successful seed germination were not established until 1922 when Lewis Knudson developed technology

for non-symbiotic seed germination (Griesbach, 2000). In the early 1900s, as consumer popularity for potted plants declined and preference for cut flowers increased, breeders focused on selecting hybrids for floral traits. After 1960, the demand for potted *Phalaenopsis* began to rise again due to new propagation techniques and improved transportation systems, and as homes became more suitable for growing *Phalaenopsis* (Griesbach, 2000). In The Netherlands, *Phalaenopsis* earned the highest turnover value among indoor plants traded at Dutch flower auctions in 2004 (VBN, 2005a) (Fig. 4). Among the almost 300 commercial orchid growers in Europe, about 90 specialize exclusively in *Phalaenopsis* (Laws, 2004). Although specific sales figures are not available for individual orchid genera sold within the U.S., it is estimated that approximately 85 to 90% of all orchids sold are of the genus *Phalaenopsis* (Nash, 2003). In Taiwan, *Phalaenopsis* account for 65% of the potted orchids produced and they are ranked as the number one potted crop (Anthura and Bureau IMAC, 2005).

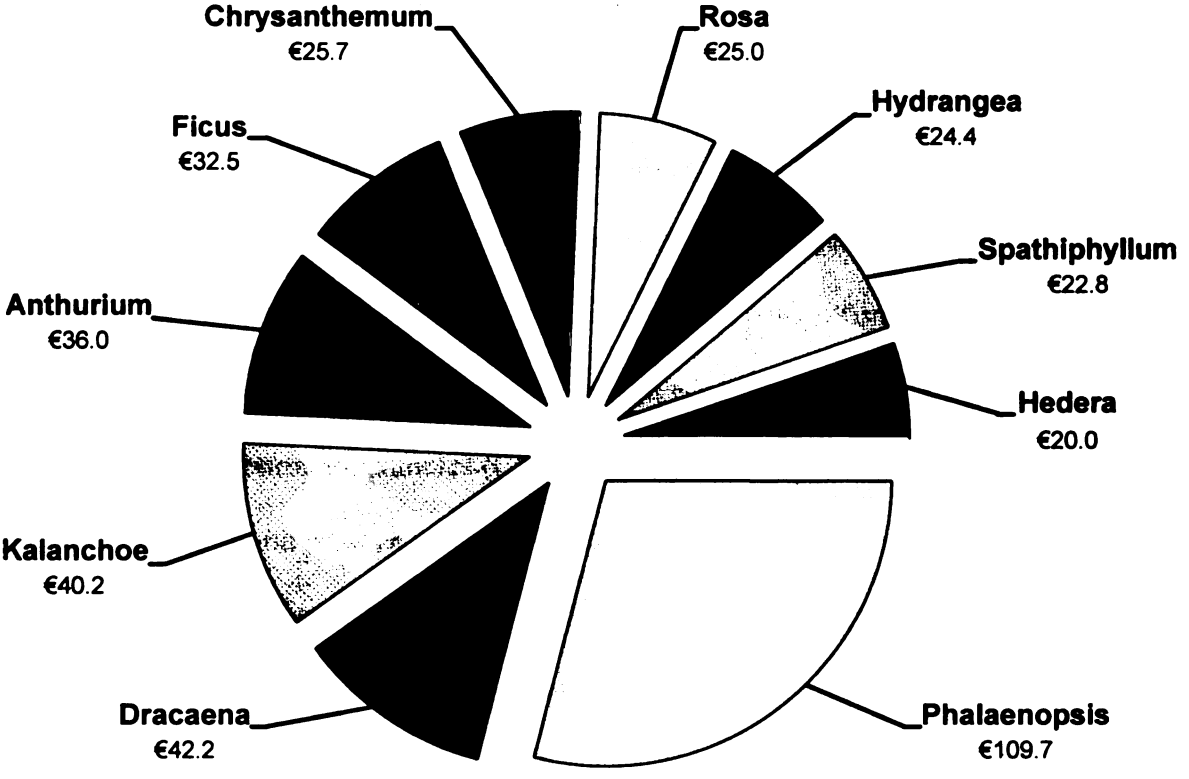

Figure 4. Turnerover value (million euro) of the most important indoor plants sold at Dutch flower auctions in 2004 (VBN, 2005a).

Plant Description

Phalaenopsis have a monopodial growth habit with short stems and are generally epiphytic, although some species are lithophytic (Pridgeon, 2000). The leaves are broad and succulent with an arching habit, allowing rainfall to potentially drain away from the crown of the plant (Christenson, 2001). Although a portion of rainwater also drains toward the crown, this leaf architecture reduces pathogen infection in nature. *Phalaenopsis* have thick roots that arise from the base of the stem or lower nodes and are usually unbranched, functioning as one of three types: aerial, prostrate epiphytic, or substrate (Christenson, 2001). The apical meristem of aerial and epiphytic roots contain chlorophyll and have photosynthetic functions, however the amount of carbon assimilation is less than the amount of carbon evolved through respiration (Dycus and Knudsen, 1957). The inflorescence, also termed spike, typically emerges from the third to fifth node below the top leaf and may consist of only a few flowers on a raceme to dozens of flowers borne on panicles (Christenson, 2001; Sakanishi et al., 1980). In all species, the sepals and petals are similar in size, shape, and color, with a labellum comprised of three lobes (Christenson, 2001) (Fig. 5). Although the most popular flower color is white, breeders are increasingly selecting *Phalaenopsis* hybrids for other colors, shades, stripes, patterns, and combinations (Nash, 2003). A recent trend has been the popularity of new harlequin-type *Phalaenopsis* created by commercial hybridizers in Taiwan, which have flowers with dark colored blotches on top of a light-colored background (Fitch, 2004a). New complex multi-species hybrids are also available with wonderful fragrances (Fitch, 2004b). The longevity of flowers varies among species and

hybrids, ranging from 30 to 120 days in *Phalaenopsis violacaea* Witte and *Phalaenopsis amabilis* (L.) Blume, respectively (Goh and Arditti, 1985).

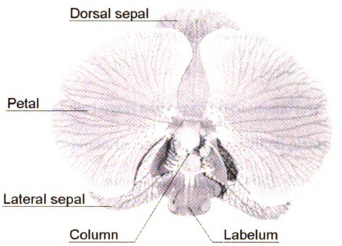

Figure 5. Structure of a *Phalaenopsis* flower.

Phalaenopsis

Phalaenopsis production occurs around the world and it has been estimated that 125 to 175 million young plants (mericlones and seedlings) are produced annually (Anthura and Bureau IMAC, 2005). The largest producing countries of potted *Phalaenopsis* include China, Germany, Japan, The Netherlands, Taiwan, and the United States (Griesbach, 2003). In 1993, potted *Phalaenopsis* orchids accounted for $103 million dollars in sales at Japanese auctions (Hew and Yong, 1997). Among all flower auctions in The Netherlands, there was a 123% increase in potted *Phalaenopsis* sales between 2001 and 2004 (VBN, 2003, 2005a) (Fig. 6). In 2004, a total of 23.8 million potted *Phalaenopsis* were traded at Dutch flower auctions with a value of €109.7 million

($136 million[1]) (VBN, 2005a). It was estimated that The Netherlands produced a total of 35 million potted *Phalaenopsis* in 2004 on approximately 80 hectares of production. *Phalaenopsis* production in China has also increased considerably during the past ten years and in 2003, 10 to 12 million plants were produced (Anthura and Bureau IMAC, 2005).

Taiwan currently has the largest number of breeders and growers with approximately 89 hectares in production, producing 36 million plants in 2002 with a wholesale value of $51 million (Fenton, 2004b; Wang, 2004). It is estimated that of the *Phalaenopsis* plants that are produced in Taiwan, 80% are exported (Anthura and Bureau IMAC, 2005). The Taiwanese government, with the goal of maintaining a central position in worldwide potted *Phalaenopsis* production, is currently developing a large scale research, production, and distribution complex, named the Taiwan Orchid Plantation (Fenton, 2004a). In 2004, the USDA amended the regulations for the importation of plants and plant products and added *Phalaenopsis* orchids from Taiwan to the list of plants that can be imported in approved growing media (USDA, 2004a). Orchid growers in the United States are challenging this ruling because it could have a negative economic impact on domestic commercial growers of potted *Phalaenopsis* orchids.

One of the primary reasons why commercial production of *Phalaenopsis* orchids has risen in the United States is that many greenhouse growers are in search of additional potted floriculture crops to expand their product line and increase profitability. Plants are generally finished and sold in 12 to 15-cm pots with six or more flower buds per plant

[1] The euro-U.S. dollar exchange rate was calculated by averaging the daily euro-U.S. dollar exchange rates for the calendar year 2004 (Federal Reserve Bank of New York, 2005). Based on this calculation, the average euro-U.S. dollar exchange rate was 1.24.

and each flower measuring ≥7.5 cm wide (Konow and Wang, 2001; Wang and Lee, 1994a). The wholesale price of a 15-cm pot varies considerably among markets within the United States, ranging from $10.00 to $26.00 in 2004 (Laws, 2004). This wholesale price is considerably higher than more traditional potted plants, such as Easter lily ($4.12), florist chrysanthemum ($2.53), and poinsettia ($4.07) (USDA, 2005b). In The Netherlands, the average wholesale price on the flower auction for potted *Phalaenopsis* was €4.61 ($5.70) in 2004 (VBN, 2005a). However, the average wholesale price varies considerably throughout the year and in 2003 ranged from €3.65 to €5.49 ($4.12 to $6.20[1]) during summer and winter periods, respectively (Anthura and Bureau IMAC, 2005).

[1] The euro-U.S. dollar exchange rate was calculated by averaging the daily euro-U.S. dollar exchange rates for the calendar year 2003 (Federal Reserve Bank of New York, 2005). Based on this calculation, the average euro-U.S. dollar exchange rate was 1.13.

Million euro

Fig
Pho

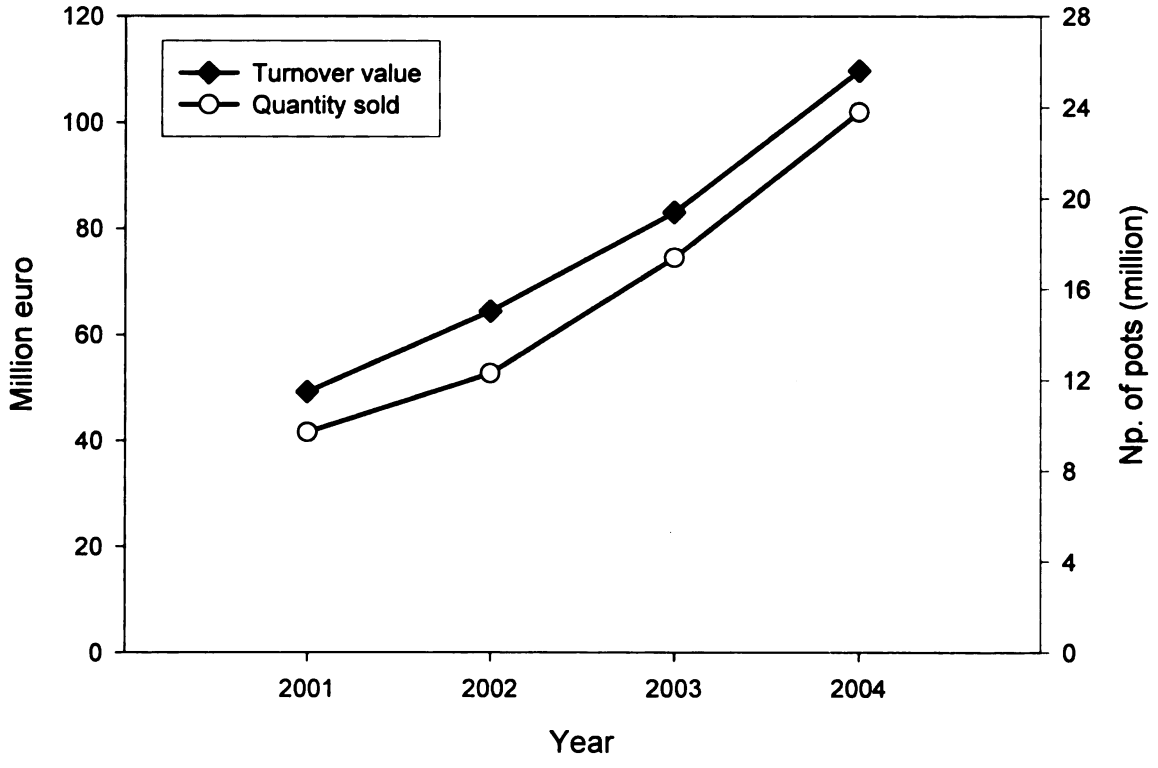

Figure 6. Turnover value [million euro (♦)] and quantity [million (○)] of potted *Phalaenopsis* sold at Dutch flower auctions from 2001 to 2004 (VBN, 2003, 2005a).

COMMERCIAL PRODUCTION OF *PHALAENOPSIS*

Commercial production of potted *Phalaenopsis* is divided into many segments: breeders, propagators, finishing greenhouse growers, wholesale florist distributors, and retailers (Laws, 2004). A segmented supply chain allows for specialization in one function and results in improved plant quality and efficient production methods.

Propagation

Consumer preference in the United States has shifted from cut flowers to potted plants, prompting breeders to develop hybrids for the mass potted plant market and to select plant material with a compact growth habit and flowers that are fragrant, long-lasting, or both. *Phalaenopsis* orchids are commercially propagated by sexual and asexual techniques, but asexual propagation is most common due to greater plant uniformity (Griesback, 2002). Plantlets propagated by tissue culture are grown in flasks, which are then transferred to community pots, thumb pots, and larger pot sizes in succession and can be sold as unfinished plants at each stage (Hew and Yong, 1997; Konow and Wang, 2001). From clonal propagation, *Phalaenopsis* generally require 24 to 36 months to reach maturity, or the capacity to flower, which is relatively short when compared with other orchid genera that can require up to 60 months (Keithly et al., 1991; Konow and Wang, 2001). Mature plants with a 25-cm to 30-cm leaf span are often purchased by commercial growers who finish the crop based on the scheduled market demand (Wang and Lee, 1994a).

Shipping Unfinished Plant Material

Commercial orchid growers in the United States commonly purchase immature and mature plant material from growers in other countries (e.g., Taiwan and The Netherlands). The USDA requires that orchid plants are imported into the United States as bare-rooted plants, without orchid media. The only exception to these regulations is the importation of *Phalaenopsis* in approved growing media from Taiwan. Shipping orchids as bare-rooted plants increases the susceptibility to temperature and water stress, which can have a negative impact on plant vigor. Su et al. (2001a) determined the effects of temperature, relative humidity, illumination, and storage duration on the amount of water loss and quantum efficiency of bare-rooted *Phalaenopsis*, and reported that temperature was the most important factor during shipping. The weight loss in plants stored at 25 °C, 70% relative humidity, and in darkness increased from approximately 3% to 20% as storage duration increased from 3 to 30 days, respectively. When temperature increased to 35 °C, weight loss decreased by approximately 28% to 62% as storage duration increased from 3 to 30 days, respectively. There was no significant decline in quantum efficiency of plants stored at 25 °C, whereas plants stored at 35 °C had a significant decrease (≤60%) in quantum efficiency when stored for up to 30 days (Su et al., 2001a).

A shipping temperature of 25 °C is recommended in another study. Wang (1997) reported that chilling injury occurred in leaves of bare-root *Phalaenopsis* when stored at 15 and 20 °C for 4, 7, or 14 days. The time to visible inflorescence was not affected by storage at 15, 20, or 25 °C for durations up to 14 days, whereas inflorescence emergence was delayed by 5 to 8 days when stored for ≥4 days at 30 °C.

Greenhouse Environment

Temperature

Vegetative Phase. *Phalaenopsis* grown at a constant temperature of ≥28 °C remain in a vegetative phase and development of the reproductive bud is inhibited (Chen et al., 1994; Sakanishi et al., 1980; Yoneda et al., 1991). Most species will tolerate periods at temperatures between 32 to 35 °C (Baker and Baker, 1991), however the maximum duration at high temperature has not been determined and the specific symptoms of heat stress have not been well described. The base temperature for *Phalaenopsis* has been calculated to be between 10.8 to 11.2 °C, and is similar for all stages of growth and development (Robinson, 2002). McConnell and Sheehan (1978) reported that *Phalaenopsis* exposed to a constant temperature of 2, 4, or 7 °C for 1 hour or more in darkness, resulted in chilling injury that was manifested as sunken, yellow, water-soaked spots on upper leaf surfaces.

Reproductive Phase. To promote the transition from a vegetative phase to a reproductive phase, commercial greenhouse growers reduce temperature to a day/night of 25/20 or 20/15 °C (Lee and Lin, 1984, 1987). After low temperature exposure for 3 to 5 weeks, an inflorescence (spike) will emerge through the leaf epidermis from the axil of the third and/or fourth node below the apical leaf (Sakanishi et al., 1980). Smaller plants (15-cm to 25-cm leaf span) that have not reached vegetative maturity may require cooler temperatures (20/15 °C) or longer exposure than larger, more mature plants (25-cm to 30-cm leaf span) (Wang and Lee, 1994b). The initiation and development of floral

primordia does not occur until the inflorescence has reached ≈5 cm in length (De Vries, 1950).

Following inflorescence emergence, there is a linear relationship between temperature and rate of development towards visible bud and anthesis (Lee and Lin 1987; Robinson, 2002). For example, the average time from inflorescence emergence to anthesis at a constant average daily temperature (ADT) of 17.7, 20.0, 22.5, or 25.7 °C was 133, 88, 64, and 53 days, respectively. The minimum time from inflorescence emergence to anthesis occurred at 26 °C. The thermal time and the base temperature (T_b) were both calculated for 1) days from inflorescence emergence to visible bud (454 degree-days; T_b=11.2 °C) and 2) days from visible bud to anthesis (333 degree-days, T_b=11.0 °C) (Robinson, 2002). The base temperature and thermal time were calculated using equations [3] and [5], respectively (pages 48 and 50).

In *Phalaenopsis* Taisuco Smile (*Phal.* Taisuco Bright × *Phal. equestris* Rchb.), forcing temperature between 17 and 26 °C did not affect the average number of nodes, flower count, final inflorescence height, or flower width (Robinson, 2002). In contrast, Lee and Lin (1984) reported that plants of *Phalaenopsis* Dos Pueblos × Juanit had shorter inflorescences and lower flower count when grown at a day/night temperature of 20/15 °C compared to plants grown at 25/20 °C. The inflorescence and flowers may abort or the inflorescence may transition back to a vegetative phase and an air plantlet will develop if plants are exposed to a high temperature (≥28 °C) before the inflorescence has reached ≈5 cm in length (De Vries, 1950; Sakanishi et al., 1980). A vegetative air plantlet is termed a keiki, the Hawaiian word for "baby" (Christenson, 2001).

Ota et al. (1991) measured the amount of CO_2 uptake in *Phalaenopsis* plants grown at constant temperatures of 10, 15, 20, 25, and 30 °C and day/night temperatures of 10/20, 25/15, 25/20, and 30/20 °C and determined that the highest amount of net CO_2 uptake occurred at 25/15 and 25/20 °C. The constant temperature for greatest CO_2 uptake was 20 °C. A similar study by Lootens and Heursel (1998) measured the amount of CO_2 uptake in single leaves of *Phalaenopsis* plants grown under a photosynthetic photon flux (*PPF*) of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and at four day/night temperature regimens of 20/15, 20/20, 25/20, or 25/25 °C, and reported that CO_2 uptake was significantly greater (14% to 21%) at 20/15 °C than at 20/20, 25/20, or 25/25 °C. A significant day/night temperature effect also existed, in which treatments with a +5 °C day/night temperature fluctuation had a 5% to 21% greater CO_2 uptake than treatments with a 0 °C day/night temperature fluctuation. These results collectively show that in *Phalaenopsis*, a positive day and night temperature fluctuation increases CO_2 absorption and presumably carbon assimilation compared to a constant temperature.

Low Temperature Requirement

The requirement of low temperature (≤25 °C) for the induction of inflorescences in *Phalaenopsis* has been well defined (De Vries, 1950; Lee and Lin, 1984, 1987; Rotor, 1952; Sakanishi et al., 1980; Yoneda et al., 1992). A 5 to 8 °C day/night fluctuation has been reported to be required for inflorescence initiation and flower development (Anthura and Bureau IMAC, 2005; Christenson, 2001). However, there has been limited research on the interaction between day and night temperature and to our knowledge, no scientific information exists to support this concept.

De Vries (1950) observed that inflorescence induction occurred in *Phalaenopsis schilleriana* Rchb.f. when the day temperature was occasionally above 30 °C and night temperature was between 19 to 21 °C. Exposure to a night temperature ≤21 °C was suggested as a requirement for inflorescence induction, and a high day temperature ≥30 °C did not have an inhibitory effect (De Vries, 1950). However, this experiment was not conducted in a climate-controlled greenhouse and the duration of the day and night was not reported. These results conflict with information by Hew and Yong (1997), in which flowering of *Phalaenopsis amabilis* and *Phalaenopsis schilleriana* did not occur when the day temperature was above 27 °C and the night temperature was between 12 to 17 °C.

Sakanishi et al. (1980) investigated the effects of increasing the duration of high temperature exposure when the average night temperature was 20 °C. As the daily hours of temperature above 28 °C increased from 0 to 24, there was a decrease in the percentage of inflorescence emergence and a delay in days to inflorescence emergence. To achieve 100% inflorescence emergence in a population of plants, they had to be exposed to at least 12 hours at a temperature of 20 °C each day (Sakanishi et al., 1980). However, this experiment was conducted under a natural photoperiod and information was not presented on when the high temperature exposure occurred in relation to the photoperiod. Furthermore, the timing of high temperature exposure during the day to inhibit inflorescence induction has not been determined. In other words, can high temperature exposure inhibit flowering during the day as well as if delivered during the night?

These experiments collectively suggest that a high day temperature can inhibit inflorescence emergence even when the night temperature is conducive for reproductive

development. Further research is merited to clarify the effects of diurnal temperature fluctuations on inflorescence emergence and development.

Irradiance

The effects of irradiance have been described during all stages of *Phalaenopsis* production (Konow and Wang, 2001; Lee, 2000; Lootens and Heursel, 1998; Wang, 1995b, 1998a; Wang and Lee, 1994a). *Phalaenopsis* plantlets grown in vitro under an instantaneous irradiance level of 40 or 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ provided by cool-white fluorescent lamps had increased root growth, wider leaves, and greater fresh weight than those grown under 10 or 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Konow and Wang, 2001). During vegetative growth in the greenhouse, the recommended irradiance for mature *Phalaenopsis* is 240 to 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but the intensity should be reduced when temperature is above 30 °C (Wang and Lee, 1994a). Lee (2000), reported that plants grown under 80 to 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and subsequently forced had significantly less root and leaf dry weight, delayed flowering, and a lower flower count compared with plants grown under 260 to 360 $\mu mol \cdot m^{-2} \cdot s^{-1}$. However, the photoperiod and daily light integral (DLI) were not presented. Lootens and Heursel (1998) determined that the saturating *PPF* for two *Phalaenopsis* hybrids grown at 20 °C was 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$. At a temperature of 25 or 30 °C, the saturating *PPF* was not found at the highest irradiance measured, 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Photoinhibition occurs in *Phalaenopsis* when grown at an irradiance above 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Lee, 2000).

Information is also available on how irradiance influences the reproductive phase of *Phalaenopsis* production. Wang (1995b) showed that plants grown at 20/15 °C day/night with a 12-h photoperiod and a DLI of 2.6 or 6.9 $mol \cdot m^{-2} \cdot d^{-1}$ initiated

inflorescences after 34 and 28 days, respectively. Plants grown under 0 or 0.35 $mol \cdot m^{-2} \cdot d^{-1}$ did not initiate inflorescences within 6 weeks. This is supported by Lee (2000), in which all plants initiated inflorescences and flowered when the DLI during forcing was ≥ 2.2 $mol \cdot m^{-2} \cdot d^{-1}$, independent of photoperiod. In *Phalaenopsis*, a reduction in light intensity has been associated with a decrease in leaf and root development, dry matter production, sugar concentration, and the amount of nitrogen absorbed (Kubota and Yoneda, 1993b).

Wang (1998a) showed that inflorescence emergence could be delayed by exposing plants to repeated weekly cycles of various days in darkness and suggested that the inability of plants to initiate inflorescences may have resulted from low concentrations of metabolites. Hisamatsu et al. (2001) reported that inflorescence initiation could be delayed by holding plants in darkness at 20 °C for ≤60 days without adverse effects on plant quality when returned to light and forced (i.e. the number of flowers, length of inflorescences, and size of flowers were not affected by dark treatment). These strategies to delay flowering could be used by *Phalaenopsis* growers in tropical and subtropical climates without the use of heating systems to maintain noninductive temperatures.

Photoperiod

Currently, there is conflicting research as to whether *Phalaenopsis* is photoperiodic; some studies have suggested that short days hasten inflorescence emergence and flowering (Goh and Arditti 1985; Rotor, 1952, 1959; Su et al., 2001b; Went, 1957; Yoneda et al., 1991). Rotor (1952, 1959) reported that plants of

Phalaenopsis amabilis grown at 18 °C under a 9-h photoperiod initiated inflorescences and flowered all year, whereas plants grown under a 16-h photoperiod had one flowering period per year. This is also supported by Went (1957), in which plants grown at 20 °C produced more inflorescences under an 8-h photoperiod than under a 16-h photoperiod. Data comparing the number of inflorescences between treatments was not provided.

Yoneda et al. (1991) observed that 6-year old mature *Phalaenopsis* grown at 22 or 23 °C and under an 8-h photoperiod initiated inflorescences and reached anthesis 7 to 9 days earlier than plants grown under a natural photoperiod. However, the effect of daylength was not significant in this study. Sakanishi et al. (1980) suggested that the facultative short-day response in *Phalaenopsis* could be a cumulative effect of low temperature.

Postharvest

The inflorescences of *Phalaenopsis* are usually braced before transport using support stakes and wire ties or clips. Stakes are often installed when the lowest bud on the inflorescence reaches the size of a marble. When plants have at least one or two open flowers they are ready for sale and are packaged for transport. The flowers of *Phalaenopsis* are susceptible to infection by pathogens. Petal blight, caused by *Botrytis* sp., can develop on open flowers as small dark spots, resulting in plants that are unsalable. This disease manifests when inflorescences and foliage remain wet for long periods or during conditions of high relative humidity (≥80%) (Anthura and Bureau IMAC, 2005; Wang, 2003).

The flowers of *Phalaenopsis* are very sensitive to small concentrations of ethylene: plants exposed to 0.1 $mg \cdot L^{-1}$ ethylene for 24 hours had complete flower and bud drop within three days of initial exposure (Wang, 2004). Applying 1-methylcyclopropene (1-MCP) at 0.2 $mg \cdot L^{-1}$ for six hours protects *Phalaenopsis* flowers from ethylene ($\leq$10 $mg \cdot L^{-1}$). The duration of ethylene protection by 1-MCP was 4, 7, and 10 days at 25 to 30, 20, and 15 °C, respectively (Wang, 2003).

Phalaenopsis are graded based on flower color, number of flowers per inflorescence, inflorescence length, lateral branching of the inflorescence, and number of inflorescences per plant. Among these characteristics, the most important grading criterion is the number of inflorescences per plant, followed by lateral branching and the number of flowers per inflorescence (Anthura and Bureau IMAC, 2005). In The Netherlands, product specifications at flower auctions require potted *Phalaenopsis* to have a minimum number of open flowers per inflorescence at time of trade. For example, at least 25% of the flower must be open from 2 March to 31 October, while from 1 November to 1 March, 25 to 50% of the flowers must be open (VBN, 2005b). Finished plants are wrapped in individual sleeves for protection, then are transported at a minimum temperature of 18 °C (Anthura and Bureau IMAC, 2005).

Plant damage can occur during long periods of shipping by airfreight or ground transportation, resulting in bud drop and high percentages (up to 15%) of unsalable plant material. In both the United States and Europe, compact and branched mini-*Phalaenopsis* hybrids are now increasingly sought by store buyers because damage during transport is reduced (Laws, 2004).

Medium and Nutrition

Growing Medium

A common growing medium used in early *Phalaenopsis* production was osmunda, the dried fibrous root mass from a fern of the genus *Osmunda*. However, osmunda is rarely used today in orchid cultivation due to its high cost, lack of quality, and limited availability because of endangerment (Christenson, 2001). The primary medium component now used in commercial production of *Phalaenopsis* is Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] bark, harvested by the logging industry on the Pacific coast of the United States (Wang, 2000). However, Douglas fir bark has several disadvantages: fresh bark has a low water-holding capacity; small or medium grade bark decomposes too quickly, resulting in high water retention; it has low nutrient retention and insufficient uniformity; and has the potential for limited availability in the future. Thus, growers usually combine fir bark with other organic and inorganic materials, including activated charcoal, chopped coconut husks and fiber (*Coco nucifera* L.), cork (*Quercus suber* L.), expanded clay, osmunda fiber, peat, perlite, redwood bark [*Sequoia sempervirens* (D. Don) Endl.], rock wool, sphagnum moss, expanded polystyrene, tree fern fiber, vermiculite, and volcanic rock (Baker and Baker, 1991; Slump, 2004).

A mixture of fine-grade fir bark and sphagnum peat (80% and 20% by volume, respectively) resulted in a greater leaf number, total leaf area, and shoot fresh mass compared to plants grown in a 100% fine-grade fir bark medium (Wang, 1998b). In a separate study, *Phalaenopsis* were grown in a mixture of fine-grade Douglas fir bark and sphagnum peat (70% and 30% by volume, respectively) or in a 100% fine-grade Douglas fir bark medium and fertilized at each irrigation with a water soluble fertilizer (20N-8.6P-

16.6K; 200 mg N l^{-1}) for one year (Wang and Konow, 2002). Plants grown in a peat and fir bark medium had a greater leaf number, total leaf area, and leaf and root fresh weight than plants grown in only bark. The differences in plant growth could be attributed to a higher water-holding capacity and cation exchange capacity of peat mix compared to fir bark alone.

One recommended media composition for growing *Phalaenopsis* is a mixture of 80% medium-grade fir bark, 10% long fiber sphagnum peat moss, and 10% coarse-grade perlite (Wang, 2003). In Japan, the primary medium for growing *Phalaenopsis* is sphagnum moss because of its high water-holding capacity, nutrient retention, slow rate of decomposition, ease of transplanting and inserting inflorescence supports, and widespread availability from New Zealand and China (Ichihashi, 1997).

The pH and electrical conductivity (EC) of the medium are also important factors to monitor during *Phalaenopsis* production. The recommended pH and EC for growing *Phalaenopsis* ranges from 5.0 to 6.0 and 1.0 to 1.5 $dS \cdot m^{-1}$, respectively (Griesbach, 1985a; Wang, 2003).

Plant Nutrition

Wang (1996) irrigated young *Phalaenopsis* seedlings with one of six water-soluble fertilizers, having various percentages of N, P, and K, and different nitrogen sources and potential acidity (10N-13.1P-16.6K, 15N-4.4P-24.9K, 15N-8.7P-20.8K, 20N-2.2P-15.8K, 20N-4.4P-16.6K, and 20N-8.7P-16.6K) at 100 or 200 mg $N \cdot L^{-1}$. After seven months of fertigation, leaf span, leaf size, total leaf area, and shoot and root fresh weight were not significantly different among fertilizers within either concentration.

These results suggest that during production of *Phalaenopsis*, different balanced fertilizers can be used with similar effects on plant growth.

Fertilizer concentration can influence the performance of *Phalaenopsis*. Increasing the rate of a 20-8.6-26.6 fertilizer from 0.25 $g \cdot L^{-1}$ to 1.0 $g \cdot L^{-1}$ (50 to 200 ppm N), increased flower count, inflorescence diameter and length, and leaf production after flowering, and hastened inflorescence emergence during the following season (Wang and Gregg, 1994). Application of a fertilizer with N at $\geq$100 $mg \cdot L^{-1}$, before and after inflorescence emergence, is reportedly important for the initiation and development of flower primordia, as well as obtaining a high flower count and quality (Wang, 2000). Griesbach (1985c) recommended applying 100 mg $N \cdot L^{-1}$ at each irrigation from a 20N-20P-20K soluble fertilizer for production of the *Phalaenopsis* hybrid 'Toyland' (*Phalaenopsis* Leucorrhoda ×*Phalaenopsis* Hummingbird).

One fertility strategy now recommended for commercial production of *Phalaenopsis* is to use a water-soluble fertilizer at each irrigation at a rate of ($mg \cdot L^{-1}$): 200 N, 25-50 P, and a minimum of 150 K (Wang, 2003). Periodic application of calcium from calcium nitrate at 100 mg $Ca \cdot L^{-1}$ and magnesium from epsom salts (magnesium sulfate heptahydrate) at 50 mg $Mg \cdot L^{-1}$ is also suggested. Table 1 provides recommended nutrient target values and sufficiency ranges for a media analysis.

Physiological Changes

The physiological changes that occur as *Phalaenopsis* transitions from a vegetative to a reproductive phase have not been completely described. During inflorescence emergence and development, exposure to low temperature has been

associated with increases in: active cytokinins in leaves; active gibberellins in inflorescences; sucrose, glucose, and fructose in inflorescences; and total nitrogen concentration and carbohydrate levels in stems (Chen et al., 1994; Chou et al., 2000; Kataoka et al., 2004; Kubota and Yoneda, 1993a; Su et al., 2001b), while a decrease in the level of active abscisic acid has been measured in roots and developing inflorescences (Wang et al., 2002).

Table 1. Element, electrical conductivity (EC), and pH target values and sufficiency ranges for *Phalaenopsis* growing media. Information from Anthura and Bureau IMAC (2005).

Element	Target value ($mg \cdot L^{-1}$)	Sufficiency range ($mg \cdot L^{-1}$)
Ammonium (NH_4^+)	<7	0 - 14
Nitrate (NO_3^-)	63	49 - 84
Phosphate (P_2O_5)	37	25 - 47
Potassium (K)	117	106 - 137
Calcium (Ca)	52	40 - 64
Magnesium (Mg)	19	10 - 29
Sulphate (SO_4)	19	10 - 29
Boron (B)	0.11	0.05 - 0.16
Chlorine (Cl)	<53	0 - 71
Copper (Cu)	0.06	0.03 - 0.09
Iron (Fe)	0.56	0.28 - 0.84
Manganese (Mn)	<0.05	0 - 0.60
Molybdenum (Mo)	0.06	0.02 - 0.10
Zinc (Zn)	0.39	0.20 - 0.59
Sodium (Na)	<35	0 - 35
EC	$1.0\ dS \cdot m^{-1}$	$0.7 - 1.3\ dS \cdot m^{-1}$
pH	5.8	5.0 - 6.5

EFFECTS OF PLANT GROWTH REGULATORS ON *PHALAENOPSIS*

Abscisic Acid

Abscisic acid (ABA) is an important hormone involved in the regulation of plant dormancy (Taiz and Zeiger, 2002). Wang et al. (2002) measured the amount of free and bound ABA in leaves, roots, and either dormant buds or flowering inflorescences of *Phalaenopsis* during three developmental stages: 1) plants grown at 28 °C without a visible inflorescence, e.g. dormant buds; 2) plants grown at 25/20 °C day/night with inflorescence length of 2 to 3 cm; and 3) plants grown at 25/20 °C with an inflorescence length of 7 to 10 cm. Plants grown at 28 °C had the highest amounts of free ABA in roots (48.5 $ng \cdot g^{-1}$) and dormant buds (31.1 $ng \cdot g^{-1}$), whereas plants grown at 25/20 °C had 46% less free ABA in roots and non-detectable levels in developing inflorescences. Levels of bound ABA, an inactive storage form, were 26 or 841% lower in roots of plants grown at 28 °C compared to plants grown at 25/20 °C with inflorescence lengths of 2 to 3 or 7 to 10 cm, respectively.

In a separate study, injection of exogenous ABA at the beginning of low temperature exposure (25/20 °C) inhibited the initiation of inflorescences (Wang et al., 2002). *Phalaenopsis* injected with ABA at 0, 0.1, or 1.0 μg per plant had inflorescence initiation percentages of 67, 17, or 0%, respectively. These results suggest that ABA could regulate the reproductive transition in *Phalaenopsis*, in which a decrease in ABA in dormant buds and roots is required for the initiation of flowering.

Auxin

To our knowledge, only one study has examined the changes in level of endogenous indole-acetic acid (IAA) during low temperature induction of *Phalaenopsis*. Fouché et al. (1997) measured the level of IAA in leaves every day following transfer to 22/17 °C and the level of IAA level abruptly increased from 135 to 450 $nmol \cdot g^{-1}$ between day two and five, followed by a second increase from 150 to 325 $nmol \cdot g^{-1}$ between day seven and nine. The relationship between fluctuations in IAA levels and the transition from vegetative to reproductive development is uncertain.

Cytokinins

In 1956, in search of compounds that promoted division of plant cells in culture, Folke Skoog isolated kinetin, N^6-furfuryladenine, a product formed during autoclaving of DNA (Taiz and Zeiger, 2002). Further studies revealed that kinetin in the presence of auxin, stimulated tobacco pith parenchyma tissue to proliferate in culture. In 1973, Letham identified a natural compound from the immature endosperm of corn, which promoted cell division similarly to kinetin. This compound, named zeatin (from the Latin for corn, *Zea mays* L.), was a *trans*-6-(4-hydroxy-3-methylbut-2-enylamino) purine (Taiz and Zeiger, 2002). Zeatin and related compounds have since been grouped under a major class of plant hormones, the cytokinins (Crozier et al., 2000).

Physiological Role

Cytokinins are biosynthesized in the apical meristem of roots and are transported through the xylem to aerial plant organs. During the past 45 years, research has shown

the involvement of cytokinins in a wide array of physiological and biochemical processes including seed germination and dormancy, cell division, organ formation and regeneration, reduction of apical dominance, response to pathogens, nutrient mobilization, floral and vascular development, fruit set, fruit ripening, and senescence of plant organs (Higuchi et al., 2004; Taiz and Zeiger, 2002). Studies have also reported a role of cytokinins during phloem loading and unloading and an effect on assimilate movement (Thomas and Blakesley, 1987).

Benzyladenine

Synthetic cytokinins include N^6-substituted adenines such as kinetin (6-furfurylaminopurine) and benzyladenine (6-benzylaminopurine, BAP). The effects of these synthetic compounds are similar to those of endogenous cytokinins. Although benzyladenine (BA) was the first synthetic cytokinin derived, BA has now been isolated as a naturally occurring cytokinin in many plants and can be considered an endogenous-like compound (Bubán, 2000).

Commercial Uses in Horticulture

Cytokinins are commonly used during all stages of micropropagation: 1) initiation into culture, 2) multiplication, 3) shoot development, and 4) root development (Thomas and Blakesley, 1987). In commercial fruit production, BA is commonly used to regulate canopy structure by promoting lateral shoot growth and increase cropping potential or as a fruit thinning agent to produce higher quality fruits and increase bloom the following season (Bubán, 2000). Cytokinins are also applied exogenously to influence chlorophyll

production and leaf senescence in many crops. During production and in postharvest environments, leaf yellowing can reduce the quality of potted plants and cut flowers. In *Limonium sinuatum* (L.) P. Mill., BA as a dip reduced chlorophyll degradation and senescence of cut flower stems (Serek and Reid, 2000). Han (1997) reported that spray application of a 25 $mg \cdot L^{-1}$ solution containing GA_{4+7} and BA prevented basal leaf yellowing in *Lilium longiflorum* Thumb. 'Nellie White'.

Benzyladenine is also used during the production of Easter cactus [*Hatiora gaertneri* (Reg.) Barthlott.] and Thanksgiving cactus [*Schlumbergera truncata* (Haw.) Moran.] to increase the number of phylloclades and flower buds (Dole and Wilkins, 2005). In Thanksgiving cactus grown under long-days, the number of phylloclades increased by almost 150% after BA (50 or 100 $mg \cdot L^{-1}$) was sprayed to runoff (Heins et al., 1981). Application of BA at 50 $mg \cdot L^{-1}$ on Easter cactus increased the total number of flowers per plant by 85% when applied as a spray 12 days after the start of long days (Boyle, 1995).

In miniature climbing rose (*Rosa* 'Jeanne la Joie') nine foliar spray applications of BAP (100 $mg \cdot L^{-1}$) applied every two days increased the number of shoots after four weeks by 21% and 68%, compared control and pinched plants, respectively (Richards and Wilkinson, 1984). The application of BAP also had a significant influence on the number of flowers eight weeks after treatment: plants treated with BAP at 10 or 100 $mg \cdot L^{-1}$ had increased flower number by 112% and 175%, respectively, compared to control plants.

Effects on Growth and Flowering of Cymbidium, Dendrobium, and Aranda

Benzyladenine is commonly used during the earliest stages of orchid production as an important component in culture media for micropropgation (Tokuhara and Mii, 1993). Several studies have suggested that the application of BA on orchids may be a useful tool to control flowering (Goh, 1977, 1979; Higuchi and Sakai, 1977; Kim et al., 1999, 2000; Sakai et al., 2000; Yoneda and Momose, 1990).

One theory that has been proposed to explain the effectiveness of BA in promoting flowering in some orchids suggests that inflorescence initiation in response to inductive temperature is a result of changes in the level of endogenous cytokinins (Chou et al, 2000; Goh, 1979). Flower initiation in many plant species is often associated with changes in hormone levels in response to environmental factors (Zeevaart, 1976). Thus, the application of BA during low temperature exposure may supplement the natural increase in endogenous cytokinins and enhance inflorescence induction.

In *Aranda* Deborah, five repeated (daily) 2 ml injections of BAP (1 *m*M) or BA+GA (1 *m*M and 1 *m*M, respectively) into stem tissues between the sixth and seventh node increased the average number of initiated inflorescences per plant by 850 and 1500%, respectively, compared to untreated plants (Goh, 1977). Information on the number of flowers per inflorescence or details on flower quality were not presented.

The effects of BA on the promotion of early flowering in *Cymbidium* sp. *in vitro* have been well described (Chang and Chang, 2003; Kostenyuk et al., 1999). Kostenyuk et al. (1999) reported that following root excision, shoots of *Cymbidium niveo-marginatum* Mak grown on a Murashige and Skoog (MS) medium supplemented with nitrogen, phosphorous, and (BA (44 μM) had a flowering percentage of 97.5% after 90

days, while control plants were nonflowering. In a similar study, callus-derived rhizomes (3 to 5 mm) of *Cymbidium ensifolium* var. *misericors* grown on a MS medium supplemented with naphthalene-acetic acid (NAA) (0.28 μM) and BA (10 to 33 μM) flowered within 100 days after culturing (Chang and Chang, 2003).

Higuchi and Sakai (1977) reported that a 1.8 *m*M solution of BA applied on *Dendrobium* Nodoka during the beginning of the short-day and low temperature treatment during forcing, increased the number of inflorescences per plant. The application method and amount of increase were not presented in English. Goh (1979) injected 1 ml of either BA (1 *m*M or 0.1 *m*M), GA (1 *m*M or 0.1 *m*M) or BA+GA (1 *m*M and 0.1 *m*M, respectively) into mature pseudobulbs of *Dendrobium* Loisae 'Dark' and observed that plants treated with BA or BA+GA initiated inflorescences 7 to 10 days after the first application, whereas untreated pseudobulbs and those treated with only GA did not initiate an inflorescence. When either BA or GA was injected into young vegetative axillary shoots (4 to 8 cm long), inflorescence initiation did not occur. This suggests that other hormonal factors may prevent floral initiation in actively growing organs (e.g., auxin), or that young shoots do not have the capacity to flower.

In *Dendrobium* Jaquelyn Thomas 'Uniwai Princess', a one-time treatment of five 0.1 ml injections of BA (10 or 100 *m*M) into 2-year old mature pseudobulbs stimulated the production of 4.0 and 6.3 inflorescences per pseudobulb, respectively, while control plants formed an average of 0.2 inflorescences per pseudobulb (Sakai et al., 2000). The average length of inflorescences stimulated by injection of BA at 10 and 100 *m*M was 17.5 and 15.3 cm, respectively, compared with 20.3 cm of control plants. In addition, flower area was reduced to 5.0 and 4.2 cm^2, respectively, compared with 5.6 cm^2 of

control plants and a high percentage of flowers were abnormal (i.e., petal-like growths from the sides of the column or two anther caps present on the column) compared to untreated plants. Incorporation of GA (10 or 100 *m*M) into the injection solution increased inflorescence length and flower area, and reduced the percentage of abnormally formed flowers (Sakai et al., 2000). The specific GA used in this study was not provided.

Campos and Kerbauy (2004) measured the concentrations of endogenous hormones during low temperature flowering induction (25/10 °C) of *Dendrobium* Second Love and reported that cytokinins (zeatin-derived forms) increased by over 360% in lateral buds when measured 15 days after the end of low temperature exposure and levels of ABA in lateral buds decreased by 31%. Levels of IAA fluctuated, decreasing 15 days after low temperature exposure and increasing thereafter. These results suggest that cytokinins may be involved during the floral transition in *Dendrobium*, which could explain the effectiveness of BA in promoting inflorescence initiation.

Effects on Flowering of Phalaenopsis

Chou et al. (2000) investigated changes in the concentration of endogenous cytokinins in the *Phalaenopsis* hybrid 'Taisuco Snow' (*Phal.* Mount Kaala × *Phal.* Wataboushi) grown at high temperature (30/25 °C day/night) and low temperature (25/20 °C). At high temperature, active cytokinins were converted into inactive forms and during exposure to low temperature, concentrations of active cytokinin in leaves increased. This suggests that cytokinins may have an important role during reproductive initiation in *Phalaenopsis*.

The application of BA during low temperature induction of *Phalaenopsis* has been reported to hasten the rate of inflorescence initiation and flowering and increase the number of inflorescences (Ichihashi, 1997; Kim et al., 1999, 2000; Yoneda and Momose, 1990). In the *Phalaenopsis* hybrid Jimmy Hall × Jimmy Hall 'Jouch Petals', a single foliar spray application of 200 $mg \cdot L^{-1}$ BA during low temperature exposure reportedly "promoted" inflorescence initiation and flowering (Ichihashi, 1997). Although BA decreased the length of inflorescences in this study, application of GA_3 at 100 $mg \cdot L^{-1}$ overcame the reduced inflorescence elongation.

A foliar spray application of BA (200 $mg \cdot L^{-1}$), GA_3 (100 $mg \cdot L^{-1}$) or BA+GA_3 (200 $mg \cdot L^{-1}$ and 100 $mg \cdot L^{-1}$, respectively) after transfer to highland culture for flowering (400 m above sea level) increased inflorescence emergence and decreased time to flower in BA and BA+GA_3 treatments (110 days) compared to GA_3 and control treatments (123 and 135 days, respectively) (Yonenda and Momose, 1990). A reproductive inflorescence generally emerges from the leaf axil of the third, fourth, or both nodes below the apical leaf (Sakanishi et al., 1980). However, in this study the percentage of inflorescences that emerged from below the fourth node was different among treatments: control (1.2%), GA_3 (8.7%), BA (18.2%), and BA+GA_3 (31.3%) (Yonenda and Momose, 1990).

Kim et al. (2000) studied the effects of two foliar spray applications of BA (100, 200, or 400 $mg \cdot L^{-1}$) or BA+GA_3 (100 $mg \cdot L^{-1}$ or 200 $mg \cdot L^{-1}$ of each) on the flowering of *Doritaenopsis* Happy Valentine (*Phal.* Otohime × *Dtps.* Odoriko). The first treatment application was made at the onset of cool temperature exposure (23/18 °C) and the second application followed 10 days later. The average number of inflorescences per plant significantly increased by 0.2 with application of BA at 200 or 400 $mg \cdot L^{-1}$

compared to untreated plants. As the application rate of BA increased from 100 to 400 $mg \cdot L^{-1}$, the length of inflorescences decreased by 2 to 7 cm. The number and length of inflorescences did not differ significantly between treatments with BA+GA_3 and untreated plants. Application of either BA (400 $mg \cdot L^{-1}$) or BA+GA_3 (100 $mg \cdot L^{-1}$ or 200 $mg \cdot L^{-1}$ of each), resulted in 5 to 13% of plants with malformed inflorescences at emergence and 3 to 7% of plants with blasted flower buds (Kim et al, 2000).

These investigations suggest that inflorescence initiation in *Phalaenopsis* is influenced by endogenous cytokinins. Application of exogenous cytokinins (e.g., BA) during low temperature exposure may hasten inflorescence emergence, increase inflorescence number and decrease inflorescence length. However, the application of BA at higher rates (400 $mg \cdot L^{-1}$), or in combination with GA_3, may result in undesirable effects on flower morphology and appearance. Further research is needed to determine the optimum rate of BA and the frequency of application required to increase inflorescence number without compromising flower quality.

Ethylene

To our knowledge, only one study has been published on the effects of ethylene application during inflorescence induction of *Doritaenopsis*. Kim et al. (2000) applied two foliar sprays of ethephon (100, 200, or 400 $mg \cdot L^{-1}$) on *Doritaenopsis* Happy Valentine during cool temperature exposure (23/18 °C). The application of ethephon did not influence the number of inflorescences, diameter and length of inflorescences, or number of flowers. However, all rates of application induced basal leaf abscission and at 400 $mg \cdot L^{-1}$, flower buds also abscised.

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Gibberellins

Endogenous gibberellins (GA) could increase during inflorescence induction and flower development in *Phalaenopsis* (Chen et al., 1994, 1997; Kubota et al., 1997; Su et al., 2001b). Chen et al. (1994) reported that an injection of 40 μg of GA_3 overcame the inhibition of flowering of *Phalaenopsis amabilis* when plants with 8-cm inflorescences were transferred to a high temperature regimen (30/25 °C, day/night). Plants treated with GA_3 and grown at the high temperature or exposed to a standard induction temperature (25/20 °C) had significantly greater concentrations of sucrose, glucose, and fructose in inflorescences compared to untreated plants grown at 30/25 °C. Gibberellin A_3 may function by stimulating the translocation of assimilates from source leaves to the apex of the inflorescence, where they are required for flower development (Chen et al., 1994). These results suggest that spraying *Phalaenopsis* with a growth retardant that inhibits the GA biosynthesis pathway or the translocation of GA could inhibit inflorescence induction.

A single application of GA_3 to *Phalaenopsis* grown in darkness does not substitute for the requirement of light during cool temperature inflorescence induction. When 5 ml of GA_3 (1 *m*M) was applied as a foliar spray to *Phalaenopsis* grown in darkness at 20 °C, inflorescence emergence was not observed within 36 days (Kubota et al., 1997). Injection of GA_3 (1, 3, or 5 μg/shoot) to plants with 2-cm to 3-cm long inflorescences grown at 30/25 °C, caused the deformation of flowers (i.e., with narrow sepals and petals) (Chen et al., 1997). These adverse effects were prevented by injection of BA into shoots at the same rate as GA_3, four days after the GA_3 treatment. Wang (1995a) made four weekly 50 μliter injections of GA_{4+7} (20,000 $mg \cdot L^{-1}$) into a leaf axil of

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vegetative plants grown during warm summer months, and inflorescence induction did not occur, although a severe phytotoxic response was reported.

Su et al. (2001b) examined changes in concentrations of endogenous GAs in inflorescences 2 to 3 cm long, following transfer to day/night treatments of: 1) 30/25 °C, 2) 30/25 °C with exogenous GA_3, or 3) 25/20 °C. Plants grown at 30/25 °C contained less biosynthetically active GA_1 and more inactive GA_8 compared to plants grown at 25/20 °C or treated with GA_3. The inhibition of inflorescence development at high temperature may be related to low levels of active GA_1. These results suggest that low temperature could reduce conversion of active GA_1 to inactive GA_8 and thus promote inflorescence induction (Su et al., 2001b).

Gibberellin Biosynthesis Inhibitors

To our knowledge, research on the effects GA biosynthesis inhibitors on growth and flowering of *Phalaenopsis* has been published once: seedlings that were dipped completely for five seconds in paclobutrazol (50, 100, 200, or 400 $mg \cdot L^{-1}$) or uniconazole (25, 50, 100, or 200 $mg \cdot L^{-1}$) before planting had a 27 to 160% decrease in inflorescence length below the first flower, compared to control plants (Wang and Hsu, 1994). Seedlings that were dipped in daminozide (2500, 5000, or 7500 $mg \cdot L^{-1}$) were delayed in flowering by 5 to 13 days, whereas paclobutrazol and uniconazole dips had no effect on time to flower. The delay in flowering of *Phalaenopsis* with daminozide may be because this compound is an acyclohexanedione. Acyclohexanediones function by interfering with the later steps of GA biosynthesis, thereby inhibiting the conversion of inactive GA precursors into active GAs (e.g., $GA_{20} \rightarrow GA_1$ or $GA_1 \rightarrow GA_8$) (Rademacher, 2000). As

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previously stated, high levels of active GA_1 may be important during stages of reproductive development in *Phalaenopsis*.

A single foliar spray application of paclobutrazol (250 or 500 $mg \cdot L^{-1}$) or uniconazole (100 or 200 $mg \cdot L^{-1}$) four weeks after inflorescence emergence, reduced inflorescence length by 3 to 6 cm (Wang and Hsu, 1994). Flower size, number of flowers and inflorescence diameter were not influenced by any chemical treatments in this study. To determine the effects of application timing on inflorescence length, a foliar application of paclobutrazol (250 $mg \cdot L^{-1}$) was made at: pre-emergence, emergence, or when the inflorescence was: 1.0, 2.5, 5.0, 7.5, or 10.0 cm in length. As the application of paclobutrazol was delayed, there was less inhibition of inflorescence elongation. For example, application of paclobutrazol at pre-emergence reduced inflorescence length by 66%, whereas application at 10.0 cm reduced inflorescence length by 20% (Wang and Hsu, 1994).

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Temperature influences many biochemical, metabolic, and physiological processes that occur during crop production, including photosynthesis, respiration, transpiration, germination, and plant development. Plant growth is defined as an irreversible increase in weight, height, or volume of a plant cell, tissue, organ, or whole plant, while development refers to a series of phenological stages that occur during the life cycle of an organism (Steininger and Pasian, 2002). Plant growth is primarily driven by light, whereas plant development is controlled by temperature. Plant responses to temperature are influenced by the average daily temperature and the relationship between the day temperature and night temperature.

Average Daily Temperature

The average daily temperature (ADT) is the mathematical average temperature during a 24-hour period. When the day and night temperature is constant, ADT can be calculated as:

$$\text{ADT} = [(\text{day temperature} \times \text{hours}\cdot\text{d}^{-1}) + (\text{night temperature} \times \text{hours}\cdot\text{d}^{-1})] \div 24 \qquad [1]$$

When day or night temperature is not constant, ADT can be calculated by measuring the air temperature with thermocouples every 10 seconds and recording hourly averages with a datalogger. Many plant responses are a function of the ADT, including the rate of leaf unfolding and the rate of progress towards flowering. The relationship

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between ADT and a rate of development is linear between the base and optimum temperature (Fig. 7).

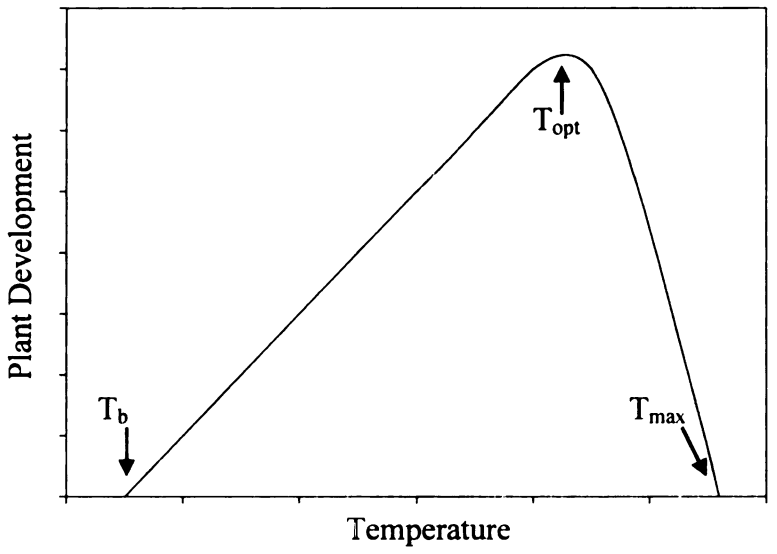

Figure 7. The effect of average daily temperature on rate of plant development.

The rate of development is calculated as the reciprocal of time for the completion of a developmental stage (e.g., time to germination or flowering). The function can be related linearly to ADT as:

$$1/\text{Days} = b_0 + b_1 \times \text{ADT} \qquad [2]$$

where rate (1/Days) is equal to the intercept (b_0) plus the product of the slope (b_1) and ADT.

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The base temperature (T_b) is the temperature at or below which the rate of progress towards a developmental stage is zero. T_b can be estimated as:

$$T_b = -b_0/b_1 \quad [3]$$

T_b can vary considerably among plant species. For example, T_b for days to flower in pansy (*Viola* ×*wittrockiana* Gams. 'Delta Primrose Blotch') was calculated to be −0.74 °C, while in tropical orchids *Zygopetalum* Redvale 'Fire Kiss' and *Phalaenopsis* Taisuco Smile, T_b for flower development from visible inflorescence to flower was 3.5 and 10.8 °C, respectively (Lopez and Runkle, 2004; Niu et al., 2000; Robinson, 2002).

The optimum temperature (T_{opt}) is the temperature at which the rate of progress towards a developmental event is maximal. All plants have an optimum temperature range for growth and development. For example, the optimum temperature for the rate of progress towards flowering in pansy and vinca (*Catharanthus roseus* L.) was calculated to be 21.7 °C and ≈35 °C, respectively (Adams et al., 1997b; Pietsch et al., 1995).

Models relating ADT and the rate of development are only valid if the following equation is true:

$$T_b \leq ADT \leq T_{opt} \quad [4]$$

When temperature exceeds T_{opt}, equation [2] becomes invalid because developmental rate begins to decrease and the response becomes nonlinear. The rate of development when temperature is $>T_{opt}$ can be described as a negative linear function of

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temperature, in which developmental rate decreases as temperature increases (Roberts and Summerfield, 1987). The decrease in plant development at high temperature results from a decline in normal protein synthesis, which is substituted by the synthesis of heat shock and stress proteins (Jones, 1992). In addition to biochemical changes, exposure to high temperature causes cellular membranes to weaken and the occurrence of ion leakage, manifested as tissue necrosis (Jones, 1992). At the maximum temperature (T_{max}), development ceases and plant death may occur.

The optimum temperature for progress towards a developmental event may not correlate with the optimal temperature for plant quality. For example, in vinca, the optimum temperature for the rate of progress towards flowering was calculated to be ≈35 °C, however flower size was greatest when plants were grown at 25 °C under the experimental light conditions (Pietsch et al., 1995). Similarly, in trailing *Petunia* Sylvana 'Malve', the rate of flowering was greatest when grown at 26 °C, but branch number at flowering was significantly greater at ≤18 °C (Adams et al., 1997a). Brøndum and Heins (1993) reported that T_{opt} for days from pinch to flower in *Dahlia pinnata* Cav. 'Royal Dahlietta Yellow' was 22.4 °C, and as ADT decreased from 22.4 to 10 °C, flower diameter and the number of flowers increased.

As stated previously, the time to reach a development event is primarily a function of ADT. The term "thermal time" is used to describe the amount of accumulated temperature that is required for the completion of a developmental event. The thermal time required to reach a developmental event θ_s at a given ADT can be calculated as:

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$$\theta_s = 1/ b_1 \quad [5]$$

where units of thermal time are degree-hour (°C·h) or degree-day (°C·d). Thermal time can be used by plant growers to predict the occurrence of a developmental event and can be calculated by subtracting T_b from the ADT and accumulating the amount of time, in units of °C·h or °C·d (Roberts and Summerfield, 1987; Steininger and Pasian, 2002).

Leaf Unfolding rate

Some floricultural crops produce a set number of leaves before the occurrence of a developmental event. The rate of progress towards an event can be quantified by tracking the number of leaves that unfold over a period of time (day or week). The rate of leaf unfolding per day is a function of the average 24-h plant temperature. Leaf unfolding rate has been modeled as a function of the average daily air or plant temperature for several commercially important potted flowering plants: African violet (*Saintpaulia ionantha* Wendl.) (Faust and Heins, 1993), begonia (*Begonia ×hiemalis* Fotsch.) (Karlsson, 1992), chrysanthemum (*Dendranthema grandiflora* Tzvelev.) (Karlsson et al., 1989), cyclamen (*Cyclamen persicum* Mill.) (Karlsson and Werner, 2001), hibiscus (*Hibiscus rosa-sinensis* L.) (Karlsson et al., 1991), Easter lily (*Lilium longiflorum* Thumb.) (Karlsson et al., 1988), and poinsettia (*Euphorbia pulcherrima* Willd. ex Klotz) (Berghage et al., 1990).

As previously stated, the response of leaf unfolding rate to ADT is linear between T_b and T_{opt}. As temperature increases above T_{opt}, the rate of leaf unfolding decreases and at temperature below T_b, leaf unfolding rate is zero. In African violet, T_b for leaf

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unfolding was ≈8.0 °C, T_{opt} was between 23.0 and 25.5 °C, and T_{max} was 30.8 °C (Faust and Heins, 1993). In Easter lily 'Nellie White', leaf unfolding rate increase linearly as temperature increased from 14 to 30 °C, and within this range, a 1 °C increase in ADT, accelerated unfolding by 0.094 leaves·d^{-1} (Karlsson et al., 1988). Berghage et al. (1990) reported that in *Poinsettia* 'Annette Hegg Dark Red', leaf unfolding rate after pinching increased from 0.13 to 0.25 leaves·d^{-1} as ADT increased from 15.3 to 27.8 °C. Another model was developed to predict the leaf unfolding rate in hibiscus: between 10 and 30 °C, an increase in 1 °C hastened leaf unfolding by 0.011 leaves·d^{-1} (Karlsson et al., 1991).

The influence of daily light integral (DLI) is often not included as a variable in plant development models. However, during certain conditions the DLI delivered to a crop can influence the rate of leaf unfolding. For example, a model was developed to predict the rate of leaf unfolding in African violet based on ADT and DLI: T_{opt} for the rate of leaf unfolding increased from 22.6 (0.18 leaves·d^{-1}) to 25.5 °C (0.27 leaves·d^{-1}) as the DLI increased from 1 to 10 mol·m^{-2}·d^{-1} (Faust and Heins, 1993).

Although the ambient air temperature is often used in plant development models, actual plant temperature is considered to be a more accurate measurement for predicting the rate of a developmental process. In a leaf unfolding rate model for African violet, using plant temperature to predict leaf development was more accurate than using air temperature. The average deviation between the predicted and observed leaf number was 63% higher when air temperature data was used compared to plant temperature data (Faust and Heins, 1993). Faust and Heins (1998) reported that the 24-h average shoot-tip temperature in vinca grown at 15, 20, or 25 °C was within 2 °C of the average air temperature, while the 24-h shoot-tip temperature of plants grown at 30 or 35 °C was

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always 4 to 6 °C below the average air temperature. The magnitude of deviation in shoot-tip temperature from air temperature is influenced by the amount of incoming solar radiation and the vapor-pressure deficit (VPD). The VPD is the difference between the vapor pressure of air when saturated with water and the actual vapor pressure (Jones, 1992). Vapor-pressure deficit affects the amount of plant transpiration during the day and night. For example, as VPD during the night increased from 0.5 to 3.0 kPa, shoot-tip temperature in vinca decreased by 1.3 °C (Faust and Heins, 1998). Actual plant temperature of African violet grown at a constant air temperature of 20 °C was almost 4 °C higher on a sunny day ($\leq$300 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and 1 to 3 °C lower on a cloudy day ($\leq$75 $\mu mol \cdot m^{-2} \cdot s^{-1}$). During the night, plant temperature was 2 to 5 °C cooler than air temperature.

Effects of Diurnal Temperature Fluctuations

The relationship between the day and night temperature can influence internode length, leaf and shoot orientation, chlorophyll content, lateral branching, and petiole elongation of plants (Erwin and Heins, 1995; Myster and Moe, 1995). The term DIF is used to describe the difference between the day temperature (DT) and night temperature (NT) and is calculated as:

$$DIF = DT - NT \qquad [5]$$

Stem Elongation

The effect of DIF on plant stem elongation has been studied on many common greenhouse crops, including begonia (Myster et al., 1997), campanula (*Campanula isophylla* Moretti) (Moe et al., 1991), chrysanthemum (Jacobson and Willits, 1998; Karlsson et al., 1989), fuchsia (*Fuchsia ×hybrida* hort. ex Sieb. and Voss) (Erwin and Heins, 1995; Maas and van Hattum, 1998), Easter lily (Erwin et al., 1989), poinsettia (Berghage, 1989; Berghage and Heins, 1991), snapdragon (*Antirrhinum majus* L.) and zinnia (*Zinnia violacea* Cav.) (Neily et al., 1997). The effects of DIF on stem elongation are not the same for all plant species. For example, in bulbous crops, such as tulip (*Tulipa ×hybrida* L.), daffodil (*Narcissus pseudonarcissus* L.), and hyacinth (*Hyacinthus orientalis* L.), DIF does not affect stem elongation (Erwin and Heins, 1995).

The night temperature was first suggested to influence stem elongation responses after Went (1944) observed different rates of stem elongation in tomato (*Lycopersicon esculentum* Mill.) at diurnally fluctuating temperatures compared to constant ones. The term "thermoperiodicity" was proposed after concluding the presence of two different "processes" during the day and night, where the dark process had a much lower temperature optimum compared to the light process (Went, 1944).

Stem elongation is promoted when the day temperature is warmer than night temperature (positive DIF). During the opposite environmental conditions, where day temperature is lower than the night temperature (negative DIF), stem elongation is inhibited. In Easter lily 'Nellie White', internode length increased by 382% as DIF increased from −16 to +16 °C (Erwin et al., 1989). Berghage and Heins (1991) reported that internode length of the second lateral shoot in *Poinsettia* 'Annette Hegg Dark Red'

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increased by approximately 2.5 cm as DIF increased from −10 to +10 °C. In snapdragon and zinnia, stem elongation during the vegetative stage increased by 38 and 13%, respectively, as DIF increased from −5 to +5 °C (Neily et al., 1997).

Stem elongation responses to DIF occur primarily from changes in cellular elongation rather than cellular division, and gibberellins (GAs) are likely involved (Grindal et al., 1998a, 1998b; Jenson et al., 1996; Myster and Moe, 1995). A reduction in the concentration of GA_1 in the plant shoot has been associated with a negative DIF in *Campanula isophylla* (Jenson et al., 1996) and pea (*Pisum sativum* L.) (Grindal et al., 1998a). Jenson et al. (1996) reported that in *Campanula isophylla* 'Hvit', the level of GA_1 was 90% lower in plants grown at negative DIF (15/21 °C, 12-h day/12-h night) compared to plants grown at positive DIF (21/15 °C). In pea plants grown at negative DIF (15.5/21.5 °C, 10-h day/14-h night), the amount of GA_1 was 60% lower than in plants grown at constant temperature (19.0 °C) (Grindal et al., 1998a). The reduction in GA_1 corresponded with a 47% decrease in stem length of plants grown at a negative DIF compared to a constant temperature.

The application of exogenous GAs can overcome the inhibition of stem elongation from a negative DIF. For example, internode elongation of begonia grown at 14/24 °C (12-h day/12-h night) and treated with GA_1 increased by 78% and 45% compared to untreated plants grown at 14/24 °C and 19/19 °C, respectively (Myster et al., 1997). Grindal et al. (1998b) reported that in pea 'Torsdag' grown at a negative DIF, endogenous bioactive GA_1 is converted into inactive GA_8 and application of exogenous GA_1 or GA_3 overcame the decreased stem elongation from a negative DIF.

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Commercial growers of greenhouse crops use DIF to manage plant height and as an alternative to the use of plant growth retarding chemicals. Mathematical models have been developed to describe the effects of DIF on stem elongation, which assist growers in managing and predicting stem elongation based upon environmental conditions. For example, Berghage and Heins (1991) constructed a model to predict how DIF influenced lateral shoot elongation after pinching of poinsettia. In chrysanthemum, internode elongation was modeled based on the effects of day and night temperature, photosynthetic photon flux, end-of-day red to far-red ratio, and the position of the internode on the stem (Jacobson and Willits, 1998).

Flowering Responses to Diurnal Temperature Fluctuations

The effects of day and night temperature on flower induction and development have been studied for many species including *Arabidopsis thaliana* (L.) Heynh. (Thingnaes et al., 2003), *Campanula isophylla* (Moe et al., 1991), chrysanthemum (Karlsson et al., 1989), *Dendrobium crumenatum* Sw. (Goh and Arditti, 1985; Went, 1944), fuchsia (Maas and van Hattum, 1998), Japaenese morning glory (*Pharbitis nil* Chois.) (Reese and Erwin, 1997), and poinsettia (Berghage, 1989). In some species, flowering is inhibited when the night temperature is excessively high. For example, flower initiation and development of poinsettia was delayed when night temperature was >25 °C (Berghage, 1989). Plants grown at a 29 °C night temperature and a day temperature between 14 and 26 °C initiated flower buds that did not develop to anthesis, while plants grown at a 29 °C day temperature and a night temperature between 14 and 26 °C developed normally (Berghage, 1989).

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Studies on *Campanula isophylla* and *Fuchsia ×hybrida* suggest that a negative DIF could slightly promote flower initiation and development (Myster and Moe, 1995). Moe et al. (1991) reported that in *Campanula isophylla* grown at a negative DIF (15/21 °C, 10-h day/14-h night), anthesis occurred 3 to 4 days earlier than plants grown at a positive DIF (21/15 °C). The total number of flowers and buds per plant was 24% greater in plants grown at a negative DIF compared to a positive DIF. However, these treatment effects may have resulted from differences in ADT between temperature regimens. Flower bud initiation and development was observed in fuchsia 'Dollar Princess' grown for 8 weeks under white or orange light at a −10 DIF (15/25 °C, 12-h day/12-h night), while plants grown at a +10 DIF (25/15 °C) did not initiate flower buds (Maas and van Hattum, 1998).

Research on several other species has reported the promotion of flowering by a negative DIF. For example, Reese and Erwin (1997) observed that in Japanese morning glory 'Violet', exposed to 16 day/night temperature combinations between 12 and 30 °C, flower induction percentage was greatest at 24/30 (day/night) and 30/30 °C. However, the duration of the day and night were not equal (8-h day/16-h night) and ADT was shown to significantly affect flower initiation. Furthermore, day and night temperature both had a significant effect on flowering percentage in this study (Reese and Erwin, 1997). The rate of flower development in three weakly photoperiodic cultivars of rice grown at 22/22, 26/22, 30/22, 22/26, or 22/30 °C (12-h day/12-h night) was hastened by ≤19.5 days at a negative DIF compared to a positive DIF (Yin et al., 1996). In comparison, the rate of flower development in several strongly photoperiodic cultivars, was hastened by ≤13.3 days at a positive DIF compared to a negative DIF.

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A negative DIF could promote flower induction in some species by increasing the availability of assimilates and respiration rate when night temperature is higher than day temperature (Yin et al., 1996). Alternatively, a negative DIF could decrease the amount of endogenous GAs (e.g., GA_1) that regulate flowering in some species (Grindal et al., 1998b; Maas and van Hattum, 1998; Myster and Moe, 1995). In pea grown at a negative DIF, it was suggested that there was a higher rate of 2β-hydroxylation of GA_1 (an active form) into GA_8 (an inactive form), which resulted in lower levels of GA_1 (Grindal et al., 1998b).

In contrast, high levels of GA_1 or GA_3 may inhibit floral initiation in some species such as fuchsia (Maas and van Hattum, 1998) and rose (*Rosa canina* L.) (Roberts et al., 1999). Wilkins (1985) reported that flower induction in the long-day plant fuchsia was inhibited by application of GA under long-day treatments, while application of GA biosynthesis inhibitors promoted flower initiation in plants grown under short days. This information is supported by King et al. (2000), in which application of either GA_1, GA_3, or GA_5 inhibited flowering in fuchsia 'Lord Byron' grown under long days. Similarly, in *Rosa canina* 'Félicité et Perpétue', flower initiation was not observed after the application of GA_1 or GA_3 to axillary shoots (Roberts et al., 1999).

Although studies have suggested the inhibition of flowering in a few species by specific GAs, more commonly long-day species show a positive correlation between increases in specific endogenous GAs and flower initiation, including *Arabidopsis* (Blázquez et al., 1998; Wilson et al., 1992), *Lolium temulentum* L. (King et al., 2003), and *Spinacia oleracea* L. (Zeevart and Gage, 1993). In a few species that require long days or vernalization for flowering, the application of GA can substitute for inductive

environmental conditions (Crozier et al., 2000). In the long-day grass *Lolium temulentum*, GA_5 is transported to the shoot apex under an inductive photoperiod, where concentrations of GA_5 increase by 100% (King et al., 2003). Evidence for GA as a floral stimulus in *Lolium temulentum* is further supported by the application of exogenous GA_5 and GA_6, which can replace the single long day required for floral initiation. Flowering in a majority of short-day species is not affected by the application of GAs (Michaels and Amasino, 1999).

Diurnal Temperature Fluctuation Requirement

Research on the requirement of a diurnal temperature fluctuation for flower induction has been limited (Goh and Arditti, 1985; Halevy, 1990; Powell et al., 1988; Went, 1944). During inflorescence development in *Dendrobium crumenatum*, flower buds develop and then become dormant (Goh and Arditti, 1985). The release from dormancy and subsequent flowering is inhibited at a constant or gradually increasing fluctuation in temperature and only occurs after a rapid decrease in temperature (Went, 1944). This response is supported by Goh and Arditti (1985) in which a 5 °C rapid drop in temperature or a gradual cooling for 24 hours resulted in simultaneous flowering nine days later. In nature, cool rain could create a drop in temperature that promotes flowering of *Dendrobium crumenatum*. Halevy (1990) reported that *Scilla autumnalis* L. and *Urginea maritima* L. Baker remained vegetative when grown at a constant temperature of 10, 15, or 20 °C, while those grown at a 20 °C day and 10 °C night flowered. The term "daily thermoperiodism", was used to describe the fluctuation between day and night temperature for these two geophytes.

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In *Cymbidium* orchids, a large positive diurnal fluctuation of 10 to 14 °C was suggested as a requirement for flower initiation (Powell et al., 1988). *Cymbidium* Astronaut 'Radjah' grown at 20/12, 26/12, or 26/18 °C (14-h day/10-h night) for 27 weeks developed a total of 3.3, 11.7, or 6.2 reproductive inflorescences per plant, respectively. The percentage of reproductive buds was highest (61.0%) at 26/12 °C compared to 20/12 °C (8.6%) and 26/18 °C (20.1%). Although flower initiation in *Cymbidium* Astronaut 'Radjah' was greatest at 26/12 °C, this study did not include treatments with a constant temperature for comparison and therefore it is unknown whether these results are because of differences in ADT or the effects of a diurnal temperature fluctuation.

A diurnal temperature fluctuation also controls seed germination in some species. In *Aristida armata* Henrard, germination was promoted at a positive fluctuating day and night temperature compared to a constant temperature (Brown, 1987). For example, the maximum germination percentage was 80% at a constant 20 °C, and ≥ 92.2% when the ADT was 20 °C, but with a ≥ 5 °C +DIF. Positive fluctuating temperature treatments with the highest germination percentages had slower rates of germination compared with constant temperature treatments. The average time to reach 80% germination when the ADT was 17.5, 20.0, or 22.5 °C was ≤ 1.1 days longer at positive fluctuating temperatures than at constant temperatures.

The Role of Day and Night Temperature

The rate of plant development is a function of the ADT (assuming $T_b \leq ADT \leq T_{opt}$) and the effects of day and night temperature are assumed to be equal (Karlsson et

al., 1988; Roberts and Summerfield, 1987; Steininger and Pasian, 2002). However, it has been suggested that the transition from vegetative to reproductive growth for some species is determined specifically by the night temperature (Berghage, 1989; Camus and Went, 1952; Roberts, 1943; Thingnaes et al., 2003; Went, 1944). Unfortunately, in many of the studies that have reported the role of night temperature in controlling the flowering response, the actual plant temperature was not recorded and the environmental conditions may not have been sufficiently controlled to provide confidence in the results. A large deviation between air temperature and plant temperature can exist during greenhouse experiments, affecting the interpretation of data. Furthermore, during these diurnal temperature fluctuation studies in controlled environments, the duration of the day and night may not have been equal (e.g., 8-h day/16-h night). As a result, many of the observations and conclusions from these studies could be related to differences in the ADT between treatments and not the specific affect of a negative or positive diurnal fluctuation.

The role of night temperature in flowering was first suggested by Roberts (1943) after observing that flower initiation was inhibited in several plant species when the day was cool (13 °C) and night was warm (24 °C) compared to treatments with reversed temperature setpoints. (The duration of the day and night was not provided in this study). Camus and Went (1952) observed similar results in tobacco (*Nicotiana tabacum* L.) and concluded that temperature during the dark period controlled stem length, leaf number, leaf shape and color, flowering time, and final fresh weight in this species. However, at least some of their conclusions could be attributed to differences in ADT among treatments.

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Thingnaes et al. (2003) reported that time to flower in *Arabidopsis thaliana*, ecotype Landsberg *erecta* (Ler), was significantly affected more by night temperature than day temperature. However, in this study there was a significant interaction of day × night temperature and DIF × ADT on flowering time, which challenges the conclusion that for this *Arabidopsis* ecotype, night temperature controls flowering time more than day temperature.

The rate of progress towards flowering in 24 cultivars of rice was compared in plants grown at five constant temperatures (22, 24, 26, 28, or 32 °C) and four diurnally fluctuating temperatures (26/22, 22/26, 30/22, or 22/30 °C; 12-h day/12-h night) (Yin et al., 1996). The effects of day and night temperature on flower development in rice were reported to be different. For example, in comparing treatments with a similar ADT, the predicted and observed days to flower deviated. When the data was analyzed using a nonlinear model, which separated the effects of the day and night temperature, T_{opt} during the day was 2 to 4 °C higher than T_{opt} during the night (Yin et al., 1996). In some cultivars used in this study, there was an interaction between day and night temperature on flowering, which may confound interpretation of these results.

Lepage et al. (1984) suggested that day and night temperature could have different effects on plant development as plants advance through developmental stages. In chrysanthemum, there was a significant correlation between the ADT and the number of days to visible flower bud, but during flower development, developmental rate was controlled more by the day than night temperature. There is likely an interaction of day temperature and irradiance during flower development, which was not considered in this

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study. Furthermore, the actual plant temperature was not recorded during this experiment.

Conclusion

In conclusion, these studies (Camus and Went, 1952; Lepage et al., 1984; Roberts, 1943; Thingnaes et al., 2003; Went, 1944; Yin et al., 1996) suggest that in some plant species, responses to temperature may not only be a function of the ADT, but also an interaction between the day and night temperature. Separating the specific effects of the day temperature or night temperature and thermoperiod may be further complicated by other environmental interactions (Roberts and Summerfield, 1987). For example, light quality, irradiance, and photoperiod have been reported to interact with diurnal temperature fluctuations to affect stem elongation in many floriculture crops (Erwin and Heins, 1995). Similar interactions may also exist when studying the effects of day and night temperature on flower induction and development.

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SECTION II

TEMPERATURE DURING THE DAY, BUT NOT DURING THE NIGHT, CONTROLS FLOWERING OF TWO PHALAENOPSIS ORCHID HYBRIDS

Temperature During the Day, But Not During the Night, Controls Flowering of Two *Phalaenopsis* Orchid Hybrids

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Introduction

Orchids are currently the second most valuable potted crop in the United States with a total reported wholesale value of $127.6 million in 2004 (U.S. Department of Agriculture, 2005). Among all of the orchid genera sold within the United States, the genus *Phalaenopsis* comprises a large percentage (85 to 90%) of the potted orchid sales (Nash, 2003) because of their ease of scheduling to meet specific market dates, high wholesale value, and long postharvest life. In The Netherlands, *Phalaenopsis* were the most valuable potted plant at Dutch flower auctions in 2004, trading 23.8 million plants valued at €109.7 million (VBN, 2005). Taiwan currently has the largest number of *Phalaenopsis* breeders and young plant growers with approximately 89 hectares in production, producing 36 million plants in 2002 with a wholesale value of $51 million (Fenton, 2004; Wang, 2004a).

During commercial production of *Phalaenopsis*, plants are often grown at a temperature of ≥28 °C to inhibit flowering and maintain vegetative growth (Chen et al., 1994; Sakanishi et al., 1980). The ability to inhibit reproductive development is important for the production of flowering plants because it allows a crop to be accurately scheduled for specific market dates. In addition, plants that flower before they have reached a marketable size are often of unacceptable quality (e.g., with few flowers and short inflorescences), and have little or no economic value.

To promote the transition from a vegetative phase to a reproductive phase in *Phalaenopsis*, Lee and Lin (1984, 1987) recommended a day/night greenhouse temperature of 25/20 or 20/15 °C. However, to our knowledge, there is no scientific

literature to support the suggested requirement of a day/night temperature fluctuation for inflorescence initiation and flowering in *Phalaenopsis*.

A diurnal temperature fluctuation has been reported to promote flowering in other plant species. For example, Halevy (1990) reported that *Scilla autumnalis* L. and *Urginea maritima* L. Baker remained vegetative when grown at a constant temperature of 10, 15, or 20 °C, while those grown at 20/10 °C day/night flowered. In *Cymbidium* orchids, a large positive diurnal fluctuation of 10 to 14 °C was suggested as a requirement for flower initiation (Powell et al., 1988). *Cymbidium* Astronaut 'Radjah' grown at 20/12, 26/12, or 26/18 °C (14-h day/10-h night) for 27 weeks developed a total of 3.3, 11.7, or 6.2 reproductive inflorescences per plant, respectively (Powell et al., 1988).

In *Phalaenopsis*, a positive day/night temperature fluctuation has been shown to increase the amount daily CO_2 uptake compared to constant temperatures with a similar average daily temperature (ADT) (Lootens and Heursel, 1998; Ota et al., 1991). Lootens and Heursel (1998) reported that daily CO_2 uptake in two *Phalaenopsis* hybrids was 14% to 21% greater at 20/15 °C than at 20/20, 25/20, or 25/25 °C. A significant day/night temperature effect also existed, in which treatments with a +5 °C day/night temperature fluctuation had a 5% to 21% greater CO_2 uptake than treatments with no temperature fluctuation. These results suggest that during inflorescence induction of *Phalaenopsis*, a diurnal temperature fluctuation could promote flowering by increasing photosynthesis.

The objectives of this study were: 1) to determine if a day/night temperature fluctuation is required for flowering and 2) to quantify how day and night temperatures influence inflorescence initiation and flowering of two *Phalaenopsis* hybrids.

Materials and Methods

Plant Material

In July 2003, mericlones of *Phalaenopsis* Brother Goldsmith '720' and *Phalaenopsis* Miva Smartissimo × Canberra '450' were transplanted into 10-cm pots in media containing 75% fine-grade Douglas fir bark,15% medium-grade perlite, and 10% sphagnum peat (by volume) and grown in a commercial greenhouse (Nurserymen's Exchange, Inc., Half Moon Bay, Calif.). Plants were grown at 26 °C under a natural photoperiod (lat. 37 °N) and a maximum photosynthetic photon flux (*PPF*) of 280 $\mu mol \cdot m^{-2} \cdot s^{-1}$. On 22 Sept. 2003, 240 plants were received in East Lansing, Mich., and were subsequently grown in a glass-glazed greenhouse at a constant temperature of 29 °C to inhibit flowering. The photoperiod was a constant 16 h (0600 to 2200 HR) consisting of natural daylengths (lat. 42 °N) with day-extension lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 20 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height [as measured with a line quantum sensor (Apogee Instruments, Inc., Logan, Utah)]. Light transmission was reduced using woven shade curtains (OLS 50; Ludvig Svensson, Charlotte, N.C.) and whitewash applied to the greenhouse glazing so that the maximum *PPF* at plant height was 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. A summary of plant material history is provided in Table 1. The average leaf span of the plant material at the beginning of the experiment was 25 to 30 cm. Leaf span was measured by extending the longest opposing leaves to a horizontal position and then measuring the length from one leaf tip to the opposite leaf tip.

Plant Culture

Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (Greencare Fertilizers, Chicago, Ill.). In Year 2, all plants were transplanted into 15-cm pots and grown in media consisting of 33% medium-grade Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] bark (Rexius Forest By-Products Inc., Eugene, Ore.), 45% medium-grade chopped coconut (*Coco nucifera* L.) coir (Millenniumsoils Coir, St. Catharines, Ont.), 11% long fiber Canadian sphagnum peat (Mosser Lee Co., Millston, Wis.), and 11% coarse-grade perlite (OFE Intl. Inc., Miami, Fla.) (by volume).

Temperature Treatments

Ten plants of each *Phalaenopsis* hybrid were placed in each of twelve glass greenhouse sections with constant temperature setpoints of 14, 17, 20, 23, 26, or 29 °C, or fluctuating day/night (12 h/12 h) temperature setpoints of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. Temperature setpoints were maintained by an environmental computer that controlled roof vents, exhaust fans, evaporative cooling, and heating as needed. The photoperiod was maintained at 12 h by pulling opaque black cloth from 1700 to 0800 HR and extended with light from incandescent lamps (2 to 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height). The photoperiod and skotoperiod paralleled the day and night temperature setpoints, respectively. A vapor pressure deficit (VPD) of 0.9 kPa was maintained at each temperature treatment by the injection of water vapor. Light transmission through the greenhouse was reduced as previously described. The average daily light integral

(DLI) per four week period during the experiment was between 2.4 and 4.4 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 2).

Air temperature was measured in each greenhouse section by aspirated thermocouples (0.127-mm type E) every 10 s and hourly averages were recorded by a CR-10 datalogger (Campbell Scientific, Logan, Utah). Temperature control during the experiment was within ±2.0 °C of the greenhouse temperature setpoints for all treatments in both years (Table 3).

The experiment was replicated in time beginning on 1 Dec. 2003 (Year 1) and on 26 Oct. 2004 (Year 2). In each year, plants were assigned randomly to each of the temperature treatments and grown for 20 weeks. After completion of the first replication until the beginning of the second replication, plants were transferred to a common glass-glazed greenhouse with a constant temperature setpoint of 29 °C to inhibit flowering. During that period, the photoperiod was a constant 16 h (0600 to 2200 HR) consisting of natural daylengths with day-extension lighting provided by HPS lamps delivering a *PPF* of 20 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. The maximum *PPF* through the greenhouse was maintained at 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ by using woven shade curtains and external whitewash.

Data Collection

The date the first inflorescence was visible without dissection (<0.5 cm) and the date that the first flower opened was recorded for each plant. Days to visible inflorescence (VI), days from VI to flowering, days to flowering, VI and flowering percentages were calculated for each treatment. The total number of visible inflorescences and the number of flower buds and flowers on the first VI were recorded

for each plant. On the date of flowering, inflorescence length from emergence to the first flower and from the first flower to the inflorescence tip was measured and the total inflorescence length was calculated. Plants without open flowers within 20 weeks of the onset of treatments were considered non-flowering. The duration of the experiment was 20 weeks because an inflorescence usually emerges after 3 to 5 weeks following exposure to an inductive temperature <25 °C (Sakanishi et al., 1980).

Data Analysis

A completely randomized block design was used during each year. Data were analyzed using SAS (SAS Institute, Cary, N.C.) mixed model procedure (PROC MIXED) and pairwise comparisons between treatments were performed using Tukey's honest significant difference (HSD) test. Arcsine square root transformation was performed on percentage data before analysis.

Results

Visible Inflorescence and Flowering Percentage

Temperature significantly influenced the percentage of plants that initiated a VI and flowered (Fig. 1). After 20 weeks, ≥80% of plants of both *Phalaenopsis* hybrids had VI when grown at 14, 17, 20, 23, 20/14 or 23/17 °C. None of the plants were reproductive within 20 weeks when grown at temperature setpoints of 29, 29/17 or 29/23 °C. In *Phalaenopsis* Miva Smartissimo × Canberra, a subset of the populations were reproductive at temperature treatments of 26, 26/14, and 26/20 °C, with VI percentages of 10, 55, and 75%, respectively. In contrast, none of the Brother Goldsmith '720' plants

had initiated an inflorescence within 20 weeks at temperature treatments of 26, 26/14, and 26/20 °C, respectively. All of the *Phalaenopsis* Miva Smartissimo × Canberra grown at 20, 23, and 23/17 °C flowered within 20 weeks, whereas in *Phalaenopsis* Brother Goldsmith, 85% and 75% had flowered when grown at 20 and 23 °C, respectively (Table 4).

Day and night temperature had different effects on promoting flowering of both *Phalaenopsis* hybrids in our study: day temperature was highly significant ($P \leq 0.001$), but night temperature was not significant (Table 5). There was a significant difference in VI and flowering percentages among some temperature treatments with a similar ADT (Table 6). For example, in *Phalaenopsis* Miva Smartissimo × Canberra grown at 23, 26/20, or 29/17 °C, VI percentage was 100, 75, and 0%, respectively. Similarly, VI percentage of *Phalaenopsis* Brother Goldsmith at 23, 26/20, and 29/17 °C was 90, 0, and 0%, respectively.

Time to Visible Inflorescence and Flower

Time to VI was not significantly different in plants grown at constant or fluctuating day/night temperature treatments with a similar ADT of 17 °C. For example, time to VI was statistically similar when grown at 17 or 20/14 °C in both *Phalaenopsis* hybrids and ranged from 32 to 45 d. The time required to reach VI was greatest in *Phalaenopsis* Miva Smartissimo × Canberra and *Phalaenopsis* Brother Goldsmith when grown at temperature setpoints of 14 or 26/14 °C, during both years (Table 7). There were no significant differences in time to VI for either hybrid grown at temperature treatments of 17, 20, and 23 °C and time to VI ranged from 23 to 39 d.

Among the treatments with flowering percentages ≥30% after 20 weeks, time from VI to anthesis and total time to anthesis for both hybrids generally decreased as ADT increased (Table 8). *Phalaenopsis* Miva Smartissimo × Canberra and *Phalaenopsis* Brother Goldsmith plants grown at 23 °C had the shortest total time to anthesis, requiring on average 102 and 111 d, respectively.

Number of Inflorescences and Flower Buds and Inflorescence Length

The number of inflorescences per plant in both *Phalaenopsis* hybrids generally increased as ADT decreased (Table 7). For example, *Phalaenopsis* Miva Smartissimo × Canberra and *Phalaenopsis* Brother Goldsmith had the greatest number of inflorescences per plant when grown at 14 °C (1.5 and 1.3, respectively). In addition, the number of flower buds on the first VI was generally greater at the cooler temperatures than at the warmer temperatures. For example, average flower bud number of *Phalaenopsis* Miva Smartissimo × Canberra grown at 26/14 °C was 2.2, while plants grown at 14 °C had on average 6.2. In *Phalaenopsis* Brother Goldsmith '720', flower bud number was greatest (5.7 or 5.8) in plants grown at 14, 17, and 20/14 °C. There were no significant differences in the number of flower buds among constant and cool day/night fluctuating treatments <26 °C with a similar ADT for both *Phalaenopsis* hybrids. The total inflorescence length at anthesis was not significantly influenced by temperature in both *Phalaenopsis* hybrids (Table 8).

Mesophyll Cell Collapse

In Year 1, after 11 weeks at the various temperature treatments, symptoms of mesophyll cell collapse (e.g., tan irregular depressions on the adaxial leaf surface) on *Phalaenopsis* Miva Smartissimo × Canberra were observed at day/night temperatures of 20/14, 26/14, 26/20, and 29/17 °C. Mesophyll cell collapse was not observed in treatments with a constant temperature setpoint or in *Phalaenopsis* Brother Goldsmith at any of the temperature treatments.

Discussion

Our results indicate that *Phalaenopsis* does not require a day/night temperature fluctuation for inflorescence initiation, at least in these two *Phalaenopsis* hybrids. Inflorescence initiation occurred in both hybrids at constant temperatures of 14, 17, 20, and 23 °C. The inhibition of inflorescence initiation in plants grown at a constant temperature of 29 °C supports previous results by Sakanishi et al. (1980) in which flowering was inhibited in *Phalaenopsis* grown at 28 °C. In *Phalaenopsis* Brother Goldsmith, none of the temperature treatments induced 100% VI during Year 1. We postulate that this may be at least partially attributed to plant immaturity in Year 1 for this hybrid. Wang and Lee (1994) reported that smaller plants that have not reached vegetative maturity may require cooler temperatures or longer exposure to initiate inflorescences than larger, more mature plants.

The difference in VI percentage among treatments with a similar ADT indicates that inflorescence initiation in *Phalaenopsis* is primarily controlled by the day temperature, and not the ADT. Wang (2004b) reported that the 'Lava Glow' clone of the

hybrid *Doritaenopsis* (*Phalaenopsis* Buddha's Treasure × *Doritis pulcherrima*) grown for 29 to 36 weeks at 25/20, 20/25, 25/15, or 15/25 °C (12-h day/12-h night) had flowering percentages of 27, 93, 0, and 100%, respectively. These results collectively suggest that the day and night temperature have separate effects on flowering of *Phalaenopsis* and that the day temperature controls flowering. When day temperature is >26 °C, inflorescence initiation is inhibited, while at day temperatures <26 °C, inflorescence initiation is promoted.

At temperature treatments of 26/14 and 26/20 °C, inflorescence initiation occurred in 55% or 75% of *Phalaenopsis* Miva Smartissimo × Canberra plants, but did not occur in the hybrid Brother Goldsmith. The difference in inflorescence initiation responses between these two *Phalaenopsis* hybrids could possibly be attributed to a difference in sensitivity to temperature from their varied genetic backgrounds. The predominate species that are in the background of *Phalaenopsis* Miva Smartissimo × Canberra are *Phalaenopsis amabilis* (L.) Blume, *Phalaenopsis aphrodite* Rchb.f., and *Phalaenopsis schilleriana* Rchb.f., while the predominate species in the background of *Phalaenopsis* Brother Goldsmith include *Phalaenopsis stuartiana* Rchb.f. and *Phalaenopsis lueddemanniana* Rchb.f. (Wildcatt, 2004). The upper temperature limit for inflorescence initiation in *Phalaenopsis* Brother Goldsmith could be lower than that of Miva Smartissimo × Canberra. As suggested previously, the more mature Miva Smartissimo × Canberra hybrid may have been less sensitive to temperature than Brother Goldsmith.

The number of inflorescences per plant and flower buds on the first VI was greatest for both hybrids when grown at the coolest temperatures (e.g., 14, 17, or 20/14

°C). Lee and Lin (1984) observed a similar cool temperature response in *Phalaenopsis* Dos Pueblos × Juanit, in which plants grown at 20/15 or 25/20 °C had on average 2.2 and 1.2 inflorescences per plant, respectively. In another *Phalaenopsis* hybrid (*Phal.* Taisuco Moonriver × *Phal. equestris* 'Alba'), the number of flower buds on the main axis of the first VI generally increased from 4.6 to 9.8 as the constant average daily forcing temperature decreased from 25.5 to 14.3 °C (Robinson, 2002).

Temperature had a significant effect on total time to anthesis of *Phalaenopsis* in our study. Robinson (2002) reported that following inflorescence emergence, there is a linear relationship between temperature and rate of development towards visible bud and anthesis. For example in *Phalaenopsis* Taisuco Smile, the average time from inflorescence emergence to anthesis decreased from 190 days to 52 days as constant ADT increased from 14.9 to 25.7 °C.

There was a significant temperature × year interaction for several observations in our study. The difference between years is probably a result of plant maturity; the same plant material was used in each year and there was an increase in the average leaf span and number of leaves in Year 2. The average days to VI and the number of flower buds per plant were also different between years and may be related to plant maturity. In all treatments except 14 °C, days to VI decreased and the number of flower buds increased between Years 1 and 2.

A major economic challenge for the production of *Phalaenopsis* orchids in temperate climates is the high cost of energy for heating a greenhouse to maintain vegetative growth. Energy is typically the second largest greenhouse production cost for growers located in temperate climates (Bartok, 2001). In our study, inflorescence

initiation was inhibited in treatments with a high day temperature setpoint (e.g., 29 °C), even when the night temperature setpoint was cool (e.g., 17 °C). Sakanishi et al. (1980) investigated the effects of increasing the duration of high temperature exposure when the average night temperature was 20 °C and reported that inflorescence emergence was inhibited when plants were exposed to ≥12 hours at a temperature of 28 °C each day. These results suggest that during *Phalaenopsis* production, a cool night temperature setpoint could be utilized to inhibit flowering if the day temperature setpoint is sufficiently warm (≥28 °C). This production strategy could have a significant economic impact for commercial growers because approximately 80% of the energy for heating a greenhouse is required at night (Bartok, 2001). Further research is necessary to determine the magnitude of high temperature and minimum daily exposure to high temperature to inhibit flowering.

The symptoms of mesophyll cell collapse on *Phalaenopsis* Miva Smartissimo × Canberra at several of the fluctuating temperature treatments may be a result of very low inlet air temperature when the day ended and the night temperature began. At the onset of the skotoperiod, cold air (often ≤0 °C) was actively drawn into the greenhouse sections until the cooler night temperature setpoint was achieved. Symptoms of mesophyll cell collapse were not observed on *Phalaenopsis* Brother Goldsmith, which could be attributed to the genetic background of this hybrid. Mesophyll cell collapse was previously observed on *Phalaenopsis* after plants were exposed to a constant temperature of 2, 4, or 7 °C for 1 hour or more in darkness (McConnell and Sheehan, 1978). The reported symptoms were dark brown, pitted areas on upper leaf surfaces, which were similar to our own observations with *Phalaenopsis* Miva Smartissimo × Canberra.

Orchids exposed to low water temperature (2 to 8 °C) can also result in symptoms of mesophyll cell collapse (Jones, 2004). However, the temperature of the irrigation water used in our study was ≈20 °C.

In conclusion, a day/night fluctuation in temperature is not required for inflorescence initiation in these two *Phalaenopsis* hybrids. Although time to flower is shortest at 23 °C, the number of inflorescences and flower buds per plant was greater at cooler temperatures. In *Phalaenopsis*, daily CO_2 uptake was reported to increase at a day/night temperature fluctuation compared to constant temperatures (Lootens and Heursel, 1998). However in our study, there was no advantage of a day/night temperature fluctuation for flowering. For example, a cool diurnal temperature fluctuation (e.g., 20/14 or 23/17 °C) did not reduce time to flower or enhance plant quality (e.g., number of inflorescences or flower buds). Flowering responses were different among some treatments with a similar ADT, suggesting that the day and night temperature have separate effects on inflorescence induction. These results also indicate that a high day temperature can inhibit inflorescence initiation and flowering even when the night temperature is conducive for reproductive development. This research information could provide commercial orchid growers with new strategies to reduce production costs and thus increase profitability.

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Table 1. Summary of production dates, container sizes, and greenhouse environmental conditions for *Phalaenopsis* Brother Goldsmith '720' and *Phalaenopsis* Miva Smartissimo × Canberra '450' preceding and during experimentation.

	Phalaenopsis hybid	
Description	Brother Goldsmith '720'	Miva Smartissimo × Canberra '450'
Received bare-root at Nurserymen's Exchange, Inc. (Half Moon Bay, Calif.)	August 2003	July 2003
Transplanted into 10-cm pots[z] Temperature: 26 °C Photoperiod: Natural daylength (lat. 37 °N) *PPF*[y]: ≤280 $\mu mol \cdot m^{-2} \cdot s^{-1}$	7 August 2003	10 July 2003
Received at Michigan State University (East Lansing, Mich.) Temperature: 29 °C Photoperiod: 16 h (0600 to 2200 HR)[x] *PPF*: ≤150 $\mu mol \cdot m^{-2} \cdot s^{-1}$	22 September 2003	
Transferred to temperature treatments for 20 weeks	1 December 2003	
Transferred from treatments to common greenhouse Temperature: 29 °C Photoperiod: 16 h (0600 to 2200 HR) *PPF*: ≤150 $\mu mol \cdot m^{-2} \cdot s^{-1}$	19 April 2004	
Transplanted into 15-cm pots[w]	July 2004	
Transferred to temperature treatments for 20 weeks	26 October 2004	
Termination of experiment	15 March 2005	

[z]Media consisting of 75% fine-grade Douglas fir bark, 15% medium-grade perlite, and 10% sphagnum peat (by volume).
[y]Photosynthetic photon flux.
[x]Natural daylengths (lat. 42 °N) with day-extension lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 20 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height.
[w]Media consisting of 33% medium-grade fir bark, 45% medium-grade chopped coconut coir, 11% long fiber Canadian sphagnum peat, and 11% coarse-grade perlite (by volume).

Table 2. Average daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$) at plant level per 4-week period during experiment for Years 1 and 2.

	4-week period				
Year	1	2	3	4	5
2003 to 2004[z]	2.4	2.6	3.5	3.8	4.1
2004 to 2005[y]	2.7	2.5	2.4	3.1	4.4

[z]Experimental period from 1 December 2003 to 19 April 2004.
[y]Experimental period from 26 October 2004 to 15 March 2005.

Table 3. Actual average air temperatures of each temperature treatment in Years 1 and 2.

Temperature setpoint (°C)	Actual temperature (°C)	
	Year 1	Year 2
14/14[z]	14.5/14.3	14.1/13.5
17/17	17.4/17.4	17.2/16.6
20/20	20.2/20.1	21.0/20.4
23/23	24.5/22.6	23.4/21.8
26/26	25.8/26.1	26.2/26.0
29/29	29.1/29.4	28.8/28.2
20/14	20.0/13.8	19.1/13.5
23/17	21.9/16.3	22.5/16.9
26/14	25.4/14.3	24.9/13.9
26/20	25.8/19.4	25.9/20.2
29/17	27.8/17.1	28.6/17.3
29/23	28.8/22.3	29.0/23.1

[z]12-h day/12-h night temperature.

Table 4. Flowering percentages for *Phalaenopsis* Miva Smartissimo × Canberra '450' and *Phalaenopsis* Brother Goldsmith '720' after 20 weeks at constant temperature setpoints of 14, 17, 20, 23, 26, or 29 °C, and fluctuating day/night temperature setpoints of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. Data for both years were pooled for analysis. Arcsine square root transformation was performed on data before analysis.

Temperature setpoint (°C)	Flowering (%)	
	Brother Goldsmith	Miva Smartissimo
14/14[z]	0	0
17/17	10	10
20/20	85	100
23/23	75	100
26/26	0	10
29/29	0	0
20/14	0	20
23/17	50	100
26/14	0	30
26/20	0	75
29/17	0	0
29/23	0	0
Significance		
Temperature	***	***

[z]12-h day/12-h night temperature.
*** Significant at $P \leq 0.001$.

Table 5. The effect of average daily temperature (ADT), average day temperature (DT), average night temperature (NT), and constant temperature (CT) on visible inflorescence (VI) percentage of *Phalaenopsis* Miva Smartissimo × Canberra '450' and *Phalaenopsis* Brother Goldsmith '720'. Arcsine square root transformation was performed on data before analysis.

Variable	ADT	DT	NT	CT
VI percentage				
Miva Smartissimo × Canberra '450'	***	***	NS	***
Brother Goldsmith '720'	**	***	NS	***

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

Table 6. Comparison of visible inflorescence percentage in treatments with a similar average daily temperature for *Phalaenopsis* Miva Smartissimo × Canberra '450' and *Phalaenopsis* Brother Goldsmith '720'. Arcsine square root transformation was performed on data before analysis.

Temperature setpoint (°C)	Visible inflorescence (%)	
	Miva Smartissimo	Brother Goldsmith
17/17[z]	100	95
20/14	100	95
Significance	NS	NS
20/20	100	85
23/17	100	80
26/14	55	0
Significance	**	***
23/23	100	90
26/20	75	0
29/17	0	0
Significance	***	***
26/26	10	0
29/23	0	0
Significance	NS	NS

[z]12-h day/12-h night temperature.

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

Table 7. Days to visible inflorescence (VI), number of flower buds on first VI, and number of inflorescences per plant for *Phalaenopsis* Miva Smartissimo × Canberra '450' and *Phalaenopsis* Brother Goldsmith '720' after 20 weeks in temperature treatments with ≥10% VI.

Temperature setpoint (°C)	Days to VI		No. of flower buds on first VI		No. of inflorescences per plant[y]
	Year 1	Year 2	Year 1	Year 2	
	Miva Smartissimo × Canberra '450'				
14/14[z]	52 b[x]	63 a	6.2 a	5.9 a	1.5 a
17/17	39 cd	32 bcd	4.0 bc	6.0 a	1.4 a
20/14	45 bc	38 bc	4.5 b	5.2 abc	1.1 b
20/20	34 d	23 d	4.2 bc	5.0 abc	1.0 b
23/17	37 cd	32 bcd	3.8 bc	5.4 ab	1.1 b
26/14	67 a	38 bc	2.2 d	4.3 bc	1.0 b
23/23	34 d	29 cd	3.9 bc	4.5 bc	1.0 b
26/20	53 b	40 b	3.2 cd	4.0 c	1.0 b
Significance					
Temperature	***	***	***	***	***
Year	***		***		NS
Temperature × Year	***		***		NS
	Brother Goldsmith '720'				
14/14	60 a[y]		5.8 a[y]		1.3 a
17/17	33 c		5.8 a		1.1 ab
20/14	40 bc		5.7 a		1.0 b
20/20	33 c		5.2 ab		1.0 b
23/17	43 b		4.5 b		1.0 b
23/23	36 bc		4.7 b		1.0 b
Significance					
Temperature	***		*		***
Year	NS		NS		NS
Temperature × Year	*		NS		NS

[z]12-h day/12-h night temperature.

[y]Data pooled for analysis.

[x]Mean separation within columns by Tukey's honest significant difference (HSD) test at $P \leq 0.05$.

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

Table 8. Days from visible inflorescence (VI) to flower, total days to flower, and total inflorescence length at flower for *Phalaenopsis* Miva Smartissimo × Canberra '450' and *Phalaenopsis* Brother Goldsmith '720' in temperature treatments with ≥30% flowering after 20 weeks.

Temperature setpoint (°C)	Days from VI to flower		Total days to flower		Total inflorescence length (cm)[y]
	Year 1	Year 2	Year 1	Year 2	
	Miva Smartissimo × Canberra '450'				
20/20[z]	80 b[x]	89 a	114 b	113 b	40 a
23/17	86 a	81 b	123 a	113 b	41 a
26/14	--[w]	87 ab	--	124 a	39 a
23/23	69 d	72 c	103 c	101 c	38 a
26/20	74 c	66 d	127 a	106 bc	41 a
Significance					
Temperature	***	***	***	***	NS
Year	NS		***		***
Temperature × Year	***		***		NS
	Brother Goldsmith '720'				
20/20	89 a	96 a	126 a[y]		26 a
23/17	90 a	--	127 a		30 a
23/23	73 b	87 b	111 b		29 a
Significance					
Temperature	***	*	***		NS
Year	***		***		NS
Temperature × Year	*		NS		NS

[z]12-h day/12-h night temperature.
[y]Data pooled for analysis.
[x]Mean separation within columns by Tukey's honest significant difference (HSD) test at $P \leq 0.05$.
[w]Not included in analysis.
[NS, *, ***]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

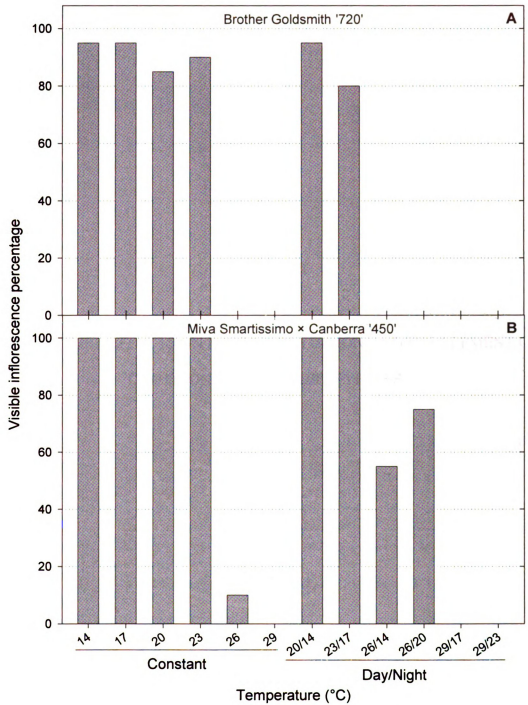

Figure 1. Visible inflorescence percentages for *Phalaenopsis* Brother Goldsmith '720' (A) and *Phalaenopsis* Miva Smartissimo × Canberra '450' (B) after 20 weeks at constant temperature setpoints 14, 17, 20, 23, 26, or 29 °C, and fluctuating day/night temperature setpoints of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. The day and night were 12 hours each. Data were pooled for Years 1 and 2.

SECTION III

TEMPERATURE EFFECTS ON FLOWER INITIATION AND DEVELPMENT OF TWO ODONTIODA ORCHID HYBRIDS

Temperature Effects on Flower Initiation and Development of Two *Odontioda* Orchid Hybrids

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Introduction

The production value of potted orchids in the United States has increased by 172% in the past decade, and they are now the second-most valuable potted flowering plant with a reported wholesale value of $127.6 million in 2004 (U.S. Department of Agriculture, 2005). In 2004, 17.2 million potted orchids were sold with an average wholesale unit value of $7.41 (U.S. Department of Agriculture, 2005). Among all of the orchid genera sold within the United States, the genus *Phalaenopsis* comprises a large percentage (85 to 90%) of the potted orchid sales (Nash, 2003).

The ability for commercial greenhouse growers to schedule orchids into flower during periods of high demand (e.g., holidays) requires knowledge of the environmental parameters that regulate flower induction. However, scientific research on growth and development of orchids has been limited to a small number of genera. Detailed commercial production information is only available for hybrids of the genus *Phalaenopsis* (Lee and Lin, 1984, 1987; Wang, 1995).

Odontioda orchids are intergeneric hybrids that are classified into the *Odontoglossum* alliance (Rittershausen and Rittershausen, 2003). These intergeneric hybrids were first created in the early 1800s by breeders in Europe that crossed two genera, *Odontoglossum* H.B.K. and *Cochlioda* Lindl. (Carpenter, 2000). The genus *Odontoglossum* is comprised of 175 species that are native to mountainous regions (1,500 to 3,500 m) of South America, while the genus *Cochlioda* is comprised of only five species that are native to the Andes Mountains (2,000 to 3,500 m) of Bolivia, Ecuador, and Peru (Pridgeon, 2000).

Odontioda are sympodial epiphytic orchids and produce green pseudobulbs that have an apical pair of long narrow leaves and a shorter pair of leaves that arise from the base of the pseudobulb (Figure 1A) (Rittershausen and Rittershausen, 2003). Similar to other sympodial orchid genera, inflorescence primordia are initiated in the axil of a leaf sheath at the base of a pseudobulb (Figure 1B) (Goh et al., 1982). *Odontioda* hybrids have been selected by breeders for their bright and showy flowers and are available in many color combinations and patterns (Rittershausen and Rittershausen, 2003). They are also appealing potted plants because of their compact growth habit (30 to 45 cm), erect-to-arching inflorescences, and long-lasting flowers (up to 30 days) (Carpenter, 2000; Rittershausen and Rittershausen, 2003).

Odontioda hybrids are generally considered among orchid hobbyists to perform best at night temperatures ranging from 7 to 13 °C and day temperatures between 24 to 27 °C (Miller, 1992; Rohrl, 2005). A diurnal temperature fluctuation has also been suggested to improve vigor and plant performance (Miller, 1992; Rohrl, 2005), although to our knowledge there is no scientific literature to support these observations. These cool growing temperatures suggest that *Odontioda* orchids could be an appealing crop to produce in temperate climates where energy for heating is a significant greenhouse production cost (Bartok, 2001). However, no scientific information is available on the environmental flowering requirements for *Odontioda* and thus, scheduling a crop to flower for specific market dates is not possible.

The objectives of this study were: 1) to determine how constant and fluctuating day and night temperatures influence flower initiation and 2) to quantify how temperature controls time from visible inflorescence to flowering in two *Odontioda* hybrids.

Materials and Methods

Plant Material

In June 2003, mericloned *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor' were transplanted into 10-cm pots in media containing 75% fine-grade Douglas fir bark,15% medium-grade perlite, and 10% sphagnum peat (by volume) and grown in a commercial greenhouse (Nurserymen's Exchange, Inc., Half Moon Bay, Calif.). Plants were grown at 24/18 °C (day/night) under a natural photoperiod (lat. 37 °N) and a maximum photosynthetic photon flux (*PPF*) of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. On 22 Sept. 2003, 240 plants were received in East Lansing, Mich., and were subsequently grown in a glass-glazed greenhouse at a constant temperature of 23 °C. The photoperiod was a constant 16 h (0600 to 2200 HR) consisting of natural daylengths (lat. 42 °N) with lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 25 to 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height [as measured with a line quantum sensor (Apogee Instruments, Inc., Logan, Utah)]. Light transmission was reduced using woven shade curtains (OLS 50; Ludvig Svensson, Charlotte, N.C.) and whitewash applied to the glazing so that the maximum *PPF* at plant height was 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. A summary of plant material history is in Table 1.

Plant Culture

Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (Greencare Fertilizers, Chicago, Ill.). In Year 2, all plants were transplanted into media consisting of 80% medium-grade Douglas fir

[*Pseudotsuga menziesii* (Mirb.) Franco] bark (Rexius Forest By-Products Inc., Eugene, Ore.), 10% long fiber Canadian sphagnum peat (Mosser Lee Co., Millston, Wis.), and 10% medium-grade perlite (Therm-O-Rock, Inc., New Eagle, Pa.) (by volume).

Temperature Treatments

Ten plants of each *Odontioda* hybrid were placed in each of twelve glass greenhouse sections with constant temperature setpoints of 14, 17, 20, 23, 26, or 29 °C, or fluctuating day/night (12 h/12 h) temperature setpoints of 20/14, 23/17, 26/14, 26/20, 29/17, or 29/23 °C. In Year 2, constant temperature setpoints of 26 and 29 °C and day/night temperature setpoints of 26/14, 26/20, 29/17, and 29/23 °C were not used because of heat stress observed at these temperatures in Year 1. Temperature setpoints were maintained by an environmental computer that controlled roof vents, exhaust fans, evaporative cooling, and heating as needed. The photoperiod was maintained at 12 h by pulling opaque black cloth from 1700 to 0800 HR and extended with light from incandescent lamps (2 to 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height). The photoperiod and skotoperiod paralleled the day and night temperature setpoints, respectively. A vapor pressure deficit (VPD) of 0.9 kPa was maintained at each temperature treatment by the injection of water vapor. Light transmission through the greenhouse was reduced as previously described. The average daily light integral (DLI) per four week period during the experiment was between 3.6 and 8.2 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 2).

Air temperature was measured in each greenhouse section by aspirated thermocouples (0.127-mm type E) every 10 s and hourly averages were recorded by a CR-10 datalogger (Campbell Scientific, Logan, Utah). Temperature control during the

experiment was within ±2.0 °C of the greenhouse temperature setpoints for all treatments in both years (Table 3).

The experiment was replicated in time beginning on 1 Dec. 2003 (Year 1) and on 26 Oct. 2004 (Year 2). In each year, plants were assigned randomly to each of the temperature treatments. After completion of the first replication on 19 April 2004 and until the beginning of the second replication, plants were transferred to a common glass-glazed greenhouse with a constant temperature setpoint of 23 °C. The photoperiod was a constant 16 h (0600 to 2200 HR) consisting of natural daylengths with day-extension lighting provided by HPS lamps delivering a *PPF* of 25 to 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. The maximum *PPF* through the greenhouse was maintained at 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as previously described. Plants that displayed symptoms of heat stress in Year 1 were not used in Year 2.

Data Collection

The date of first visible inflorescence (VI) without dissection (<0.3 cm) and the date that the first flower opened was recorded for each plant. Days to VI, days from VI to flower, days to flower, VI percentage and inflorescence abortion percentage were calculated for each treatment. The total number of visible inflorescences and the number of flower buds and flowers on the first VI were recorded for each plant. On the date of flowering, flower diameter (Year 2 only) and total inflorescence length from emergence to the tip of the inflorescence were measured. In Year 2, leaf length and pseudobulb diameter were measured at the beginning of the experiment and at flowering and the increase in pseudobulb diameter and leaf length were calculated. Pseudobulb diameter

was measured at the widest point of the pseudobulb from the outer edge of a basal leaf to the outer edge of the opposing leaf sheath using a digital caliper. Pseudobulb diameter and leaf length measurements for plants that did not have a VI were made after 31 weeks in each temperature. In both years, plants that did not have a VI after 20 weeks of the onset of treatments were considered not reproductive. In Year 2, the experimental period was 33 weeks in order to collect flowering data.

Data Analysis

A completely randomized block design was used during each year. Data were analyzed using SAS (SAS Institute, Cary, N.C.) mixed model procedure (PROC MIXED) and pairwise comparisons between treatments were performed using Tukey's honest significant difference (HSD) test. Visible inflorescence percentages were analyzed using generalized model procedure (PROC GENMOD) with a binomial distribution and logit transformation. For each *Odontioda* hybrid, rates of progress for time from VI to flower were modeled as a function of average daily temperature (ADT). Data for time from VI to flower were converted to rates by calculating the reciprocal (1/days) and linear regression analysis was performed using linear models procedure (PROC REG). The intercept (b_0) and slope (b_1) of the regression lines were used to estimate the base temperature ($T_b = -b_0/b_1$) and the amount of thermal time (units of degree-days) that are required from VI to flower ($°C \cdot d^{-1} = 1/b_1$) in each hybrid (Roberts and Summerfield, 1987).

Results

Plant performance

During Year 1, plants of both hybrids displayed symptoms of heat stress (e.g., severe necrosis on leaf margins and apices) when grown at constant temperature setpoints of 26, 29, and fluctuating day/night temperatures of 26/14, 26/20, 29/17, or 29/23 °C. The percentage of plants that had a VI and days to VI were variable among these treatments and many inflorescences aborted within each population (Table 4). Data in these treatments were not included in further analysis.

Visible Inflorescence Percentage

Temperature had a significant influence on the percentage of plants that initiated a VI and developed to flowering in *Odontioda* George McMahon 'Fortuna' (Years 1 and 2) and *Odontioda* Lovely Penguin 'Emperor' (Year 2) (Fig. 2). During Year 1, inflorescence initiation in *Odontioda* Lovely Penguin 'Emperor' was variable and ≤50% of plants initiated inflorescences in all treatments. After 20 weeks at the various temperature setpoints, ≥90% of plants of *Odontioda* George McMahon and *Odontioda* Lovely Penguin (Year 2 only) had a VI when grown at 14 and 17 °C, while ≤50% plants grown at 23/17 °C had a VI during the experiment.

Time to Visible Inflorescence and Flower

In both *Odontioda* hybrids the average time to VI varied among treatments (52 to 86 d) and the effect of temperature was not significant (Table 5). However, time from VI to flower in both *Odontioda* hybrids decreased with increasing ADT (Fig. 3). For

example, as temperature increased from 14 to 23 °C, time from VI to flower in *Odontioda* George McMahon decreased from 94 to 55 d. Similarly in *Odontioda* Lovely Penguin, as temperature increased from 14 to 20 °C, the average time decreased from 105 to 73 d.

The rate of progress from VI to flower was linear for both *Odontioda* George McMahon and *Odontioda* Lovely Penguin within ADT ranges of 14.2 to 23.6 °C and 14.2 to 20.1 °C, respectively. In *Odontioda* George McMahon, the base temperature for development from VI to flower was calculated as 1.8 °C and thermal time for completion of the event was estimated at 1250 $°C \cdot d^{-1}$ (Table 6). The base temperature and thermal time from VI to flower in *Odontioda* Lovely Penguin was calculated to be 2.6 °C and require 1111 $°C \cdot d^{-1}$, respectively.

Inflorescence Characteristics

The number of inflorescences per plant in *Odontioda* George McMahon was slightly affected by temperature and ranged from 1.0 to 1.6 inflorescences per plant (Table 5). In *Odontioda* Lovely Penguin, temperature had no significant affect on the number of inflorescences per plant. The number of flower buds on the first VI were not significantly different among treatments and averaged 8.9 and 7.4 in *Odontioda* George McMahon and *Odontioda* Lovely Penguin, respectively. The total inflorescence length at flower was not significantly influenced by temperature in *Odontioda* George McMahon and *Odontioda* Lovely Penguin and averaged 26.8 and 35.0 cm, respectively (data not presented). The diameter of the first open flower was influenced by temperature for both

Odontioda hybrids and showed a significant linear decreasing trend ($P \leq 0.01$) as constant temperature increased from 14 to 23 °C (Fig. 4).

Pseudobulb Diameter and Leaf Length

Temperature had a significant influence on the increase in pseudobulb diameter and the final pseudobulb diameter of both *Odontioda* hybrids ($P \leq 0.001$) (Table 7). As temperature increased from 14 to 23 °C, pseudobulb diameter showed a decreasing trend (Fig. 5). The final pseudobulb diameter was greatest in plants grown at 14 or 17 °C and averaged 5.4 to 6.1 cm in both hybrids. The occurrence of inflorescence initiation in all temperature treatments was quantified based on pseudobulb diameter (Fig. 6). In *Odontioda* George McMahon and *Odontioda* Lovely Penguin, pseudobulbs with a diameter ≥3.5 and ≥5.0 cm, respectively, had developed a VI in ≥60% of plants. The increase in leaf length and final leaf length were not significantly different among treatments (Table 7) and final leaf lengths varied from 24.6 to 30.3 cm (data not presented).

Discussion

In our study, a high percentage of inflorescences aborted and leaf necrosis occurred when *Odontioda* orchids were grown at temperatures of 26 or 29 °C for 12 or 24 h daily. These plants were determined to be of unacceptable quality for commercial sales. A similar response to high temperature has been reported in the ladybird orchid, *Zygopetalum* Redvale 'Fire Kiss', where flower buds on plants transferred to ADTs of 25.4 to 28.6 °C developed necrotic lesions and aborted within 20 d (Lopez and Runkle,

2004). Although inflorescence initiation occurred in both *Odontioda* hybrids when grown at day temperatures of 26 or 29 °C, many of the inflorescences did not subsequently develop.

In both *Odontioda* hybrids, the percentage of plants that initiated a reproductive inflorescence and developed to open flowers was greatest when grown at constant temperatures of 14 or 17 °C. Flowering in response to low temperature has been previously reported in other orchid genera. For example, Lopez et al. (2005) reported that plants of *Miltoniopsis* Augres 'Trinity' had the highest flowering percentage (≥80%) when grown under a 9-h photoperiod at 20 °C for four to eight weeks and transferred to 14 °C for eight to twelve weeks. In *Phalaenopsis*, flowering was inhibited at constant temperatures ≥28 °C and exposure to temperatures ≤25 °C for 3 to 5 weeks was required for inflorescence initiation (Chen et al., 1994; Sakanishi et al., 1980).

There was no advantageous effect of a diurnal temperature fluctuation on inflorescence initiation in both hybrids compared to constant temperature treatments with a similar ADT. For example, in *Odontioda* George McMahon grown at 17 or 20/14 °C, VI percentages after 20 weeks were 95 and 70%, respectively. These results suggest that a high day temperature (20 to 23 °C) reduced the percentage of plants that initiated an inflorescence and developed, even when the night temperature was low (14 to 17 °C). In *Odontioda* Lovely Penguin, the low inflorescence initiation observed during Year 1 may have been attributed to plant immaturity. As with other flowering plants, a juvenility period also exists in orchids, in which a specific stage of maturity must be reached before plants are capable of reproductive development (Goh et al., 1982).

In our study, a minimum pseudobulb diameter was required for uniform inflorescence initiation: pseudobulbs with a diameter ≥5.5 cm, developed a VI in 93% of plants of both *Odontioda* hybrids. Plants grown at the coolest temperatures (14 or 17 °C) had the greatest increase in pseudobulb diameter and thus the greatest final pseudobulb diameter. This suggests that temperature controls the final pseudobulb size and that pseudobulbs must be relatively large before inflorescence initiation can occur. Ichihashi (1997) reported that in *nobile*-type *Dendrobium* orchids, flower initiation only occurs on mature pseudobulbs when exposed to temperatures of 7.5 to 20 °C (Ichihashi, 1997). The specific physiological changes that occur during pseudobulb maturation in response to cool temperatures are unknown. However, plants of *Dendrobium* Malones required a high specific gravity (≥106 $mg \cdot ml^{-1}$), dry matter content (≥10.5%), or both for inflorescence initiation (Ichihashi, 1997).

The rate of inflorescence development was modeled as a function of ADT for both *Odontioda* hybrids and the predicted days to flower at a given temperature was very similar to the actual time. For example, in *Odontioda* George McMahon grown at an ADT of 17.0 °C, the average time from VI to flower was 82 d, while the model predicted 74 d (1250 $°C \cdot d^{-1}$/17.0 °C). The time from VI to flower in *Odontioda* grown at 17 °C was considerably longer than the estimated time for *Zygopetalum* Redvale 'Fire Kiss' (39 d), but shorter than the estimated time for several *Phalaenopsis* hybrids (139 d) (Lopez and Runkle, 2005; Robinson, 2002). The average time from VI to flower in *Odontioda* Lovely Penguin grown at 23 °C was 22 d greater than plants grown at 20 °C. This suggests that constant temperatures of 23 °C may be superoptimal for inflorescence development in this hybrid.

The calculated base temperatures of *Odontioda* George McMahon and *Odontioda* Lovely Penguin during inflorescence development were similar: 1.8 and 2.6 °C. This estimated base temperature for *Odontioda* is 1.3 °C lower than the estimated base temperature of another native South American orchid genus, *Zygopetalum* (Lopez and Runkle, 2004; Pridgeon, 2000). The lower base temperature in *Odontioda* could be attributed to the genetic background of these intergeneric hybrids. The predominate species in the background of *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor' is *Odontoglossum crispum* Lindl., which is native to high elevations (2,200 to 3,000 m) of the Andes Mountains in Columbia (Pridgeon, 2000; Wildcatt, 2004). In comparison, *Zygopetalum* is native to mid-elevations of 300 to 1,500 m (Pridgeon, 2000).

In conclusion, *Odontioda* orchids should be grown at temperatures ≤26 °C to avoid heat stress and inflorescence abortion. Cool constant temperatures between 14 to 17 °C can be utilized to promote both inflorescence initiation and development in these two *Odontioda* hybrids. At this temperature range, pseudobulbs will attain a minimum size required for uniform flowering. Time from inflorescence initiation to flowering is related to the ADT and can be predicted with our model. Although time from VI to flower was shortest at warmer temperatures, flower size decreased as temperature increased. This information could be used by commercial orchid growers when producing *Odontioda* orchids in flower for specific market dates.

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Table 1. Summary of production dates, container sizes, and greenhouse environmental conditions for *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor' preceding and during experimentation.

	Odontioda hybrid	
Description	George McMahon 'Fortuna'	Lovely Penguin 'Emperor'
Received bare-root at Nurserymen's Exchange, Inc. (Half Moon Bay, Calif.)	29 October 2002	13 June 2003
Transplanted into 7.5-cm pots[z] Temperature: 24/18 °C (day/night) Photoperiod: Natural daylength (lat. 37 °N) *PPF*[y]: ≤500 μmol·m^{-2}·s^{-1}	29 October 2002	--
Transplanted into 10-cm pots	2 June 2003	13 June 2003
Received at Michigan State University (East Lansing, Mich.) Temperature: 23 °C Photoperiod: 16 h (0600 to 2200 HR)[x] *PPF*: ≤300 μmol·m^{-2}·s^{-1}	22 September 2003	
Transferred to temperature treatments for 20 weeks	1 December 2003	
Transferred from treatments to common greenhouse Temperature: 23 °C Photoperiod: 16 h (0600 to 2200 HR) *PPF*: ≤300 μmol·m^{-2}·s^{-1}	19 April 2004	
Transplanted into new media[w]	July 2004	
Transferred to temperature treatments for 33 weeks	26 October 2004	
Termination of experiment	14 June 2005	

[z]Media consisting of 75% fine-grade Douglas fir bark, 15% medium-grade perlite, and 10% sphagnum peat (by volume).
[y]Photosynthetic photon flux.
[x]Natural daylengths (lat. 42 °N) with day-extension lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 25 to 50 μmol·m^{-2}·s^{-1} at plant height.
[w]Media consisting of 80% medium-grade fir bark, 10% long fiber Canadian sphagnum peat, and 10% medium-grade perlite (by volume).

Table 2. Average daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$) at plant level per 4-week period during experiment for Years 1 and 2. The maximum photosynthetic photon flux at plant height was 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

	4-week period						
Year	1	2	3	4	5	6	7
2003 to 2004[z]	3.8	4.0	5.1	6.0	6.1	--[w]	--
2004 to 2005[y]	4.1	3.6	3.8	4.8	6.9	8.2	4.5

[z]Experimental period from 1 December 2003 to 19 April 2004.
[y]Experimental period from 26 October 2004 to 7 June 2005.
[w]Data not collected.

Table 3. Actual average air temperatures of each temperature treatment in Years 1 and 2.

	Temperature setpoint (°C)					
Year	14/14[z]	17/17	20/20	23/23	20/14	23/17
1	14.5/14.3	17.4/17.4	20.2/20.1	24.5/22.6	20.0/13.8	21.9/16.3
2	14.1/13.5	17.2/16.6	21.0/20.4	23.4/21.8	19.1/13.5	22.5/16.9

[z]12-h day/12-h night temperature.

Table 4. Visible inflorescence (VI) and inflorescence abortion percentages and days to VI for *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor' after 20 weeks during Year 1 at constant temperature setpoints of 26 or 29 °C, and fluctuating day/night temperature setpoints of 26/14, 26/20, 29/17, or 29/23 °C. All plants displayed symptoms of heat stress and were considered unmarketable. Data are for Year 1.

		VI (%)		Inflorescence abortion (%)		Days to VI	
Temperature setpoint (°C)	Actual temperature (°C)	George McMahon	Lovely Penguin	George McMahon	Lovely Penguin	George McMahon	Lovely Penguin
26/26[z]	25.8/26.1	50	30	50	30	78	89
29/29	29.1/29.4	--[y]	--	--	--	--	--
26/14	25.4/14.3	100	10	40	0	65	27
26/20	25.8/19.4	90	20	20	20	71	107
29/17	27.8/17.1	90	20	80	20	68	72
29/23	28.8/22.3	--	--	--	--	--	--

[z]12-h day/12-h night temperature.
[y]All plants died.

Table 5. Days to visible inflorescence (VI), number of flower buds on first VI, and number of inflorescences per plant for *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor' in temperature treatments with ≥10% VI. Data for both years were pooled for analysis.

	Days to VI		No. of flower buds on first VI		No. of inflorescences per plant	
Temperature setpoint (°C)	George McMahon	Lovely Penguin	George McMahon	Lovely Penguin	George McMahon	Lovely Penguin
14	59 a[y]	66 a	7.9 a	5.8 a	1.4 ab	1.1 a
17	60 a	77 a	9.5 a	7.4 a	1.2 ab	1.0 a
20	77 a	63 a	8.3 a	7.5 a	1.6 a	1.1 a
23	66 a	86 a	9.4 a	9.9 a	1.0 b	1.1 a
20/14[z]	61 a	53 a	8.5 a	7.9 a	1.6 a	1.0 a
23/17	57 a	52 a	10.0 a	5.8 a	1.3 ab	1.0 a
Significance						
Temperature	NS	NS	NS	NS	*	NS
Year	*	***	**	NS	NS	NS
Temperature × Year	NS	NS	NS	NS	NS	NS

[z]12-h day/12-h night temperature.

[y]Mean separation within columns by Tukey's honest significant difference test at $P \leq 0.05$.

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

Table 6. Parameters of linear regression analysis relating temperature to rate of progress for time from visible inflorescence to flower in *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor'. The slope (b_1) and intercept (b_0) were used to calculate the base temperature (T_b) and degree-days (°C·d^{-1}).

Odontioda hybrid	Intercept (b_0) (1/days)	Slope (b_1) (1/days)/°C	T_b (°C)	°C·d^{-1}	r^2
George McMahon 'Fortuna'	-0.0014 ± 0.0011[z]	0.0008 ± 0.0001	1.8	1250	0.74***
Lovely Penguin 'Emperor'	-0.0023 ± 0.0024	0.0009 ± 0.0001	2.6	1111	0.56***

[z]Standard error.
***Significant at $P \leq 0.001$.

Table 7. The effect of temperature on final pseudobulb diameter and leaf length, and pseudobulb diameter increase and leaf length increase of *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor'. Data were collected at flower or after 31 weeks in temperature treatments. Data for Year 2 only.

Odontioda hybrid	Pseudobulb diameter	Leaf length	Pseudobulb diameter increase	Leaf length increase
George McMahon	**	NS	*	NS
Lovely Penguin	**	NS	**	NS

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

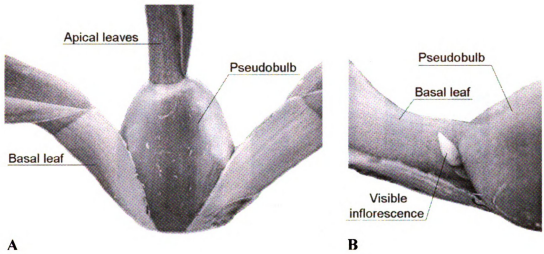

Figure 1. Pseudobulb of an *Odontioda* orchid with pairs of apical and basal leaves (A) and a visible inflorescence in the axil of a leaf sheath at the base of a mature pseudobulb (B).

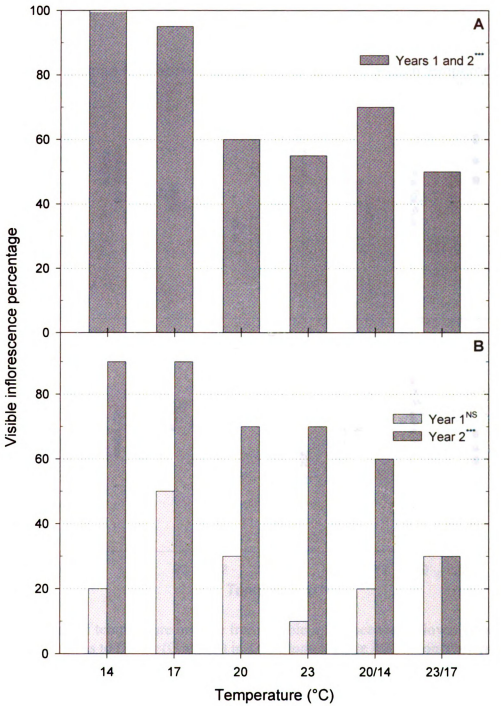

Figure 2. Visible inflorescence (VI) percentages for *Odontioda* George McMahon 'Fortuna' (A) and *Odontioda* Lovely Penguin 'Emperor' (B) after 20 weeks at constant temperature setpoints of 14, 17, 20, or 23 °C, and fluctuating day/night temperature setpoints of 20/14 or 23/17 °C. The day and night were 12 hours each. VI percentages were analyzed using a binomial distribution with logit transformation. Data for *Odontioda* George McMahon was pooled for Years 1 and 2. NS, *** Nonsignificant or significant at $P \leq 0.001$.

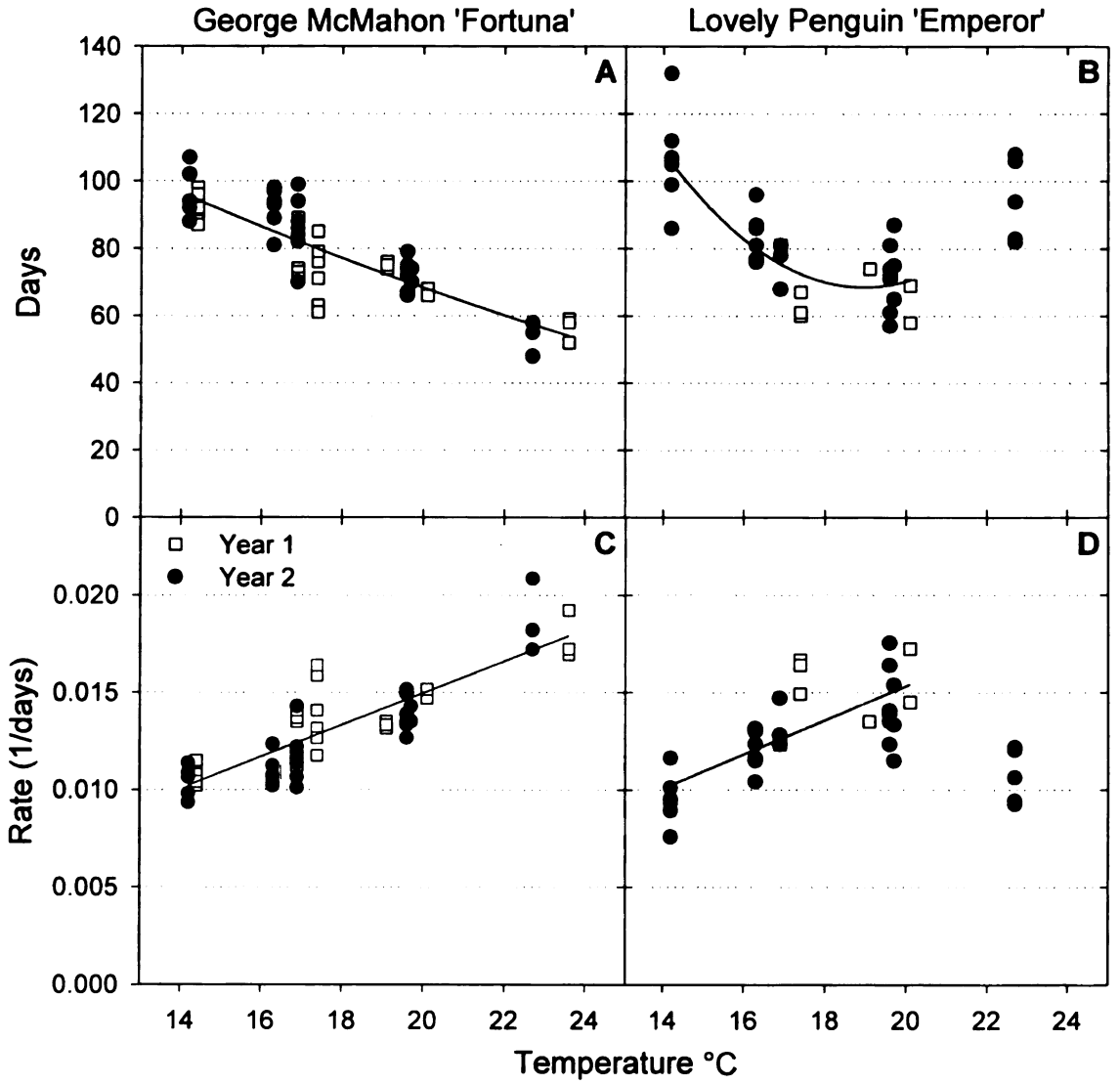

Figure 3. Effect of temperature on time from visible inflorescence to flower (A and B) and rate of progress to flower (C and D) in *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor'. Each symbol represents an individual plant. The solid lines represent the regression equation using pooled data for Years 1 (□) and 2 (●). Data at 23 °C for *Odontioda* Lovely Penguin were not included in regression analysis. The average daily temperature was reported for treatments with a fluctuating day and night temperature. Parameters of linear regression analysis are presented in Table 6.

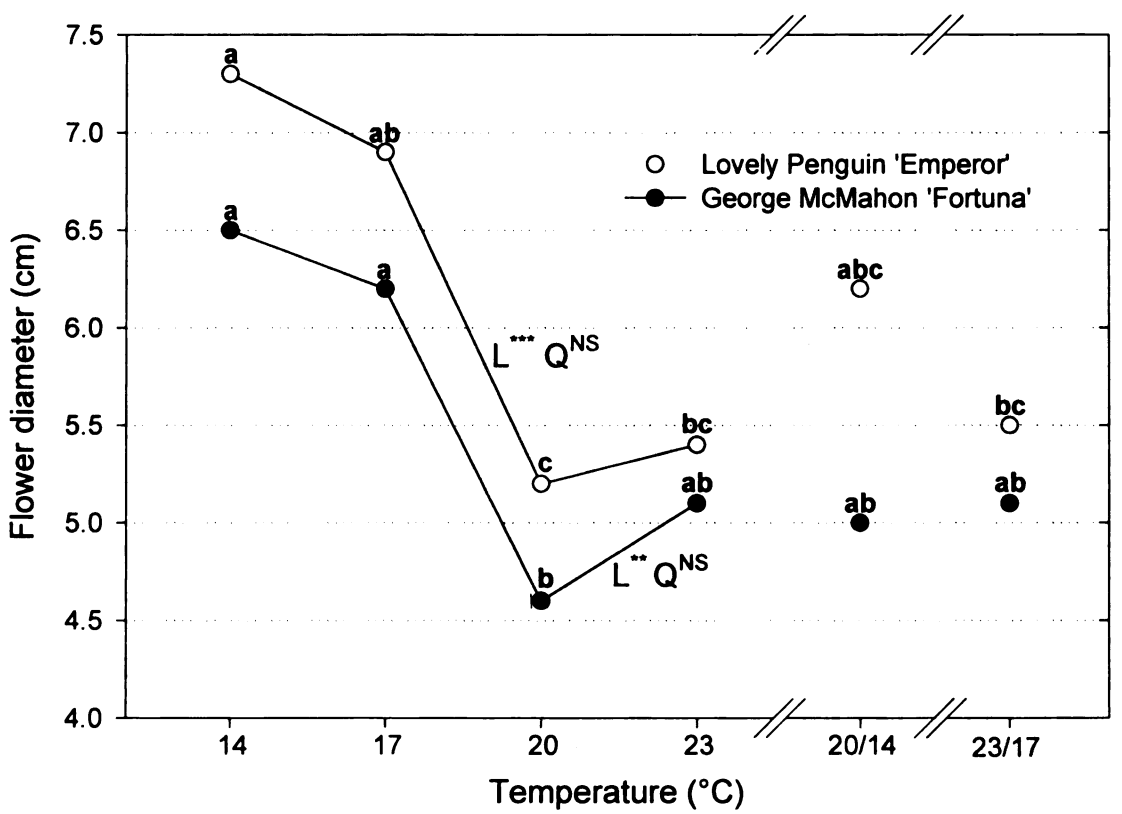

Figure 4. Influence of temperature on average flower diameter in *Odontioda* George McMahon 'Fortuna' (●) and *Odontioda* Lovely Penguin 'Emperor' (○) at constant temperature setpoints of 14, 17, 20, or 23 °C, and fluctuating day/night temperature setpoints of 20/14 or 23/17 °C. The day and night were 12 hours each. Mean separation within each hybrid by Tukey's honest significant difference (HSD) test at $P \leq 0.05$. L = linear, Q = quadratic trends; NS, **, *** Nonsignificant or significant at $P \leq 0.01$ or 0.001, respectively. Data for Year 2.

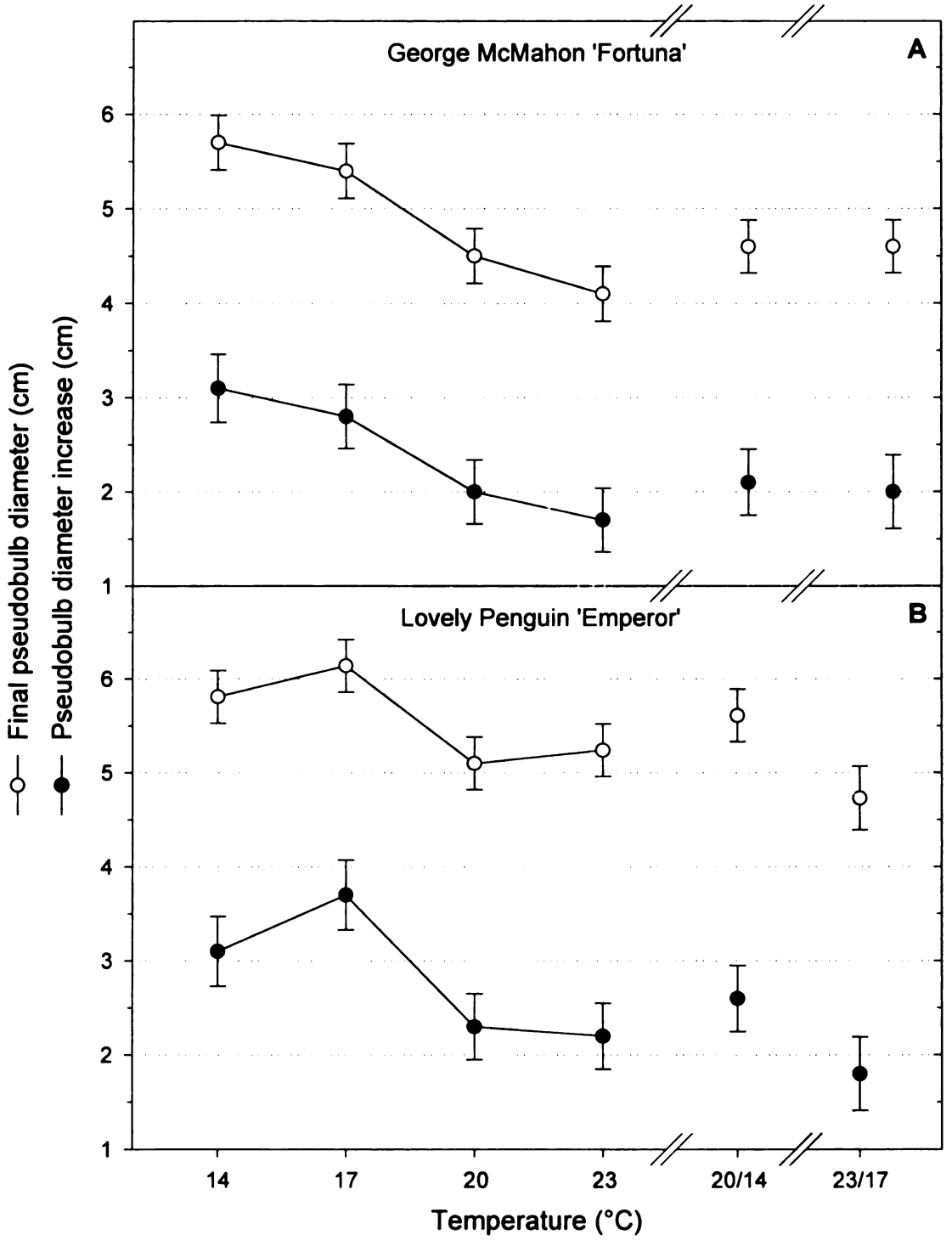

Figure 5. Influence of temperature on final pseudobulb diameter (○) and pseudobulb diameter increase (●) in *Odontioda* George McMahon 'Fortuna' (A) and *Odontioda* Lovely Penguin 'Emperor' (B) at constant temperature setpoints of 14, 17, 20, or 23 °C, and fluctuating day/night temperature setpoints of 20/14 or 23/17 °C. The day and night were 12 hours each. Each symbol represents the average of 10 plants. Vertical bars indicate standard errors about the treatments means. Data for Year 2.

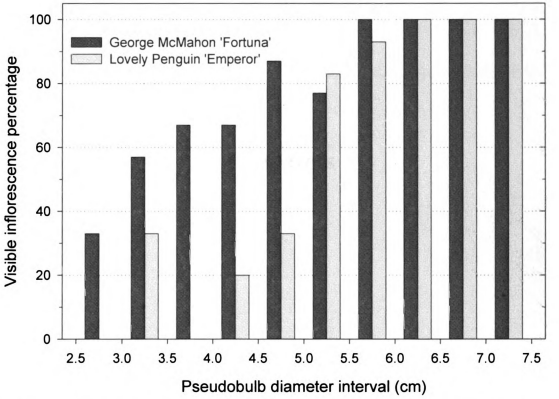

Figure 6. Influence of pseudobulb diameter on visible inflorescence percentage in *Odontioda* George McMahon 'Fortuna' and *Odontioda* Lovely Penguin 'Emperor'. Pseudobulb diameter was measured at flower or after 31 weeks in temperature treatments. Data for Year 2.

APPENDICES

APPENDIX A

EFFECTS OF DAILY LIGHT INTEGRAL ON GROWTH AND FLOWERING OF POTTED PHALAENOPSIS ORCHIDS

Introduction

Orchids are currently the second most valuable potted crop in the United States with a total reported wholesale value of $127.6 million in 2004 (U.S. Department of Agriculture, 2005). Among all of the orchid genera sold within the United States, the genus *Phalaenopsis* comprises a large percentage (85 to 90%) of the potted orchid sales (Nash, 2003) because of their ease of scheduling to meet specific market dates, high wholesale value, and long postharvest life. In The Netherlands, *Phalaenopsis* were the most valuable potted plant at Dutch flower auctions in 2004, trading 23.8 million plants valued at €109.7 million (VBN, 2005). Taiwan currently has the largest number of *Phalaenopsis* breeders and growers with approximately 89 hectares in production, producing 36 million plants in 2002 with a wholesale value of $51 million (Fenton, 2004; Wang, 2004).

The commercial production of *Phalaenopsis* consists of two basic phases: a vegetative phase and a reproductive phase. During the vegetative phase, *Phalaenopsis* plants are grown at temperatures ≥28 °C to inhibit flowering and maintain vegetative growth (Chen et al., 1994; Sakanishi et al., 1980). To promote the transition from a vegetative phase to a reproductive phase in *Phalaenopsis*, a day/night greenhouse temperature of 25/20 or 20/15 °C has been recommended (Lee and Lin (1984, 1987).

The effects of irradiance on *Phalaenopsis* have been described for both the vegetative and reproductive production phases (Konow and Wang, 2001; Wang, 1995, 2004). Konow and Wang (2001) reported that plants of *Phalaenopsis* Atien Kaala grown under a maximum photosynthetic photon flux (*PPF*) of 75, 125, or 320 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 52 weeks had average fresh weights of 17, 36, and 61 g, respectively. Information is also

available on how irradiance influences the reproductive phase of *Phalaenopsis* production. Wang (1995) reported that plants grown at 20/15 °C day/night with a 12-h photoperiod and a constant daily light integral (DLI) of 2.6 or 6.9 $mol \cdot m^{-2} \cdot d^{-1}$ initiated inflorescences after 34 and 28 d, respectively. Plants grown under 0 or 0.35 $mol \cdot m^{-2} \cdot d^{-1}$ did not initiate inflorescences within 6 weeks (Wang, 1995).

The recommended irradiance for vegetative growth of *Phalaenopsis* is relatively low (100 to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Wang, 2004). However, to our knowledge, the effect of light intensity during the vegetative phase on subsequent flowering has not been reported. The objective of this study was to quantify the effects of DLI during the vegetative phase on vegetative growth and subsequent flowering of four *Doritaenopsis* and *Phalaenopsis* orchid hybrids.

Materials and Methods

Plant Material

On 2 Nov. 2004, clones of three bare-root immature *Phalaenopsis* hybrids (Pink Twilight '173', Sharon Bay '163', and Brother Showpiece) and one *Doritaenopsis* hybrid (*Dtps.* White Castle × *Phal.* Moon World) '717' were received in East Lansing, Mich., from a commercial greenhouse (Floricultura Orchidaceae B.V., Heemstede, Holland). The initial average leaf span of the plant material was 21 to 27 cm. Leaf span was measured by extending the longest opposing leaves to a horizontal position and then measuring the length from one leaf tip to the opposite leaf tip. Plants were planted into 11.5-cm pots in media consisting of 33% medium-grade Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] bark (Rexius Forest By-Products Inc., Eugene, Ore.), 45%

medium-grade chopped coconut (*Coco nucifera* L.) coir (Millenniumsoils Coir, St. Catharines, Ont.), 11% long fiber Canadian sphagnum peat (Mosser Lee Co., Millston, Wis.), and 11% coarse-grade perlite (OFE Intl. Inc., Miami, Fla.) (by volume). Plants were grown in a glass-glazed greenhouse at a constant temperature of 28 °C to inhibit flowering. The photoperiod was a constant 16 h (0600 to 2200 HR) consisting of natural daylengths (lat. 42 °N) with day-extension lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 20 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height [as measured with a line quantum sensor (Apogee Instruments, Inc., Logan, Utah)]. Light transmission was reduced using woven shade curtains (OLS 50; Ludvig Svensson, Charlotte, N.C.) and whitewash applied to the glazing so that the maximum *PPF* at plant height was 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. A summary of plant material history is provided in Table 1.

Daily Light Integral Treatments

On 23 Nov., 2004, 15 plants of each hybrid were transferred to a glass-glazed greenhouse with three DLI treatments created using woven shade curtains (OLS 30 and OLS 50; Ludvig Svensson) with different light transmission values and varying irradiances from HPS lamps (Fig. 1). The photoperiod was a constant 14 h (0600 to 2000 HR) consisting of natural daylengths with lighting provided by HPS lamps delivering a maximum *PPF* of 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Plants were grown at a constant temperature of 28 °C and a vapor-pressure deficit (VPD) of ≈1.0 kPa was maintained by the injection of water vapor.

After 20 weeks, 12 of the largest plants of each hybrid were transferred to a common greenhouse with a temperature setpoint of 23 °C to induce flowering. The

photoperiod was 16 h (0600 to 2200 HR) consisting of natural daylengths with lighting provided by HPS lamps delivering a *PPF* of 20 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Light transmission through the greenhouse was reduced so that the maximum *PPF* at plant height was 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Air Temperature and Plant Culture

Air temperature was measured in each greenhouse section by aspirated thermocouples (0.127-mm type E) every 10 s and hourly averages were recorded by a CR-10 datalogger (Campbell Scientific, Logan, Utah).

Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (Greencare Fertilizers, Chicago, Ill.).

Data Collection

Light intensity under each treatment was measured using a quantum sensor (LI-COR, Inc., Lincoln, Nebr.) located at plant level. The calculated average DLIs during the 20-week period were 2.5±0.9, 5.5±1.8, and 9.8±2.9 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 2). Plant leaf span from opposing leaf tips were measured and the number of leaves were recorded at the beginning of the experiment and after 20 weeks under each DLI treatment and the increase in leaf span and number of leaves were calculated. The ratio of variable to maximal chlorophyll fluorescence (F_v/F_m) was measured for each plant at 20 weeks using a portable chlorophyll fluorometer (Plant Efficiency Analyzer, Hansatech Instruments Ltd., Norfolk, England). Measurements were made between 1400 and 1600 HR. For

each plant, the center of the most recently matured leaf was selected and the adaxial surface was clipped using the manufacturer's plastic/foam clips. Leaves were dark adapted for 15 min before measurements were recorded.

After transfer to a common greenhouse for forcing, the date of first visible inflorescence (VI) without dissection (<0.5 cm) and the date that the first flower opened was recorded for each plant. Days to VI, days from VI to flowering, days to flowering, VI percentage, inflorescence abortion percentage, and flowering percentage were calculated for each treatment. On the date of flowering, the total number of flower buds and flowers were recorded for each plant and the total inflorescence length from emergence to the tip of the inflorescence was measured. Plants that did not have a VI after 10 weeks of forcing at 23 °C were considered not reproductive. Ten weeks was used because in other *Phalaenopsis* hybrids grown at 23 °C, the average time to VI was 29 to 39 d (Blanchard, 2005). Light intensity was measured as described above and the calculated average DLI during forcing was 3.8±1.5 $mol \cdot m^{-2} \cdot d\text{-}^{1}$ (Table 2).

Data Analysis

A completely randomized block design was used during each year. Data were analyzed using SAS (SAS Institute, Cary, N.C.) mixed model procedure (PROC MIXED) and pair-wise comparisons between treatments were performed using Tukey's honest significant difference (HSD) test. Visible inflorescence, inflorescence abortion percentage, and flowering percentage were analyzed using generalized model procedure (PROC GENMOD) with a binomial distribution and logit transformation. Pair-wise comparisons for percentage data were performed using chi-square (χ^2) test.

Results

Vegetative Growth and Chlorophyll Fluorescence

After 20 weeks under the three DLI treatments, all hybrids except *Phalaenopsis* Brother Showpiece grown under a low DLI (2.5 $mol \cdot m^{-2} \cdot d^{-1}$) had a significantly greater increase in leaf span compared to plants grown under the highest DLI (9.8 $mol \cdot m^{-2} \cdot d^{-1}$) (Figure 2). For example, in *Phalaenopsis* Pink Twilight, the average leaf span increase of plants grown under 2.5, 5.5, or 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ was 4.8, 3.1, and 3.0 cm, respectively. The average increase in number of leaves per plant ranged from 0.5 and 1.8 and was not significantly different among DLI treatments (data not presented)

Chlorophyll fluorescence was influenced by DLI and plants of all hybrids grown under a low DLI had a significantly higher F_v/F_m ratio compared to plants grown under the highest DLI (9.8 $mol \cdot m^{-2} \cdot d^{-1}$) (Fig. 3A). The average F_v/F_m ratio for all four hybrids grown under 2.5, 5.5, or 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ was 0.78, 0.71, and 0.65, respectively.

Visible Inflorescence, Inflorescence Abortion, and Flowering Percentage

After 10 weeks following transfer to a common greenhouse for flower induction, ≥58% of all hybrids except *Phalaenopsis* Pink Twilight had a VI when previously grown for 20 weeks at an average DLI of 2.5 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 3 and Fig. 3B). Inflorescence initiation percentage of plants grown under an average DLI of 5.5 $mol \cdot m^{-2} \cdot d^{-1}$ varied among hybrids and ranged from 17% to 75%. All hybrids except *Phalaenopsis* Pink Twilight grown for 20 weeks at 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ had a significantly lower inflorescence initiation percentage (≤50%) compared to plants grown under 2.5 $mol \cdot m^{-2} \cdot d^{-1}$.

The percentage of plants with an inflorescence that aborted was not affected by DLI; however there was a significant difference among hybrids (Table 3). Plants of *Phalaenopsis* Pink Twilight had the greatest inflorescence abortion percentages (8% to 33%) among all hybrids. All hybrids except *Phalaenopsis* Pink Twilight had a lower flowering percentage when grown for 20 weeks at 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ compared to plants grown under 2.5 $mol \cdot m^{-2} \cdot d^{-1}$.

Flowering Characteristics

The average time to VI, time from VI to flower, and total time to flower was not influenced by DLI; however there was a significant difference among hybrids (Table 4). Plants of *Phalaenopsis* Brother Showpiece had the shortest time to VI (25 or 26 d), while plants of *Phalaenopsis* Sharon Bay required the longest time (42 to 45 d). Time from VI to flower was greatest in *Phalaenopsis* Brother Showpiece (72 d), while in *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', time from VI to flower decreased by ≈13 days. The number of flowers per plant varied between 2.9 to 4.8 and was not significantly different among any DLI treatment or hybrid. In all hybrids, total inflorescence length was not influenced by DLI and ranged from 20.1 to 32.6 cm.

Discussion

Phalaenopsis plants grown under a low DLI (2.5 $mol \cdot m^{-2} \cdot d^{-1}$) during vegetative growth had an increased leaf span and higher F_v/F_m ratio than plants grown under a DLI of 9.8 $mol \cdot m^{-2} \cdot d^{-1}$. Chlorophyll fluorescence can provide information on the state of photosystem II, which is the most susceptible component of the photosynthetic apparatus

to damage from excess quantities of light (Maxwell and Johnson, 2000). Thus, chlorophyll fluorescence values can be used to estimate the photosynthetic efficiency of a plant (Maxwell and Johnson, 2000). In our study, plants grown under 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ had a consistently lower F_v/F_m ratio than plants grown under 2.5 $mol \cdot m^{-2} \cdot d^{-1}$. These results suggest that plants grown under 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ were exposed to high irradiance levels above the light saturation point, resulting in photoinhibition. Lootens and Heursel (1998) determined that the saturating *PPF* for two *Phalaenopsis* hybrids grown at 20 °C was 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$. At a temperature of 25 or 30 °C, the saturating *PPF* was not found at the highest irradiance measured, 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Lee (2000) reported that photoinhibition occurs in *Phalaenopsis* when grown under a *PPF* above 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In our study, plants grown under the high DLI treatment were exposed to a maximum *PPF* of 900 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

The greater inflorescence initiation percentages among plants grown under an average DLI of 2.5 $mol \cdot m^{-2} \cdot d^{-1}$ suggest that higher DLI values may not be advantageous for subsequent forcing. The relatively low flowering percentages among all treatments indicate that the populations of plants were not fully mature when transferred to 23 °C for forcing, regardless of the average DLI. Runkle et al. (2005) recommended that for uniform inflorescence initiation and flowering of *Phalaenopsis*, plants should have a minimum average leaf span of 25 cm. In our study, the average leaf spans of *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', *Phalaenopsis* Pink Twilight '173', *Phalaenopsis* Sharon Bay '163', and *Phalaenopsis* Brother Showpiece at the beginning of forcing were 31.8 ± 3.5, 24.5 ± 2.4, 26.3 ± 2.4, and 24.6 ± 3.4 cm,

respectively. The percentage of plants that were reproductive would have likely increased if the duration of vegetative growth at 28 °C was extended.

We observed that *Doritaenopsis* and *Phalaenopsis* hybrids had different inflorescence initiation percentages when compared to other hybrids grown under the same DLI. This variation among hybrids may be attributed to differences in plant maturity or their varied genetic backgrounds.

In this study, several flowering characteristics were not significantly affected by DLI: time to VI, time from VI to flower, total time to flower, number of flowers, and inflorescence length. In other greenhouse crops, light quantity has been shown to have a significant effect on floral evocation and flower development (Moe, 1997). Pramuk and Runkle (2005) studied the effects of DLI during the seedling stage of several bedding plants on subsequent flowering under a common DLI. Seedlings grown under an average DLI of 14.2 $mol \cdot m^{-2} \cdot d^{-1}$ flowered 4 to 12 d earlier than seedlings grown under 4.1 $mol \cdot m^{-2} \cdot d^{-1}$. However, plant quality (e.g., flower bud number and plant shoot dry weight) at first flowering generally decreased as the seedling DLI increased (Pramuk and Runkle, 2005). In our study, differences in flowering characteristics among DLI treatments were not observed and these results may be confounded by immaturity of the plant material.

In summary, our results indicate that during vegetative production of *Phalaenopsis*, plants grown under a low DLI (2.5 $mol \cdot m^{-2} \cdot d^{-1}$) will have a greater increase in leaf span and higher photosynthetic efficiency than plants grown under a higher DLI (9.8 $mol \cdot m^{-2} \cdot d^{-1}$). In general, plants grown under a lower DLI during vegetative growth will also have higher flowering percentages during subsequent forcing. Several characteristics (e.g., time to VI) in this study were not significantly influenced by

DLI and may be related to the immaturity of plant material. Further experiments need to be performed to validate our results before recommendations can be made.

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Table 1. Summary of production dates, container sizes, and greenhouse environmental conditions for *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', *Phalaenopsis* Pink Twilight '173', *Phalaenopsis* Sharon Bay '163', and *Phalaenopsis* Brother Showpiece preceding and during experimentation.

Description	Date
Grown at Floricultura Orchidaceae B.V. (Heemstede, Holland) in community trays	--
Received bare-root at Michigan State University (East Lansing, Mich.)	02 November 2004
Transplanted into 11.5-cm pots[z] Temperature: 28 °C Photoperiod: 16 h (0600 to 2200 HR)[x] *PPF*[y]: ≤150 $\mu mol \cdot m^{-2} \cdot s^{-1}$	02 November 2004
Transferred to three daily light integral (DLI) treatments for 20 weeks: Calculated average DLIs: 2.5 ± 0.9, 5.5 ± 1.8, and 9.8 ± 2.9 $mol \cdot m^{-2} \cdot d^{-1}$ Temperature: 28 °C Photoperiod: 14 h (0600 to 2000 HR)[x] Vapor-pressure deficit (VPD): ≈1.0 kPa	23 November 2004
Transferred to a common greenhouse for flowering Temperature: 23 °C Photoperiod: 16 h (0600 to 2200 HR)[x] *PPF*: ≤150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ Calculated average DLI: 3.8 ± 1.5 $mol \cdot m^{-2} \cdot d^{-1}$	13 April 2005
Termination of experiment	8 August 2005

[z]Media consisting of 33% medium-grade fir bark, 45% medium-grade chopped coconut coir, 11% long fiber Canadian sphagnum peat, and 11% coarse-grade perlite (by volume).
[y]Photosynthetic photon flux.
[x]Natural daylengths (lat. 42 °N) with day-extension lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 25 to 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height.

Table 2. Average daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$) at plant level per month during vegetative and forcing periods.

Light quantity treatment	*Vegetative period*[z]					
	Dec.	Jan.	Feb.	March	April	Average
Low	1.9	2.5	2.7	2.9	2.8	2.5 ± 0.9
Medium	4.1	4.9	5.6	6.8	7.1	5.5 ± 1.8
High	6.9	9.0	10.0	12.5	11.3	9.8 ± 2.9
	Forcing period[y]					
	April	May	June	July	Aug.	Average
	5.9	3.0	3.4	4.0	3.8	3.8 ± 1.5

[z]23 November 2004 to 12 April 2005.
[y]13 April 2005 to 8 August 2005.

Table 3. Visible inflorescence percentage, inflorescence abortion percentage, and flowering percentage for *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', *Phalaenopsis* Pink Twilight '173', *Phalaenopsis* Sharon Bay '163', and *Phalaenopsis* Brother Showpiece following 20 weeks of vegetative growth at 28 °C under an average daily light integral (DLI) of 2.5, 5.5, or 9.8 $mol \cdot m^{-2} \cdot d^{-1}$. Plants were subsequently forced at 23 °C under an average DLI of 3.8 $mol \cdot m^{-2} \cdot d^{-1}$. Percentages were analyzed using a binomial distribution with logit transformation.

Average DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Visible inflorescence (%)	Inflorescence abortion (%)	Flowering (%)
Dtps. White Castle			
2.5	58	25	33
5.5	33	0	33
9.8	17	0	17
Phal. Pink Twilight			
2.5	42	8	33
5.5	58	33	25
9.8	67	17	50
Phal. Sharon Bay			
2.5	83	0	83
5.5	17	0	17
9.8	33	0	33
Phal. Brother Showpiece			
2.5	67	0	67
5.5	75	0	75
9.8	17	0	17
Significance			
Hybrid	NS	**	NS
DLI	**	NS	*
Hybrid × DLI	**	NS	**

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

Table 4. Days to visible inflorescence (VI), days from VI to flower, total days to flower, number of flowers, and total inflorescence length for *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', *Phalaenopsis* Pink Twilight '173', *Phalaenopsis* Sharon Bay '163', and *Phalaenopsis* Brother Showpiece following 20 weeks of vegetative growth at 28 °C under an average daily light integral (DLI) of 2.5, 5.5, or 9.8 $mol \cdot m^{-2} \cdot d^{-1}$. Plants were subsequently forced at 23 °C under an average DLI of 3.8 $mol \cdot m^{-2} \cdot d^{-1}$.

Average DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Days to VI	Days from VI to flower	Total days to flower	Flower no.	Total inflorescence length (cm)
Dtps. White Castle					
2.5	44 a[z]	60 d	99 abc	3.0 a	24.9 ab
5.5	39 ab	59 d	98 bc	3.0 a	26.0 ab
9.8	37 abc	59 d	95 c	3.0 a	26.4 ab
Phal. Pink Twilight					
2.5	31 bcd	66 bc	98 bc	3.0 a	20.1 b
5.5	32 bc	66 bcd	96 c	3.3 a	22.5 ab
9.8	28 cd	70 ab	98 bc	3.3 a	21.7 ab
Phal. Sharon Bay					
2.5	44 a	63 cd	107 a	4.0 a	30.4 ab
5.5	45 a	62 cd	106 ab	3.5 a	27.1 ab
9.8	42 a	63 cd	105 abc	4.8 a	32.6 a
Phal. Brother Showpiece					
2.5	25 d	72 a	97 c	2.9 a	21.3 ab
5.5	26 d	72 a	97 bc	3.3 a	22.1 ab
9.8	25 cd	72 a	98 bc	3.0 a	22.5 ab
Significance					
Hybrid	***	***	**	NS	**
DLI	NS	NS	NS	NS	NS
Hybrid × DLI	NS	NS	NS	NS	NS

[z]Mean separation within columns by Tukey's honest significant difference (HSD) test at $P \leq 0.05$.

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

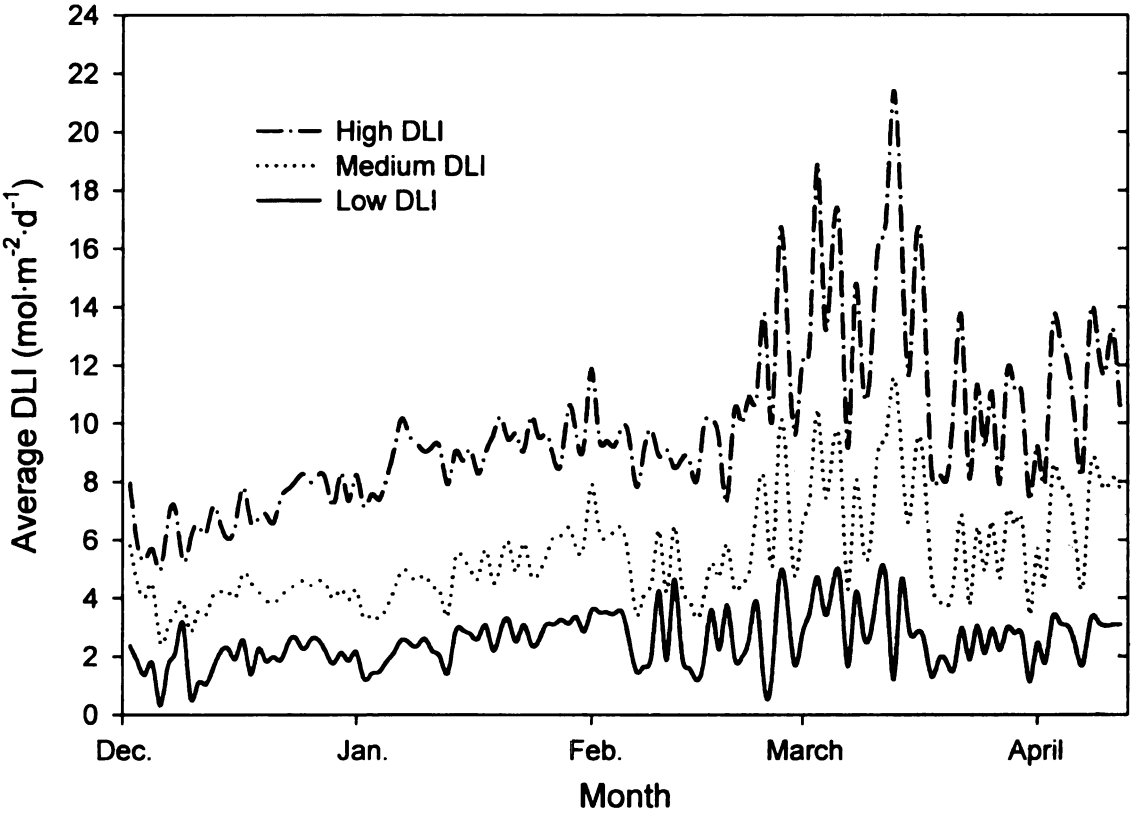

Figure 1. Daily light integral (DLI) at plant level under each light treatment during a 20-week period of vegetative growth at 28 °C.

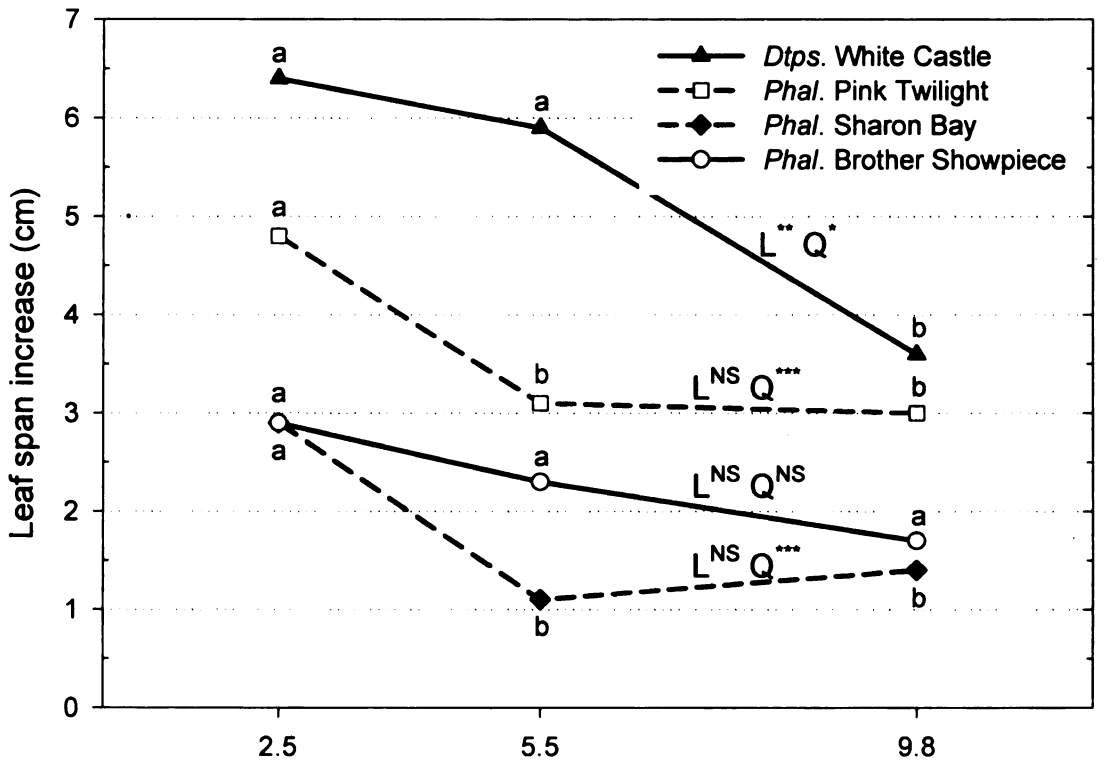

Figure 2. Average leaf span increase of *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', *Phalaenopsis* Pink Twilight '173', *Phalaenopsis* Sharon Bay '163', and *Phalaenopsis* Brother Showpiece under an average daily light integral (DLI) of 2.5, 5.5, or 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ for 20 weeks at 28 °C. Mean separation within hybrids by Tukey's honest significant difference (HSD) test at $P \leq 0.05$. L = linear, Q = quadratic trends; NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

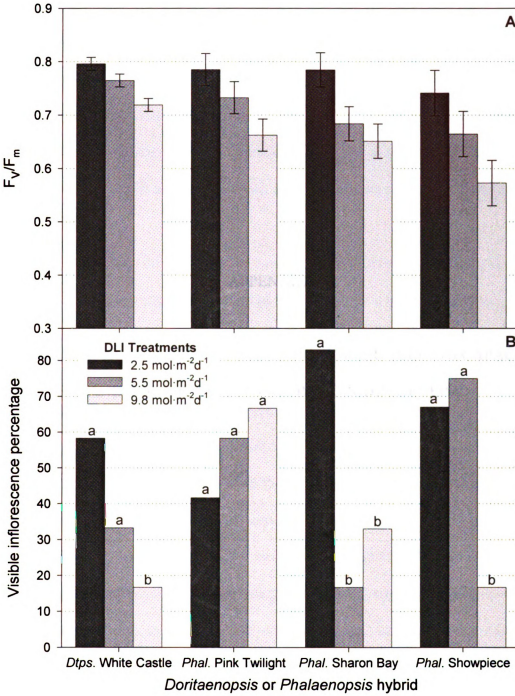

Figure 3. Chlorophyll fluorescence ratios (A) and visible inflorescence (VI) percentages (B) for *Doritaenopsis* (*Dtps.* White Castle × *Phal.* Moon World) '717', *Phalaenopsis* Pink Twilight '173', *Phalaenopsis* Sharon Bay '163', and *Phalaenopsis* Brother Showpiece following 20 weeks under an average daily light integral (DLI) of 2.5, 5.5, or 9.8 mol·m^{-2}·d^{-1}. Error bars represent 95% confidence intervals. VI percentages were analyzed using a binomial distribution with logit transformation and pair-wise comparisons within hybrids by chi-square (χ^2) test at $P \leq 0.05$.

APPENDIX B

EFFECTS OF TEN ORCHID MEDIAS ON PH, WATER-HOLDING CAPACITY, AND PERFORMANCE OF THREE ORCHID GENERA

Introduction

Orchids are currently the second most valuable potted crop in the United States with a total reported wholesale value of $127.6 million in 2004 (USDA, 2005a). Since 1996, when the United States Department of Agriculture (USDA) began collecting data for wholesale value of potted orchids, sales have increased by 172% (USDA, 2005b). In 2004, 17.2 million potted orchids were sold at wholesale with an average unit value of $7.41 (USDA, 2005b).

During commercial orchid production, growers use many different organic and inorganic materials to comprise the growing media, including activated charcoal, chopped coconut husks and fiber (*Coco nucifera* L.), cork (*Quercus suber* L.), Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] bark, expanded clay, osmunda fiber, peat, perlite, redwood bark [*Sequoia sempervirens* (D. Don) Endl.], rock wool, sphagnum moss, expanded polystyrene, tree fern fiber, vermiculite, and volcanic rock (Baker and Baker, 1991; Slump, 2004). Among all of these materials, the primary medium component used is Douglas fir bark, harvested by the logging industry on the Pacific coast of the United States (Wang, 2000). However, Douglas fir bark has several disadvantages: fresh bark has a low water-holding capacity; small or medium grade bark decomposes too quickly, resulting in high water retention; it has low nutrient retention and poor uniformity.

In addition, Douglas fir bark has the potential for limited availability in the future. The possible limited availability is related to the spread of a fungus, *Phytophthora ramorum* S. Werres and A.W.A.M. de Cock, which causes a disease known as sudden oak death (SOD) in the western United States (Wang and Barnes, 2004). In December

2004, The Animal and Plant Health Inspection Service (APHIS) issued a federal order restricting the interstate movement of nursery stock from all commercial nurseries in California, Oregon, and Washington (APHIS, 2004). Greenhouse grown orchids and Douglas fir bark are both currently exempt from this federal regulation, but these exemptions may change in the future. As a result of this and the many other problems associated with Douglas fir bark, commercial orchid growers are looking for alternative media combinations that have a reduced or no amount of fir bark.

The objective of this study was to determine how different percentages of fir bark, chopped coconut coir, perlite, and sphagnum moss influence pH, water-holding capacity and root and foliar performance of *Miltoniopsis*, *Paphiopedilum*, and *Phalaenopsis*. *Phalaenopsis* were chosen because of their popularity among commercial orchid growers and for their thick and smooth roots. *Miltoniopsis* were chosen for their fine root system, while *Paphiopedilum* were selected for their thick and hairy roots.

Materials and Methods

Plant Material

On 22 Sept. 2004, 100 plants each of *Miltoniopsis* Eastern Bay 'Claret Punch', *Paphiopedilum* Clair de Lune × Enchanted Orient, and *Phalaenopsis* Brother Goldsmith '720' were received in East Lansing, Mich. from a commercial greenhouse (Nurserymen's Exchange, Inc., Half Moon Bay, Calif.). *Miltoniopsis* and *Paphiopedilum* were received in 38-cell packs in media containing 60% medium-grade perlite and 40% sphagnum peat (by volume). *Phalaenopsis* were received in 10-cm pots in media containing 75% fine-grade Douglas fir bark,15% medium-grade perlite, and 10%

sphagnum peat (by volume). Plants of *Miltoniopsis* and *Paphiopedilum* were grown in a glass-glazed greenhouse at a constant temperature of 23 °C, while *Phalaenopsis* were grown at 29 °C to inhibit flowering. The photoperiod was a constant 16 h (0600 to 2200 HR) consisting of natural daylengths (lat. 42 °N) with day-extension lighting provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 20 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height [as measured with a quantum sensor (Apogee Instruments, Inc., Logan, Utah)]. Light transmission was reduced using woven shade curtains (OLS 50; Ludvig Svensson, Charlotte, N.C.) and whitewash applied to the glazing so that the maximum *PPF* at plant height was 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. A summary of plant material history is provided in Table 1.

Media Treatments

In Oct. 2003, ten plants of each genus were randomly selected and transplanted into one of ten orchid media mixes. These media mixes consisted of various percentages of medium-grade Douglas fir bark (Rexius Forest By-Products Inc., Eugene, Ore.), medium-grade chopped coconut coir (Millenniumsoils Coir, St. Catharines, Ont.), medium-grade perlite (Therm-O-Rock, Inc., New Eagle, Pa.), and long fiber Canadian sphagnum peat (Mosser Lee Co., Millston, Wis.) (Table 2). Plants of *Miltoniopsis* and *Phalaenopsis* were transplanted into 11.5-cm pots, while plants of *Paphiopedilum* were transplanted into 10-cm pots. *Miltoniopsis, Paphiopedilum*, and *Phalaenopsis* were grown in a glass-glazed greenhouse at a constant temperature of 20, 23, and 29 °C, respectively, and under a maximum *PPF* of 300, 140, and 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. Light transmission was reduced and the photoperiod was maintained as previously described. Each individual plant was irrigated as necessary with reverse osmosis water

supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (Greencare Fertilizers, Chicago, Ill.). Plants were irrigated pot-by-pot and not based on a fixed watering schedule.

Data Collection

Visual evaluations of foliage and root appearance and foliage and root development were made after 33, 52, and 83 weeks in each of the media mixes. On the day of evaluation, a plant of each hybrid in each media mix was randomly selected and removed from the growing medium to evaluate the roots. On several days during the experiment, one plant in each media mix was selected and the pH was measured with a pH meter (Orion Soil pH Meter, Model 410; Orion Research Inc., Boston, Mass.) using a 1:2 dilution method (1 part medium to 2 parts reverse osmosis water by volume).

At the beginning of the experiment and after 83 weeks, a sample from one plant in each growing media was collected and immersed in reversed osmosis water for 16 h. After 16 h, each media sample was poured into a 15-cm pot and allowed to drain for 1 h to achieve field capacity. The volume and weight of each media were measured and each sample was subsequently placed into a drying oven at a constant temperature of 38 °C. After seven days, samples were removed and weighed and the bulk density, porosity, and gravimetric moisture content were calculated for each media. Bulk density (BD) was calculated as:

$$\text{Bulk density} = W_s/V_s + V_p \qquad [1]$$

where BD is equal to the oven-dry weight of the sample (W_s) divided by the volume of solids (V_s) plus volume of pore space (V_p) (Brady and Weil, 1999). Porosity is expressed as the percentage of soil volume that is occupied by water and air and can be calculated using the equation:

$$\text{Porosity (\%)} = (1 - \text{BD/PD}) \times 100 \quad [2]$$

where particle density (PD) is assumed to be 1.0 $g \cdot cm^3$ (Brady and Weil, 1999). The gravimetric moisture content (GMC) is the percentage of water per oven-dry weight of the sample and is calculated using the equation:

$$\text{Moisture (\%)} = [(\text{moist soil weight} - \text{oven-dry weight})/\text{oven-dry weight}] \times 100 \quad [3]$$

Results and Discussion

Foliar and Root Evaluations

We performed several subjective evaluations throughout a 19-month period to determine differences in foliar and root development of the orchid genera grown in ten media mixes. Evaluations at week 33 and 52 showed that vegetative growth and foliar appearance were not influenced by any of the orchid media mixes for all orchid genera. However, root development and growth were noticeably different among orchid media mixes. For example, orchid media mixes that were composed of a high percentage (≥50%) of coconut coir (e.g., treatments 2, 4, 7, 8, and 9) had reduced root growth

compared to the other media mixes. Treatments with a high percentage of coconut coir also had dark discolored roots indicating possible infection by pathogens. Media mixes that consisted of 25% coconut coir had similar vegetative growth and root growth compared to other media mixes not containing coconut coir.

Evaluations at week 83 showed that vegetative growth and development were distinctly different among media mixes for all orchid genera. Plants that were grown in media mixes with a high percentage of coconut coir showed less vegetative growth than other treatments. For example in *Miltoniopsis*, the number of new pseudobulbs and leaf length were greater in plants grown in media mixes consisting of lower percentages ($\leq$25%) of coconut coir. Evaluations of root growth and development among all genera were consistent with the results from evaluations made at 33 and 52 weeks. Several plants of all three orchid genera in a media mix that consisted of 75% coconut coir died.

Miltoniopsis and *Paphiopedilum* grown in a media containing 80% bark (treatment 10) had less root growth compared to all other treatments except treatment 2, while *Phalaenopsis* performed well in 80% bark. The production of *Phalaenopsis* in media containing 80% fir bark was recommended in a previous study: Wang (1998) reported that a mixture of fine-grade fir bark and sphagnum peat (80% and 20% by volume, respectively) resulted in a greater leaf number, total leaf area, and shoot fresh mass compared to plants grown in a 100% fine-grade fir bark medium.

Bulk Density, Porosity, and Gravimetric Moisture Content

The initial and final bulk densities ranged from 0.07 to 0.17 $g \cdot cm^3$ and were variable among all media mixes (Table 3). Media mixes that consisted of $\geq$50% coconut

coir generally had the greatest initial and final porosities. For example, a medium composed of 50% coconut coir, 25% perlite, and 25% sphagnum peat (by volume) had a final porosity of 92.7%. In all media mixes porosity increased between initial and final measurements. These porous medias may be advantageous for commercial production because tropical epiphytic orchids perform best in substrates that allow air around their roots (Rittershausen and Rittershausen, 2003).

The initial GMC varied considerably different among all treatments and was generally greatest in media mixes with the highest proportion of coconut coir. The GMC was calculated to be ≥100% for all media mixes. These high GMC percentages are likely influenced by the high amounts of organic material, which can increase the water-holding capacity of the medium (Brady and Neil, 1999). In all media mixes, GMC increased between initial and final measurements. This increase in GMC during the study suggests that decomposition occurred in the media mixes. During decomposition of organic material there is an increase in water-holding capacity (Brady and Neil, 1999).

pH

The pH of each media mix was measured several times throughout the study and all media mixes showed a decreasing trend over time (Fig. 1). For example, in *Phalaenopsis* Brother Goldsmith '720', the initial and final pH values for treatment 6 were 5.1 and 4.2, respectively. This decreasing trend was similar for all three orchid genera and only data for *Phalaenopsis* Brother Goldsmith '720' is presented. In *Phalaenopsis*, the lowest pH occurred in treatment 10 (3.8) and may be related to the high percentage (80%) of fir bark included in this media mix. The final pH of all media

mixes was considerably below the recommended range (5.0 to 6.5) for growing *Phalaenopsis* (Anthura and Bureau IMAC, 2005). These low pH values indicate plants should be transplanted into fresh media or the pH should be raised.

In conclusion, these results suggest that during orchid production, the percentage of Douglas fir bark used in growing media can be reduced and supplemented with coconut coir. In general, orchid media consisting of 25% coconut coir could be used during the production of *Miltoniopsis*, *Paphiopedilum*, and *Phalaenopsis*. The increased percentage of coconut coir in orchid media could alleviate many of the problems that are associated with bark. In addition, we postulate that an orchid media containing 25% coconut coir will not degrade as rapidly as a media containing a higher percentage of fir bark. The incorporation of higher percentages (≥50%) of coconut coir in orchid media resulted in decreased foliar and root development and growth, pathogen infection, and sometimes death. Thus, to avoid these problems, orchid media should not consist of ≥50% coconut coir. This information could be beneficial to orchid growers seeking alternative media mixes with reduced amounts of fir bark.

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Table 1. Summary of production dates, container sizes, and greenhouse environmental conditions for *Miltoniopsis* Easter Bay 'Claret Punch', *Paphiopedilum* Claire de Lune × Enchanted Orient, and *Phalaenopsis* Brother Goldsmith '720' preceding and during experimentation.

	Plant material		
Description	*Milt.* Eastern Bay 'Claret Punch'	*Paph.* Claire de Lune × Enchanted Orient	*Phal.* Brother Goldsmith '720'
Received at Nurserymen's Exchange, Inc. (Half Moon Bay, Calif.)	November 2002 flask	7 June 2002 community flat	August 2003 bareroot
Transplanted	4 November 2002 38-cell pack[z]	10 February 2003 38-cell pack[z]	7 August 2003 10-cm pot[y]
Received at Michigan State University (East Lansing, Mich.)	22 September 2003	22 September 2003	22 September 2003
Transplanted into one of ten media mixes[x]	October 2003 11.5-cm pot	October 2003 10-cm pot	October 2003 11.5-cm pot
First foliar and root evaluation (33 weeks)	3 June 2004	3 June 2004	3 June 2004
Second foliar and root evaluation (52 weeks)	14 October 2004	14 October 2004	14 October 2004
Third foliar and root evaluation (83 weeks)	19 May 2005	19 May 2005	19 May 2005
Termination of experiment	19 May 2005	19 May 2005	19 May 2005

[z]Media consisting of 60% medium-grade perlite and 40% sphagnum peat (by volume).
[y]Media consisting of 75% fine-grade Douglas fir bark, 15% medium-grade perlite, and 10% sphagnum peat (by volume).
[x]Media mixes used in this study are provided in Table 2.

Table 2. Percentages and ratios of fine-grade Douglas fir bark, medium-grade chopped coconut coir, medium-grade perlite, and long fiber Canadian sphagnum peat (by volume) used in ten different orchid media mixes during experiment.

Treatment number	Material (%) by volume				
	Fir bark	Coconut coir	Perlite	Sphagnum peat	Ratio
1	75	0	12.5	12.5	6:0:1:1
2	0	75	12.5	12.5	0:6:1:1
3	50	25	12.5	12.5	4:2:1:1
4	25	50	12.5	12.5	2:4:1:1
5	50	25	25	0	2:1:1:0
6	50	25	0	25	2:1:0:1
7	25	50	25	0	1:2:1:0
8	25	50	0	25	1:2:0:1
9	0	50	25	25	0:2:1:1
10	80	0	10	10	8:0:1:1

Table 3. Initial and final bulk density, porosity, and gravimetric moisture content (GMC) of ten media mixes from *Phalaenopsis*. The change in GMC was caluclated by subtracting the initial GMC from the final GMC. Equations [1], [2], and [3] were used to calculate bulk density, porosity, and GMC, respectively.

Treatment number	Ratio[z]	Bulk density ($g \cdot cm^3$)		Porosity (%)		GMC (%)		Change in GMC (final - initial)
		Initial	Final	Initial	Final	Initial	Final	
1	6:0:1:1	0.17	0.12	84.9	87.8	170	358	+ 188
2	0:6:1:1	0.09	0.08	90.3	91.5	330	470	+ 140
3	4:2:1:1	0.13	0.11	87.1	89.5	246	314	+ 68
4	2:4:1:1	0.08	0.12	89.1	90.8	321	365	+ 44
5	2:1:1:0	0.15	0.11	85.3	89.1	203	318	+ 115
6	2:1:0:1	0.09	0.10	87.7	90.4	289	383	+ 95
7	1:2:1:0	0.13	0.09	87.1	91.4	245	428	+ 183
8	1:2:0:1	0.08	0.09	89.1	91.2	356	362	+ 7
9	0:2:1:1	0.08	0.07	90.2	92.7	399	414	+ 14
10	8:0:1:1	0.13	0.12	85.9	88.3	175	238	+ 64

[z]Ratio of fine-grade Douglas fir bark, medium-grade chopped coconut coir, medium-grade perlite, and long fiber Canadian sphagnum peat used in media mix.

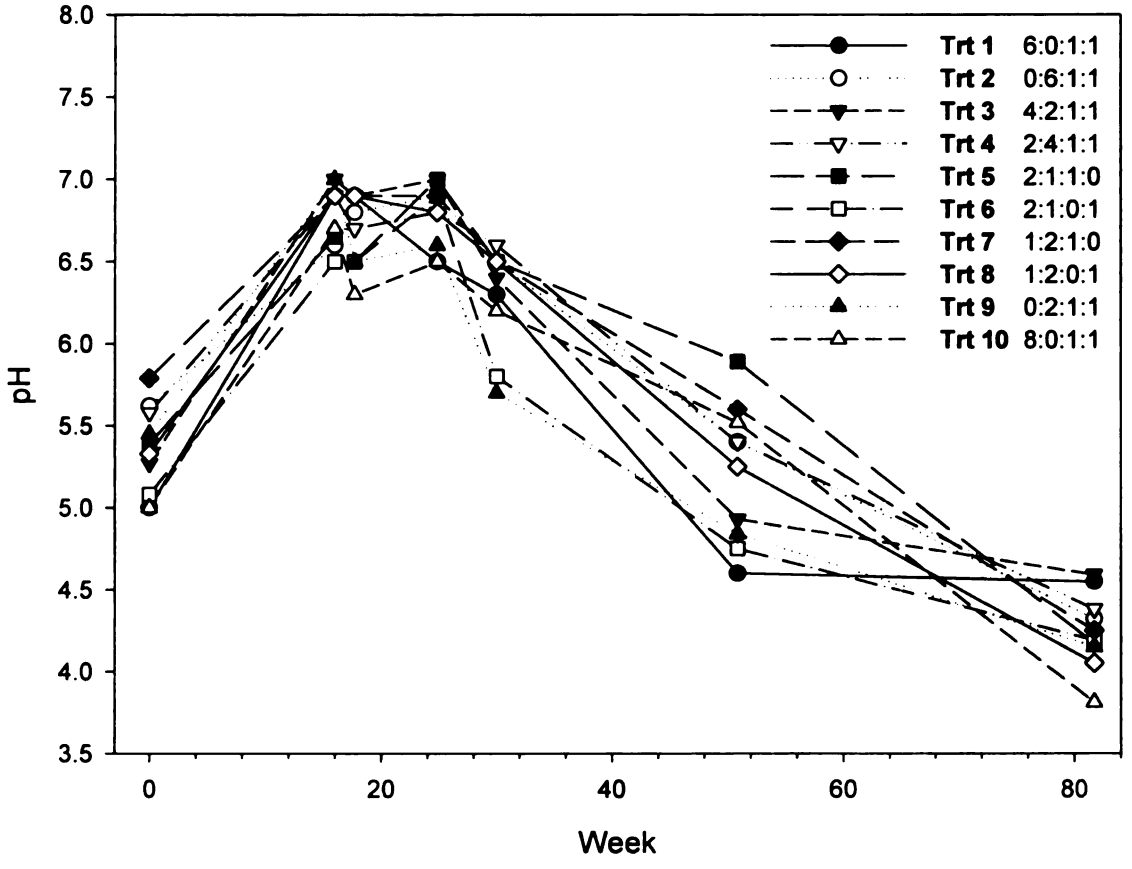

Figure 1. Effect of ten orchid media mixes on media pH of *Phalaenopsis* Brother Goldsmith '720' during a 19-month period from 20 October 2003 to 19 May 2005. Treatment ratios represent the proportion of fine-grade Douglas fir bark, medium-grade chopped coconut coir, medium-grade perlite, and long fiber Canadian sphagnum peat used in each media mix. The pH of each media was measured using a 1:2 dilution method (1 part medium to 2 parts reverse osmosis water by volume).