

The Effect of Temperature on Leaf and Flower Development and Flower Longevity of *Zygopetalum* Redvale ‘Fire Kiss’ Orchid

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Abstract. The vegetatively propagated ‘Fire Kiss’ clone of the hybrid *Zygopetalum* Redvale orchid has appealing potted-plant characteristics, including fragrant flowers that are waxy lime-green and dark maroon with a broad, three-lobed, magenta and white labellum. We performed experiments to quantify how temperature influenced leaf unfolding and expansion, time from visible inflorescence to flower, and longevity of individual flowers and inflorescences. Plants were grown in controlled-environment chambers with constant temperature setpoints of 14, 17, 20, 23, 26, and 29 °C and an irradiance of 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 9 h·d⁻¹. As actual temperature increased from 14 to 25 °C, the time to produce one leaf decreased from 46 to 19 days. Individual plants were also transferred from a greenhouse to the chambers on the date that an inflorescence was first visible or the first flower of an inflorescence opened. Time from visible inflorescence to open flower decreased from 73 days at 14 °C to 30 days at 26 °C. As temperature increased from 14 to 29 °C, flower and inflorescence longevity decreased from 37 and 38 days to 13 and 15 days, respectively. Data were converted to rates, and thermal time models were developed to predict time to flower and senescence at different temperatures. The base temperature was estimated at 6.2 °C for leaf unfolding, 3.5 °C for time to flower, and 3.7 °C for flower longevity. These models could be used by greenhouse growers to more accurately schedule *Zygopetalum* flowering crops for particular market dates.

Potted flowering orchids are produced in large quantities throughout the world. For example, in 1995, the world demand for potted orchids was estimated at 1.22 billion units of plant stock (Hew and Yong, 1997). Orchids are the second most valuable flowering potted crop in the United States, with an estimated wholesale value in 2002 of approximately \$105.6 million (U.S. Department of Agriculture, 2003). However, environmental effects on growth and development of most orchid species are poorly understood, or not at all. Notable exceptions include some species and hybrids of *Phalaenopsis*, *Cattleya*, *Cymbidium*, and *Dendrobium*. In these genera, low temperature, short photoperiods, or both regulate the flowering process (Ichihashi, 1997; Rotor, 1952; Sakanishi et al., 1980).

Zygopetalum, or the ladybird orchid, is a sympodial terrestrial and epiphytic South American genus composed of 20 species (Rittershausen and Rittershausen, 2000). They are native to neotropical mountains (1,300 to 1,700 m) of Brazil, Guiana, Venezuela, and Peru (Rose,

1993). The hybrid *Zygopetalum* Redvale ‘Fire Kiss’ has attributes that make it an appealing potted plant. It is moderately compact (25 to 40 cm tall) and has exotic, waxy flowers with lime-green and dark-maroon sepals and petals, a broad magenta and white three-lobed labellum, and a strong, sweet, and spicy fragrance. Flowering of *Zygopetalum* is promoted by short days (SDs) followed by cool temperatures (e.g., 14 °C), but the effects of temperature on growth and inflorescence development and longevity have not been determined (Lopez et al., 2003).

In the United States, potted flowering plants are commonly produced, marketed, and purchased for holidays such as Christmas, Valentine’s Day, Easter, and Mother’s Day. This requires an understanding of the flowering process so that greenhouse growers can schedule crops into flower for specific market dates. Plants that do not have flowers or have flowers that are too immature (e.g., only flower buds) or are all open are often not sold or are sold for a lower price. Therefore, scheduling a crop of *Zygopetalum* to flower for a specific, predetermined market date has not been possible.

Temperature controls the rate of plant development, including time to unfold a leaf and time for an inflorescence to develop open flowers. Mathematical models have been developed to assist greenhouse growers with scheduling of flowering crops [e.g., *Lilium longiflorum* Thunb. (Fisher et al., 1996; Healy and Wilkins, 1984)]. Once plants have been grown at a variety of temperatures and time to reach a particular event (e.g., flowering) is quantified, data can be converted into rates. For example, the reciprocal

of days to flower becomes the rate of progress toward flowering. Developmental rate is zero at or below a species-specific base temperature (T_b) and is maximum at the optimal temperature (T_{opt} ; Roberts and Summerfield, 1987). Between T_b and T_{opt} , rate of development is linear and can be described as

$$1/\text{days} = b_0 + b_1 T \quad [1]$$

where days is days to flowering, T is temperature, and b_0 and b_1 are species-specific constants. The base temperature, T_b , can be calculated as

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

Thermal time, or time to reach a particular developmental stage, can be quantified in degree-days ($^{\circ}\text{C}\cdot\text{d}^{-1}$), which is calculated as

$$^{\circ}\text{C}\cdot\text{d}^{-1} = 1/b_1 \quad [3]$$

Therefore, if the average daily temperature is T_a , the days necessary to complete a developmental process can be calculated by $(^{\circ}\text{C}\cdot\text{d}^{-1})/(T_a - T_b)$.

In addition to time to flower, temperature also influences flower longevity of potted plants. For example, the overall flower longevity of potted *Rhipsalidopsis gaertneri* Reg. (Moran), an epiphyte with a geographic distribution similar to that of *Zygopetalum*, decreased from 43 to 26 d as temperature increased from 18 to 24 °C (Hartley et al., 1995). To maximize cut flower longevity, *Cattleya*, *Cymbidium*, and *Dendrobium* orchid flowers are often stored at 10 to 14 °C; however, temperatures below this range can cause chilling injury (Sacalis, 1989, 1993).

Information on the time required to reach a developmental stage is critical to developing crop production schedules. The objectives of this study were to determine the relationship between temperature and 1) leaf unfolding rate (LUR) and expansion; 2) time from visible inflorescence to flower; and 3) flower and inflorescence longevity of *Zygopetalum* orchids.

Materials and Methods

Plant material. Vegetatively propagated ‘Fire Kiss’ clone of the hybrid *Zygopetalum* Redvale (*Zygopetalum* Artur Elle \times *Zygopetalum* Titanic) plants were grown in a commercial greenhouse (Nurserymen’s Exchange, Inc., Half Moon Bay, Calif.), transplanted into 38-cell plug trays in June 2000, and then into 10-cm pots in April 2001. Plants were grown at 16 to 26 °C under natural photoperiods (lat. 37 °N) with a maximum photosynthetic photon flux (PPF) of 350 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Five hundred plants in a fine-grade 4 fir bark : 1 perlite-based media were received in East Lansing, Mich., on 6 May 2001. They were maintained at 24 ± 2 °C in a glass-glazed greenhouse until experiments began. The photoperiod was a constant 16 h (0600 to 2200 HR), consisting of natural daylengths (lat. 42 °N) with day-extension lighting from high-pressure sodium (HPS) lamps, which delivered a supplemental PPF of 20 to 35 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height [as measured with

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Table 1. Actual average daily air temperatures of environmental chambers for each experiment.

Experiment	Year	Air temp setpoint (°C)					
		14	17	20	23	26	29
1	1	13.4	16.7	19.5	22.4	24.8	28.6
	2	13.4	17.3	19.5	22.4	25.5	---
2	1	13.5	17.4	19.5	22.0	25.5	---
	2	12.2	17.6	21.1	23.5	25.7	---
3	1	13.4	17.1	19.5	25.9 ^y	25.4	28.6
	2	13.3	17.4	19.6	22.3	25.5	---

^zTemperature not used.

^yPlants were grown in a greenhouse.

a line quantum sensor (Apogee Instruments, Inc., Logan, Utah)].

Plant culture. In Year 1, plants were fertilized at every irrigation using well water containing 95, 34, and 29 mg·L⁻¹ Ca, Mg, and S, respectively, supplemented with water-soluble fertilizer to provide the following (mg·L⁻¹): 125 N, 12 P, 125 K, 13 Ca, 1.0 Fe, 0.1 B and Mo, and 0.5 Mn, Zn, and Cu (MSU Special; Greencare Fertilizers, Chicago, Ill.). Water was acidified with H₂SO₄ to a titratable alkalinity of ≈140 mg·L⁻¹ CaCO₃. In Year 2, plants were irrigated as necessary with reverse osmosis water supplemented with water-soluble fertilizer to provide the following (mg·L⁻¹): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo.

Temperature and photoperiod control. All experiments were performed in walk-in controlled-environment chambers with constant temperature set points of 14, 17, 20, 23, and 26 °C. In Year 1 of Expts. 1 and 3 (see below), an additional chamber set at 29 °C was used. In Expt. 1, Year 1, the 23 °C treatment was provided in a greenhouse. Air temperature in each chamber was measured by an aspirated thermocouple every 10 s and hourly averages were recorded by a datalogger (CR-10; Campbell Scientific, Logan, Utah). The average daily air temperatures for all experiments were calculated (Table 1).

For Expt. 1, Year 1, each chamber was divided in half with black plastic, and two photoperiods were created: 9 h of light with or without a 4-h (2200 to 0200 HR) night interruption (NI). The 9-h SD base photoperiod was provided by a combination of cool-white fluorescent (VHOF96T12; Philips, Bloomfield, NJ) and incandescent lamps from 0800 to 1700 HR at 150 μmol·m⁻²·s⁻¹. NI lighting (2 to 3 μmol·m⁻²·s⁻¹ at canopy level) was provided by incandescent lamps. In Year 2, only a 9-h photoperiod was provided because photoperiod did not influence leaf development in Year 1.

Leaf development (Expt. 1). The experiment was replicated in time, beginning on 12 June 2001 (Year 1) and 19 Feb. 2002 (Year 2). Experimental treatments were identical between years, unless otherwise noted. Ten plants were assigned randomly to each of the SD and NI sections of the walk-in controlled-environment chamber. At the beginning of the experiment, one immature pseudobulb was identified and leaf unfolding was recorded weekly by counting the number of leaves from the top of the medium to the terminal end of the pseudobulb. A new leaf was counted as it became visible at the apex. The leaf length of a marked immature leaf was measured weekly (measured

from the medium surface to the leaf tip) and the incremental increase in leaf expansion was calculated. Plants were grown for 20 weeks, except for those at 29 °C, in which observations were terminated after 13 weeks because of declining growth and plant mortality.

Flower development (Expt. 2). The experiment was replicated in time, beginning on 12 Apr. 2002 (Year 1) and 19 Mar. 2003 (Year 2), with 10 plants per treatment. Plants were grown in a glass greenhouse, and on the date at which the first inflorescence was visible (visible

inflorescence, or VI) without dissection (<1 cm long), plants were transferred to one of the five growth chambers until 10 plants were in each chamber. The date each plant was placed in the chamber and the date the first and subsequent flowers opened were recorded for each plant. At flowering, the number of flower buds and nodes on immature pseudobulbs below the inflorescence were counted and inflorescence length was measured. Days to flower and air temperature during that period were calculated for each plant.

Flower and inflorescence longevity (Expt. 3). The experiment was replicated in time, beginning on 8 Aug. 2001 (Year 1) and 14 Feb. 2002 (Year 2). Plants were grown in a glass greenhouse, and on the date that the first flower of an inflorescence opened on each plant, it was transferred to one of the growth chambers. The date that each plant was placed in a chamber and the date of flower mortality (senescence) of the first and subsequent flowers were recorded for each plant. The date of flower senescence was defined as the day that half of the labellum

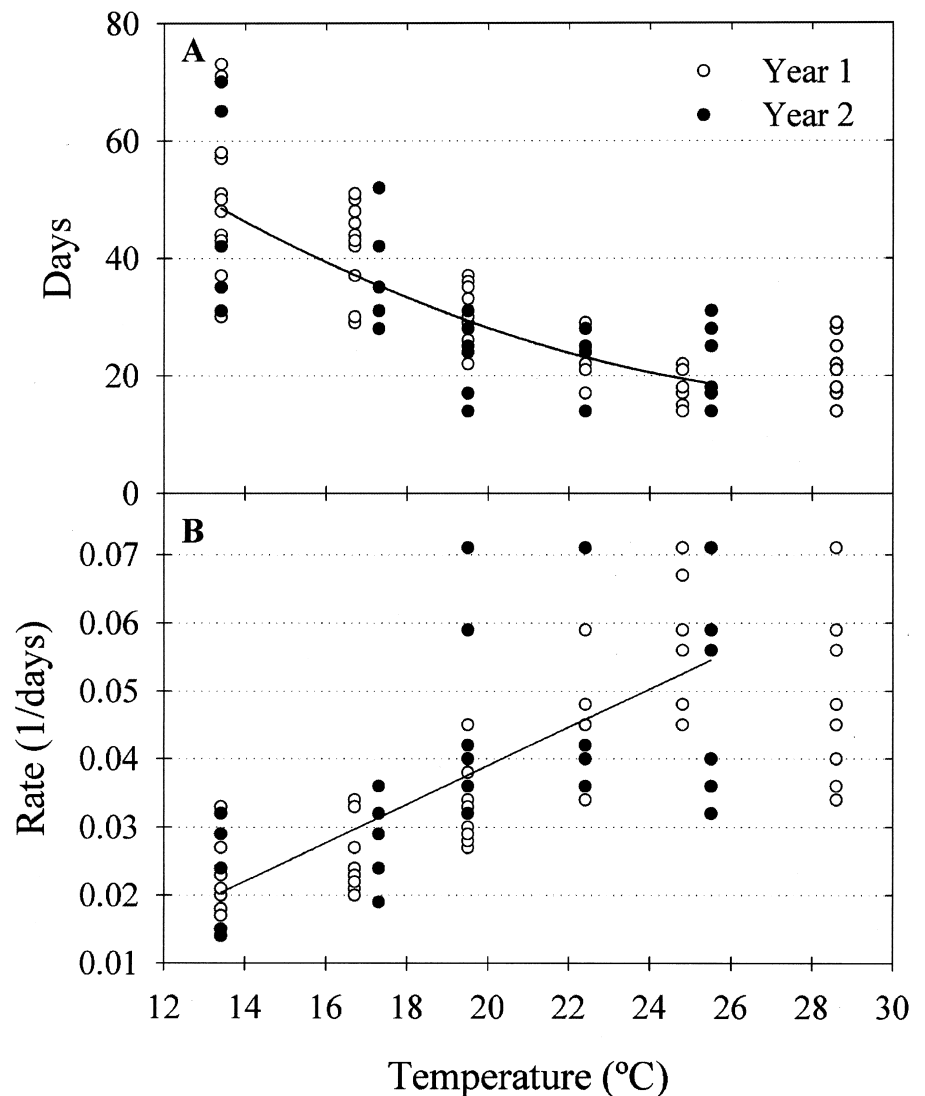


Fig. 1. Influence of forcing temperature on individual leaf unfolding of *Zygopetalum* Redvale 'Fire Kiss'. Each symbol represents an individual plant. The solid lines represent the regression equations using pooled data for Years 1 and 2. Data at 28.6 °C were not included in the regression equation. Statistical analysis is presented in Table 2.

Table 2. Parameters of linear regression analysis relating temperature to rate of progress for leaf development, time from visible inflorescence to flower, flower longevity of the first flower, and inflorescence longevity in *Zygopetalum* Redvale 'Fire Kiss'.^z

Developmental stage	Intercept (b_0) (1/days)	Slope (b_1) (1/days)/°C	T_b (°C)	°C·d ⁻¹	r^2
Leaf unfolding	-0.0174 ± 0.0038 ^y	0.0028 ± 0.0002	6.2	357	0.60***
Visible inflorescence to flower	-0.0053 ± 0.0016	0.0015 ± 0.0001	3.5	667	0.89***
Longevity of first flower	-0.0100 ± 0.0047	0.0027 ± 0.0002	3.7	370	0.66***
Inflorescence longevity	-0.0094 ± 0.0042	0.0026 ± 0.0002	3.6	385	0.69***

^zThe intercept and slope were used in Eqs. [1] and [2] to calculate base temperature (T_b) and thermal time to complete a particular developmental stage (°C·d⁻¹).

^yStandard error.

***Significant at $P \leq 0.001$.

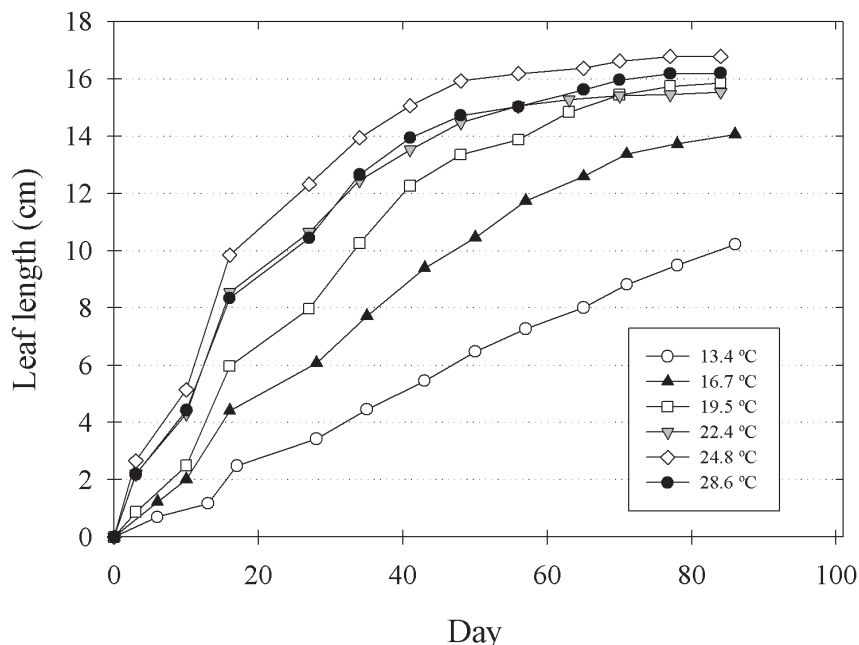


Fig. 2. Influence of forcing temperature on increase in leaf length (measured from the medium surface to the leaf tip) in *Zygopetalum* Redvale 'Fire Kiss'. Each symbol represents the average of 20 plants.

was discolored or wilted. Individual flower and inflorescence longevity was calculated for each plant at each temperature.

Data analysis. Each year, a completely randomized block design was used. Data were analyzed using SAS (SAS Institute, Cary, N.C.) mixed model procedure (PROC MIXED) for analysis of variance and linear models procedure (PROC REG) for regression models. Data were pooled in each experiment for all measured characteristics. The mean time to flower, LUR, and flower and inflorescence longevity at each temperature were converted to rates by taking the reciprocal (1/days). The relationship between rate of progress to flowering, leaf development or flower senescence (1/days) and mean temperature T in °C were determined by Eqs. [1], [2], and [3] to calculate T_b and °C·d⁻¹. Within each developmental stage, slopes and intercepts were computed.

Results

Leaf development (Expt. 1). Photoperiod had no significant effect on leaf unfolding or leaf expansion, and thus data for both photoperiods were pooled. Time to unfold one leaf decreased as temperature increased, until it reached a minimum at ≈25 °C (Fig. 1). The

time required to produce one leaf averaged 46 d at 14 °C and 19 d at 25 °C. The rate of leaf unfolding was a linear function of temperature until ≈25 °C (Table 2). The base temperature for LUR was estimated at 6.2 °C, and the degree-days required to develop one leaf was 357 °C·d⁻¹ (Table 2).

As temperature increased from 13 to 25 °C, leaf expansion increased ($P \leq 0.001$) (Fig. 2). Leaves became mature earlier at higher temperatures, and thus the incremental increase in leaf length began to decrease earlier at the higher temperatures. For example, at 28.6 °C leaves achieved their maximum size earliest (<80d), and at 13.4 °C, >100 d elapsed after the start of the experiment before leaf length began to reach a maximum (data not shown).

Flower development. Time from VI to flower opening decreased with increasing temperature, with an average of 73 d at 14 °C and 30 d at 26 °C (Fig. 3). Rate of progress from VI to flowering was linear within the range of temperatures tested (Fig. 3). The base temperature was estimated at 3.5 °C for time from VI to flower, and estimated thermal time was 667 °C·d⁻¹ (Table 2). The average flower count of each inflorescence was 3.8 and was not significantly influenced by temperature (data not presented). Average inflorescence length

varied among the temperature treatments (26 to 37 cm), however no significant trends existed (data not presented).

Flower and inflorescence longevity. As temperature increased from 14 to 29 °C, longevity of the first open flower decreased from 37 d to 13 d (Fig. 4). Inflorescence longevity followed a similar pattern, decreasing from 38 d at 14 °C to 15 d at 29 °C. Flower longevity of the second and subsequent flowers decreased by 1 to 3 d in comparison to the longevity of the first open flower at all temperatures studied (data not presented).

Flower and inflorescence longevity data were converted to rates, and a thermal time model was developed to predict senescence at different temperatures. Rate of progress to senescence of individual flowers and inflorescences was linear within the range of temperatures tested (Table 2). The base temperatures were estimated at 3.7 and 3.6 °C, and the accumulated thermal time lifespan was 370 and 385 °C·d⁻¹, respectively.

Discussion

As temperature increased from 14 to 26 °C, the developmental rate at various stages of growth and development of *Zygopetalum* increased. Increasing temperature from 14 to 25 °C hastened leaf unfolding and expansion, accelerated time from VI to flower, and reduced the longevity of open flowers and inflorescences. Temperatures >25 °C were generally superoptimal. For example, some flower buds of plants grown at the warmest temperatures developed necrotic lesions and aborted within 20 d. In addition, leaf development (unfolding and expansion) was maximal around 25 °C and was retarded when the constant daily temperature was greater. Therefore, the optimal temperature for most rapid growth and development of *Zygopetalum* appears to be about 25 °C. The calculated base temperature of *Zygopetalum* was also similar among developmental phases and was between 3.5 and 6.2 °C.

A similar response to temperature has been observed in *Phalaenopsis* orchid. As temperature increased from 14 to 26 °C, the rate of leaf, bud, and flower development increased linearly in several hybrids (Robinson, 2002). The optimal temperature for growth of *Phalaenopsis*, which is native to tropical and subtropical areas of the South Pacific Islands and Asia, appeared to be 26 °C (Robinson, 2002). The calculated base temperature of *Phalaenopsis* was between 8 and 12 °C, which is 4 to 6 °C higher than that reported here for *Zygopetalum*. This is not surprising, because *Zygopetalum* species are native to neotropical mid-elevation mountains (1,300 to 1,700 m) that have moderate climates (Rose, 1993).

Leaf development and flower longevity were modeled as a function of temperature and were found to accurately predict the time of these developmental processes. To complete a developmental process, a plant must experience a specific number of units of degree-days (or thermal time) above the base temperature characteristic of that process (Roberts and Summerfield, 1987). For example, the model predicted

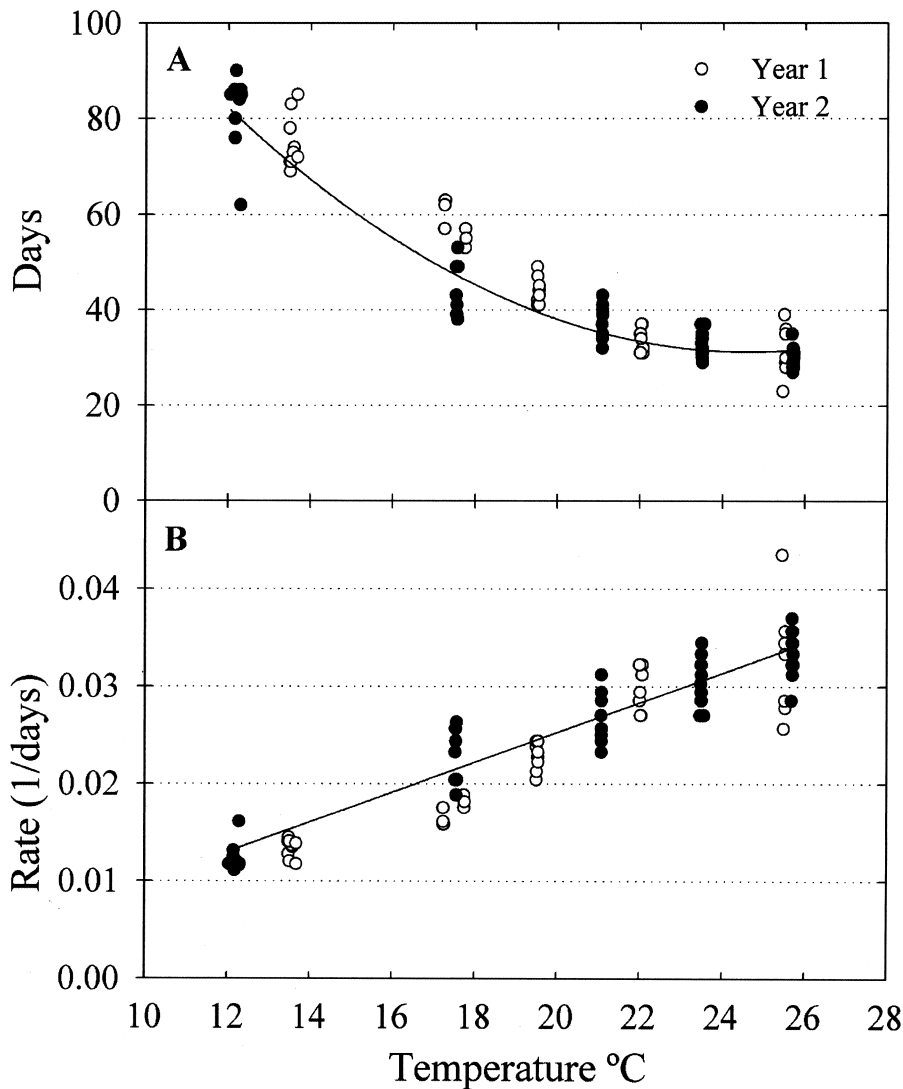


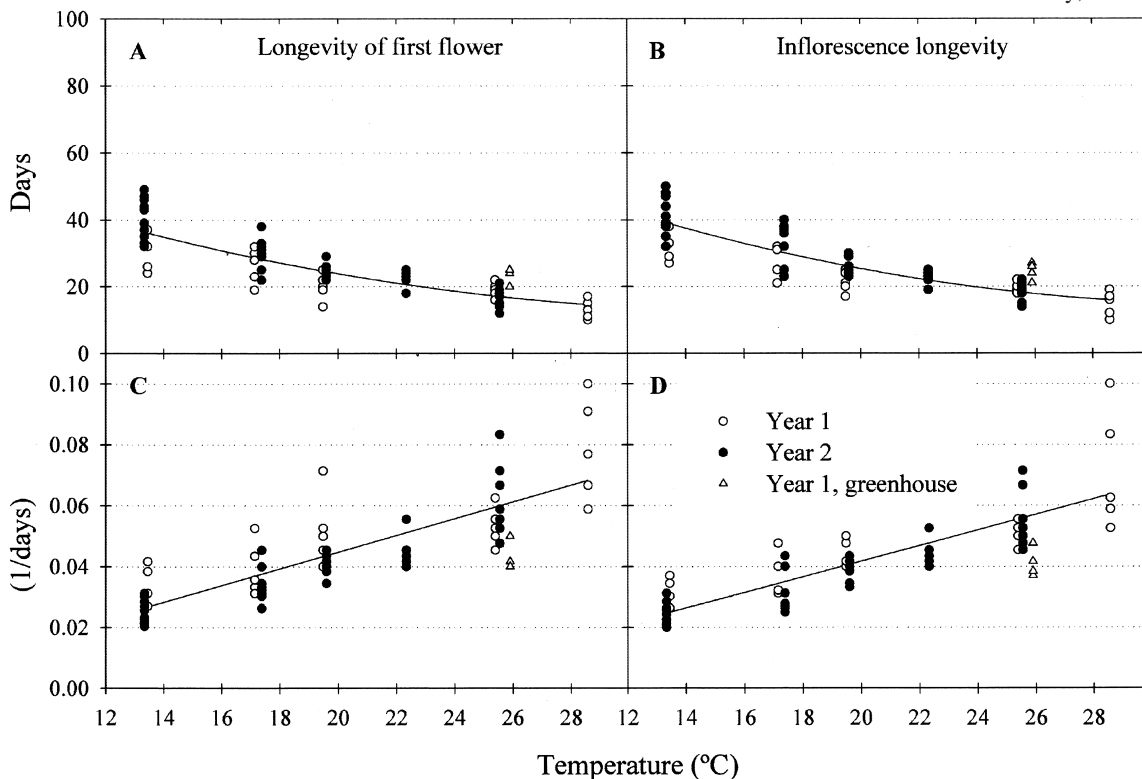
Fig. 3. Influence of forcing temperature on time from visible inflorescence (VI) to flower in *Zygopetalum* Redvale 'Fire Kiss'. Each symbol represents an individual plant. (A) Days from VI to flower. The solid line represents the regression equation using pooled data for Years 1 and 2. The line in (B) represents predicted values for the rate of progress (1/days) to flowering according to linear regression. Statistical analysis is presented in Table 2.

that time from VI to flower for *Zygopetalum* grown at 26.0 °C ($T_b = 3.5$ °C) is estimated at 667 °C·d⁻¹/(26.0 ± 3.5 °C) = 30 d.

Actual time from VI to flower for plants forced at 26 °C was 30 d. Flower longevity was also accurately predicted by our model; plants grown at 14 °C ($T_b = 3.7$ °C) had an estimated accumulated thermal time lifespan of (370 °C·d⁻¹/10.3 °C) = 36 d. Actual flower longevity observed was 37 d. Therefore, these models could be used by greenhouse growers to coordinate flowering with specific market dates and to maximize flower longevity.

Thermal time models can also be used to maximize the flower life of potted flowering plants. Providing optimal shipping and storage temperatures between production greenhouses and retail outlets could significantly improve flower longevity. Our flower longevity experiments were performed at temperatures from 14 to 29 °C, and our model estimated that the T_b for flower longevity was 3.6 °C. However, previous studies have shown that potted *Zygopetalum* develop symptoms of chilling injury at temperatures ≤ 8 °C (unpublished data). Therefore, the optimal temperature for flower and inflorescence longevity is likely between 8 and 14 °C, which agrees with temperatures recommended to maximize cut flower life of orchids (10 to 14 °C; Sacalis, 1989, 1993).

In summary, these experiments suggest that



an optimal temperature for vegetative growth of *Zygopetalum* is between 20 and 25 °C, and further increases in temperature have little impact on the rate of leaf development.

Fig. 4. Influence of forcing temperature on longevity of the first open flower (A and C) and inflorescence (B and D) of *Zygopetalum* Redvale 'Fire Kiss'. Each symbol represents an individual plant. The solid lines represent the regression equation using pooled data for Years 1 and 2. Lines in C and D represent predicted values for the rate of progress (1/days) to the indicated developmental stage according to linear regression. Statistical analysis is presented in Table 2.

For example, according to our model, plants grown at 23 °C developed one leaf about 2 d slower than plants grown at 26 °C. Following flower induction, a finish forcing temperature of 20 to 23 °C is suggested for relatively rapid flower development and acceptable flower quality. However, temperature can be adjusted using our model to help meet specific finish dates. Flower and inflorescence longevity of *Zygopetalum* placed in the average home or office (20 °C) is estimated at 23 d if light and water are not limited.

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