This is to certify that the

thesis entitled

Temperature Effects on Timing and Bud Development of Coreopsis verticillata 'Moonbeam' and Flower Induction of Long-day Perennials under Different Night Temperatures

presented by

Alison J. Frane

has been accepted towards fulfillment
of the requirements for

Masters degree in Horticulture

William H. Carlson
Major professor

Date February 11th, 1999

TEMPERATURE EFFECTS ON TIMING AND BUD DEVELOPMENT OF COREOPSIS VERTICILLATA 'MOONBEAM' AND FLOWER INDUCTION OF LONG-DAY PERENNIALS UNDER DIFFERENT NIGHT TEMPERATURES

By

Alison J. Frane

A THESIS

Submitted to

Michigan State University

in partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

Department of Horticulture

1999

ABSTRACT

TEMPERATURE EFFECTS ON TIMING AND BUD DEVELOPMENT OF COREOPSIS VERTICILLATA 'MOONBEAM' AND FLOWER INDUCTION OF LONG-DAY PERENNIALS UNDER DIFFERENT NIGHT TEMPERATURES

By

Alison J. Frane

Effects of forcing temperature on flowering of *Coreopsis verticillata* 'Moonbeam' were recorded. Plants were initially cooled for twelve weeks and then grown under 16-hr long days (4-h night interruption in the first year) in greenhouses set at 17, 20, 23, 26, and 29°C. Flower size, flower number and time to flower decreased as temperature increased. The relationship between flower bud diameter, temperature and time to flower was modeled as a sigmoid logistic function. Models for time to visible bud (VB), flower (FLW) and from VB to FLW were developed using a linear function of rate of development.

The effectiveness of a four-hour night interruption (NI) to induce flowering in several species of long-day herbaceous perennials was tested at six different night temperatures. Eight herbaceous perennials were grown under natural short days augmented with a four-hour NI. Night temperatures were set at 2.5, 5, 10, 15, 20, and 25 °C with a day temperature of 25 °C for all treatments. While some species showed an increase in the number of nodes developed prior to flower induction and a lower flowering percentage at night temperature treatments above 20° C, night temperatures as low as 3.9° C (4.9°C in the second year) did not inhibit flowering of any species.

To my brother, Alex

who always makes me laugh

ACKNOWLEDGMENTS

I want to thank my advisor, Dr. Will Carlson, for believing in me, encouraging me when my spirits lagged and for giving me the benefit of his prodigious insight into human nature. I'd like to thank the other members of my committee as well: Dr. Royal Heins for his helpful and informative guidance in analyzing data and working on experiments; Dr. Art Cameron for his knowledge and undying enthusiasm regarding perennials; and last but not least, Dr. Ken Poff for asking the difficult questions and saying what no one else will say.

I would also like to thank the other graduate students et al.: Emily Clough, Beth Fausey, Leslie Finical, Antonis Kanavouras, Paul Koreman, Bin Liu, Mary-Slade Morrison, Genhua Niu, Erik Runkle, Cara Wallace and Cathy Whitman for their company, advice and support as well as Shiying Wang and Hiroshi Shimizu for their help analyzing data.

Tom Wallace, Dan Tschirhart, and all the undergraduate workers at the greenhouse were also invaluable in carrying out the experiments. It would not have been possible without them.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LITERATURE REVIEW

Many plants develop and flower in a seasonal pattern. It is advantageous for a plant to flower during a season in which it has adequate moisture and light, and moderate temperatures. Just as important is the avoidance of stressful conditions not conducive to growth and reproduction.

How do plants regulate developmental events to occur at the optimal time? If plants simply responded to the presence or absence of favorable weather conditions, accurate and consistent timing of developmental events would be a rarity. In the natural environment, many plants use photoperiod to regulate timing, as this is one of the most reliable indicators of the time of year. In temperate zones, plants may also use the process of vernalization to detect whether the unfavorable conditions of winter have passed.

Temperature during the growing season also has a marked effect on development and timing. In a controlled environment, we can manipulate the timing and magnitude of flowering for our own purposes by adjusting photoperiod and temperature. This review will focus on photoperiodic response, modeling temperature effects on rate of development, and how temperature can alter the photoperiodic response.

Photoperiod

The term photoperiod literally means period, or duration of the cycle, of light. Thus photoperiod is the length of the light period (also referred to as daylength). Under natural conditions, however, the length of the light period is directly related to the length of the dark period. While photoperiodic responses

could be dependent on the length of the light period or the length of the dark period, or their relative lengths, it turns out that for most plants night length is actually most important in determining photoperiodic response (Thomas and Vince-Prue, 1984).

The photoperiodic responses of plants can be divided into three basic categories, based on daylength. First, there are those plants that flower only if the photoperiod is short enough (night is long enough), or which flower faster or more profusely as days become shorter (nights become longer). These are commonly called short-day plants (SDP). Other plants flower only if the length of the photoperiod is long enough (night is short enough), or their flowering response increases as the length of the photoperiod increases (night length decreases). These are termed long day plants (LDP.) Finally, there are the aptly named day neutral plants (DNP) in which flowering response is not linked to photoperiod at all. There also exist plants with dual daylength requirements i.e. a period of short days and then a period of long days, or vice versa (SLDP and LSDP respectively) (Thomas and Vince-Prue, 1997).

Plants that respond to photoperiod have been further divided into two categories: qualitative or quantitative. A qualitative response (also known as an obligate response) is characterized by a response to the quality of the photoperiod — either inductive or not inductive (Thomas and Vince-Prue, 1997). For instance, a qualitative LDP flowers only when the photoperiod is longer than a certain daylength, termed the critical photoperiod (Thomas and Vince-Prue, 1984) Below the critical photoperiod, an obligate LDP will not flower. Similarly, a

qualitative SDP flowers only when the photoperiod is shorter than a certain daylength, also termed the critical photoperiod.

A quantitative, or facultative response, on the other hand, is characterized by a flowering response that varies with the quantity of light and darkness (measured in hours) (Thomas and Vince-Prue, 1997, p.3.) For a quantitative LDP, the longer the photoperiod, the greater the magnitude of flowering response (as measured by how fast or profusely the plant blooms.) A quantitative SDP flowers faster or more profusely with shorter photoperiods. A quantitative plant will eventually bloom under any photoperiod (Thomas and Vince-Prue, 1984)

Perception of Photoperiod

In order for plants to have any photoperiodic response, they must be able to perceive daylength in some manner. This mechanism must also be fairly precise if it is to accurately determine the time of year, especially at lower latitudes, where the change in daylength throughout the year is relatively small. For a long time, it was thought that plants measured the photoperiod by some sort of "hourglass" mechanism, whereby a series of chemical steps was thought to occur in the dark period. The plant would sense night length by how many steps had been completed by the end of the night. This theory has largely been replaced by a circadian rhythm theory (Thomas and Vince-Prue, 1997).

The word circadian comes from the Latin for "around one day," a circadian rhythm being a cyclic response throughout the natural 24 hr period of a day.

Organisms with circadian rhythms are not simply responding to the light and dark periods that occur during that day, however. The rhythmic response is coupled to an unseen internal oscillator, which continues even if these stimuli are taken away, although usually not indefinitely. The period of this rhythm, now referred to as "free running," in the absence of external stimuli, may be slightly more or less than 24 hrs (Thomas and Vince-Prue, 1997)

This free running period cannot be started in an environment without stimuli, however. Some event, usually a transition between light and dark, is required. The circadian oscillator is said to be entrained to such an event, called a *zeitgeber,* or time-giver. In order to accommodate the changing photoperiod throughout the year, and still ensure that coupled responses occur at the appropriate time of day, the entrainment of the oscillator is adjusted if the *zeitgeber* occurs at some other phase of the cycle than the phase entrained to it (Thomas and Vince-Prue, 1997).

In photoperiodic perception, the event coupled to the circadian oscillator is thought to be a phase of relative sensitivity to light called the inducible phase (ϕ_i.) In SDP, coincidence of light with ϕ_i, would prevent flowering, while in LDP, it would induce flowering. Light then plays two roles in the circadian rhythm of photoperiodic perception: that of entraining the oscillator to the correct phase, and that of inducing or inhibiting flowering. This theory is based upon a system of what is dubbed external coincidence, in other words, the coincidence of an external stimulus (light) with a circadian oscillator (Thomas and Vince-Prue, 1997)

Other theories are based upon a system of internal coincidence — the interaction of two internal oscillators such that the correct phases of each coincide. External stimuli, such as light would not serve a direct inducing or inhibiting purpose, but would affect the entrainment of one or both oscillators so that they are no longer in phase with each other. This type of system has not been extensively explored for plants, however, and the internal coincidence theory currently prevails (Thomas and Vince-Prue, 1997)

Vernalization and Cold Treatment

Vernalization is a process whereby exposure to cold temperatures is required for floral induction. It should be distinguished from instances where the cold treatment does not affect induction, but initiation and early development, as in *Iris* Wedgewood, brussels sprouts and onion (Thomas and Vince-Prue, 1997). In still other plants, a cold treatment is not required for induction, but merely promotes subsequent flower development. For example, in many fruit trees in the Rosaceae, flower buds are induced and initiated during the season prior to bloom, and require a cold treatment to break dormancy (Gur, 1985).

Vernalization may be the only process necessary to induce flowering, or there may be a photoperiodic requirement as well after the vernalization process. As with photoperiodic responses, plants can have an obligate or facultative cold requirement to flower. In some plants, a photoperiodic treatment, in particular a SD treatment, is interchangeable with a cold requirement to induce flowering . All plants in which SD can substitute for a cold treatment are LDP, interestingly

enough. Thus, plants such as *Campanula medium* or *Coreopsis grandiflora* which have this type of response could be classified as short-long-day plants (SLDP) without cold, or simply LDP after cold (Napp-Zinn, 1984; Runkle, 1996; Ketellapper and Barbaro, 1966). In other plants, such as *Leucanthemum vulgare*, SD cannot fully substitute for a cold requirement, but SD during the cold treatment can enhance the vernalization process (Heide, 1995).

Effects of Forcing Temperature on Rate

Temperature can affect plants in many different ways. It is well known that higher temperatures increase rate of reactions in general, and more specifically, developmental processes in living organisms. Temperature responses are generally modeled by finding the amount of time necessary to reach a developmental event, and converting it into a rate. Rates of development in plants will generally have some optimum temperature (T_{opt}) where developmental rate reaches a maximum (R_{max}), some base temperature (T_b) below T_{opt} where the rate becomes zero, and some maximum temperature (T_{max}) above T_{opt} where the rate also becomes zero (Larsen, 1990).

Rate of development is often modeled as a linear function of temperature in the sub-optimal range (Whitman et. al., 1997; Yuan, 1998; Larsen, 1990), and sometimes in the supra-optimal range. The slope of the line in the supra-optimal range may have an equal but opposite slope to the line in the sub-optimal range, creating a "roof" shaped graph (Pearson et. al. 1993), or it may have a different slope, usually steeper.

The wider the range of temperatures selected, the less likely it is that one will be able to model the data with a straight line. In cases like these, rate may also be modeled by a quadratic equation (Larsen, 1990) as Wang et. al. (1998) did with *Hibiscus moscheutos*. Brøndum and Heins (1993) used an asymmetrical "hoop" shaped curve to describe rates of development to flower in dahlia. Finally, yet another way to model rates above and below T_{opt} is to use a "double exponential" function where one exponential function describes the response below T_{opt}, and one describes the response above T_{opt} (Larsen, 1990). This also allows the model to take into account the possible asymmetry of the response.

Pivotal to the process of modeling developmental events as a straight line with respect to temperature are the concepts of T_b and degree-days (°d) or thermal time (sometimes abbreviated as θ, or CTT: cumulative thermal time). Using a linear model in the sub-optimal phase, rate of progress toward an event is often described using an equation such as:

$$\frac{1}{\mathrm{DTE}} = i + sT \qquad [1]$$

where DTE is the days to event (such as days to flowering or the unfolding of a leaf), *i* and *s* are constants representing intercept and slope respectively and T is temperature. Using this model, base temperature (T_b) can then be calculated as:

$$T_b = \frac{-i}{s} \qquad [2]$$

Thermal time is measured in units of degree-days, and represents the

average number of degrees above the base temperature experienced by the plant on a given day. Thus a plant which experiences an average daily temperature (ADT) one degree above it's T_b accumulates one degree-day. Two days at that ADT and it will accumulate two degree days, just as it will accumulate two degree-days if it experiences one day at an ADT two degrees above its T_b. Cumulative thermal time (CTT) indicates the number of degree-days necessary for a plant to accumulate in order to achieve a given developmental event, and can be expressed as:

$$CTT = \frac{1}{s} \qquad [3]$$

Base temperature (T_b) is never derived directly, but is always extrapolated from the data, since when rate = 0, time to the event is infinite. It is necessary to know T_b in order to find how many degree-days a plant is accumulating, or if it is accumulating any at all. Then, knowing how fast degree-days are being accumulated, it is possible to estimate time to an event at a given temperature.

Leaf unfolding rate (LUR) is often modeled to predict biomass production, progress towards flowering, or final height. Models incorporating LUR have been developed for sugar beets (Milford, et. al., 1985), and summer squash (NeSmith, 1997) to predict crop growth and yield. Such models can aid in cultivar selection and management decisions such as pesticide sprays and harvesting schedules.

NeSmith (1997) found that by using thermal time rather than days after sowing, four different cultivars of summer squash could be modeled using one equation. This method of modeling differs from most others in that instead of

modeling using rates at different temperatures, he used CTT for a crop grown at varying temperatures. Leaf unfolding rates for Easter lily (Karlsson et. al., 1988), and chrysanthemum (Karlsson et. al., 1989) were found to have a linear relationship to temperature.

For crops such as cut flowers, bedding plants, perennials and flowering potted plants, there is much interest in the effects of temperature on time to flower. Song et. al. (1993) found that increasing average daily temperature decreased days to flower (from 17/15 to 25/23°C D/N temperature) for a variety of cultivars of *Platycodon grandiflorus*. The timing of Easter lily crops is also commonly controlled by adjusting temperature, higher temperatures causing faster flowering (Karlsson et. al., 1988). Whitman et. al. (1996) found that, for *Lavandula angustifolia* 'Munstead', as temperatures increased from 15 to 27°C, the number of days to flower was reduced. Above 23°C, however, fewer plants flowered in the treatment group containing the smallest plants (7-9 nodes at beginning of forcing), which suggests that perhaps 23°C is near to the optimum flowering temperature for flowering in this species.

In the interests of modeling time to flower, bud development has also often been modeled, using measurements of bud length or diameter as growth progresses and comparing the pattern and rate of expansion at different temperatures. The most notable application of this type is the bud meter concept developed by Healy and Wilkins (1984) whereby a model was incorporated into a measuring tool. When the bud meter is held up to the bud, the tip of the bud lines up with the number of days to flower at several given

temperatures.

Fisher et. al. (1996) refined the Easter lily bud meter by using a different equation to model bud expansion. They found that an exponential model fit the data better and had fewer parameters than the original Healy-Wilkins model which modeled bud expansion in two linear phases with a junction at the point where bud length reached 6 mm.

Wang et. al. (1998) found that diameter of *Hibiscus moscheutos* buds could be also be modeled using an exponential equation. While neither a bud meter nor predictive tables were developed for *Hibiscus*, these could easily be created from their model.

Thermocycles to Induce Flowering

A regular variation in temperature throughout the day, referred to as a thermocycle (C. Mirolo et. al., 1990), can affect flowering response in some plants. *Xanthium* normally has a very restrictive photoperiodic requirement for flower induction. *Xanthium* is a qualitative SDP which requires at least a single long dark period of 9 hr or greater to induce flowering (deZeew, 1957). Even a short light break in the middle of this long night prevents flower initiation (Thomas and Vince-Prue, 1997, p.15).

De Zeeuw (1957) found that it is possible to achieve flowering in *Xanthium pennsylvanicum* under normally non-inductive long day conditions by using

thermocycles. He exposed the plants to a 16- hr photoperiod, half of which was at 4°C and the other half at 26°C. One group of plants received cold at the beginning of the light period (T3) and one group received cold at the end of the light period (T2). Control groups received 16 hr of light at continual 4°C (T4) or continual 26°C (T1). The dark period was kept at 26°C for all treatments. These treatments lasted for four days before the plants were returned to normal long days (temperature not specified). It was found that both T2 and T3 flowered but the flower development proceeded more rapidly in the group that received cold at the beginning of the light period (T3). Treatment 4 was not expected to flower as it had been shown that *Xanthium* has a requirement for a certain amount of high light at high temperatures. The experiment was repeated with the treatments lasting only two days, with similar results, but slower flower development.

Table 1. Thermoperiodic flowering of *Xanthium* under normally non-inductive photoperiods. Adapted from de Zeeuw, 1957

	Treatment (8hrs)	(8hrs)	(8hrs)	dissection after: 1 wk	2 wks
T1	26°C	26°C	26°C	vegetative	vegetative
T2	26°C	**4°C**	26°C	stage 3.5	stage 7
T3	**4°C**	26°C	26°C	stage 8	6mm bud
T4	**4°C**	**4°C**	26°C	vegetative	vegetative
	(light)	(light)	(dark)	stages as defined by Salisbury (1955)	

Mirolo (1990) repeated T3 with a slight variation. He used *Xanthium strumarium* and had the warmer temperature set at 23°C. He confirmed that *Xanthium* could be induced to flower under non-inductive photoperiods by using thermocycles. He also confirmed de Zeeuw's finding that only two such thermocycles were necessary to cause induction, but that flowers developed

faster with more thermocycles.

Knowing that gibberellic acid has a promotive effect only on induced *Xanthium* plants, Mirolo also tested to see whether this would be the case with thermocyclicly induced *Xanthium*. He found that found that two thermocycles with one 5×10^{-4} M treatment per day of gibberellic acid to the roots was comparable to normal short-day induction of *Xanthium*, in terms of the differentiation of the terminal male inflorescence in the two weeks following induction.

It is unclear what mechanism these thermocycles would be affecting in the induction of *Xanthium*. It could be hypothesized that the relatively cold temperature during the day either prevents the plant from perceiving that period as light, or prevents or slows the transmission of the resulting signal, causing the plant to develop as if it had experienced a long night.

Temperature Effects on Photoperiod Response of Long Day Plants

In some cases, cold temperatures can prevent or reduce normal flowering response to an inductive photoperiod. Shillo and Halevy (1982) carried out a series of experiments on the long day plant, *Gypsophila paniculata* (Baby's Breath), cv. 'Bristol Fairy. To investigate the interaction between temperature and photoperiod, they placed plants under two photoperiods, either SD (8 hr) or LD (16 hr), and one of three temperature regimes, 27/22, 22/17, 17/12°C day/night.

They found that none of the plants flowered under short days, but under

long days, the percentage of plants flowering depended strongly on the temperature, although there was no temperature at which all plants failed to flower. The higher the temperature, the greater was the promotive effect of the long photoperiod. This agreed with field observations that at low night temperatures during the winter, plants often failed to flower. They also concluded that high night temperatures were only required for initiation and the early stages of elongation and bud formation. This was inferred from the fact that plants started earlier in the fall flowered during the winter without additional heat, while those planted later did not flower until spring.

Table 2. Flowering of *Gypsophila* under SD or NI lighting and different temperature regimes. Adapted from Shillo and Halevy, 1982

Temp. (°C)	Flowering plants (%)	
day/night	SD	LD
27/22	0	83
22/17	0	12

Hicklenton et. al. (1993) later confirmed experimentally that it is indeed the night temperature which is the limiting factor in flower induction. They tested two cultivars of *Gypsophila paniculata* ('Bristol Fairy' and 'Bridal Veil') to determine the optimum irradiance and night temperature for each. Night temperature treatments were 8, 12, 16, or 20°C. Day temperature was at 20°C for all treatments. Half of the plants received 710 $\mu mol \cdot s^{-1} \cdot m^{-2}$, and half receive 450 $\mu mol \cdot s^{-1} \cdot m^{-2}$ for 9 hrs, resulting in daily light integrals of 23 and 14.6 $mol \cdot m^{-2}$. They found that at low night temperatures 'Bristol Fairy' often failed to initiate flower buds (only 33% of the plants flowered at a night temperature of 8°C). This occurred at both irradiances tested, but the effect was more marked at 450 $\mu mol \cdot s^{-1} \cdot m^{-2}$. Percentage of plants flowering of cv. 'Bridal Veil' was almost

completely unaffected by light level or night temperature.

In another experiment (Shlomo et. al., 1985), it was found that gibberellin treatments could substitute for this high night temperature requirement under long days. They grew *G. paniculata* 'Bristol Fairy' plants under short (10 hr) or long (4 hr day extension) photoperiod. Plants were sprayed twice weekly (11 times) with GA at varying concentrations. Plants receiving LD treatment were sprayed with concentrations of 0, 125, 250 or 500 $mg \cdot l^{-1}$, while plants receiving SD treatment were sprayed with concentrations of 0 or 250 $mg \cdot l^{-1}$. All plants in the LD treatment that received GA flowered, whereas only 33% flowered under LD without GA. Number of stems per plant and total weight of flowering stems per plant increased while time to flower decreased with increasing GA concentration. No plants under SD flowered regardless of GA treatment, although there were some partially elongated stems which resulted in "blind" shoots or which had rosette-like vegetative growth at the end.

GA substitution for the high night requirement for flowering under long days is interesting to note because unlike many other LDP, gibberellin treatments cannot substitute for the long-day requirement itself in *Gypsophila paniculata* (Shillo and Halevy, 1982; Shlomo et. al., 1985). As with *Xanthium*, gibberellin enhances the flowering response, but cannot substitute for the photoperiodic requirement itself. Also like *Xanthium*, the interaction of temperature and photoperiod could be related to the lack of perception of the light administered during the drop in temperature. On the other hand, it could also be related to a lack of realization of the photoperiodic response.

Brøndum and Heins (1993) reported an interaction between temperature and photoperiod in tuberous root formation, lateral shoot count, lateral shoot length, and primary shoot length of *Dahlia pinnata* 'Royal Dahlietta Yellow'. They created twenty-four temperature × photoperiod factorial treatments with four temperatures, set at 15, 20, 25 or 30°C, and six photoperiods of 10, 12, 14, 16, 20, or 24 hrs. At lower temperatures and shorter photoperiods, tuberous root formation was promoted: above 14 hrs or 25°C, there was little to no tuberous root formation. The number of lateral shoots increased with photoperiod up to 14 hrs. At photoperiods above 14 hrs, there were fewer lateral shoots at 25°C, than at 15 or 20°C. Lateral shoot length increased with photoperiod from 10 to 14 hrs, while above 14 hrs, shoot length was more dependent on temperature — the higher the temperature, the shorter the lateral shoots.

Temperature and photoperiod also interacted to affect some aspects of flowering. Flower development was more strongly affected by temperature, although photoperiod did have some effects. For instance, at 25°C, flower buds formed at photoperiods greater than 14 hrs aborted, while at 30°C, no flower buds were formed at all (Brøndum and Heins, 1993).

The interaction between temperature and photoperiod for overall production of dahlia is very complex because of the many variables of plant development that are affected. Variation in photoperiod often seems to affect the magnitude of the response to temperature. Brøndum and Heins concluded from this study that there are very narrow temperature and photoperiod ranges for optimum production of *Dahlia pinnata* 'Royal Dahlietta Yellow', namely,

photoperiods between 12 and 14 hrs and temperatures around 20°C. Optimum was defined as producing plants of a satisfactory height that develop quickly and have many flower buds.

Temperature Effects on Photoperiod Response in Short Day Plants

In some SDP, critical photoperiod is dependent on temperature. For example, in poinsettia or chrysanthemum, raising temperature causes the critical photoperiod to change. Langhans and Miller (1963) subjected poinsettias *(Euphorbia pulcherrima)* to three different temperature regimes (60, 70 and 80°F), and photoperiods between 8 hrs and 12 hrs (see table) for varying numbers of days before returning them to 13 hr photoperiods.

They found that as temperature increased, the photoperiod required for

Table 3. Number of days from the start of short day treatment to visible bud (top number) and flowering (bottom number) in poinsettia 'Barbara Ecke Supreme.' Adapted from Langhans and Miller (1963) [n/a = event occurred, but the number of days was not recorded; dash = event did not occur in 100 days]

# of short days	Temperature (°F) and photoperiod (hours)														
	60°F				70°F					80°F					
	8	10	11½	12	8	10	10½	11½	12	8	8½	9	9½	10	12
20	40 83	41 88	40 93	53 93	55 ---	49 ---	49 ---	--- ---	--- ---	n/a ---	69 ---	69 ---	64 ---	62 ---	--- ---
30	38 87	39 89	40 87	43 93	32 62	34 62	33 62	38 ---	57 ---	42 ---	40 ---	47 ---	52 ---	71 ---	--- ---
40	35 85	38 88	37 87	45 93	33 62	32 62	32 61	41 ---	55 ---	40 62	42 ---	44 ---	40 ---	45 ---	--- ---
50	37 87	41 87	41 87	44 99	34 62	32 61	35 63	40 64	48 ---	41 62	38 62	44 72	44 n/a	53 74	--- ---

induction became more restrictive, and that different conditions were required for flower initiation than for flower development. For example, as temperature and photoperiod increased and number of short days decreased, more plants produced buds which never produced flowers. This suggests that shorter photoperiods, lower temperatures, and more days of inductive treatments are required for flower development than for flower induction.

Poinsettia could be termed "short day-shorter day plants", with respect to flowering, meaning that they are SDP for which the critical photoperiod gets shorter for subsequent flower development. Horticulturally they are often grown using blackcloth to artificially shorten photoperiod until natural daylength is short enough to satisfy the requirement for induction/initiation. Continued shortening of days would naturally satisfy the more restrictive requirement for flower development.

In more recent research at Michigan State University, it has been shown that it is night temperature, rather than average daily temperature, which is actually a limiting factor for flowering in poinsettia (Heins, 1990). Poinsettia were grown at six different night temperatures and six different day temperatures, ranging from 14-29°C. Heins (1990) found that at night temperatures above 26°C, no plants flowered, regardless of the day temperature.

A similar interaction between temperature and photoperiod was reported in the SDP *Dendranthema grandiflora* (formerly *Chrysanthemum morifolium*) (Cathey, 1957). Several varieties of chrysanthemum were subjected to seven photoperiodic treatments in combination with three minimum night temperatures.

Like Langhans and Miller, Cathey found that the requirements for initiation and flowering differed and that they were both affected by interactions between temperature and photoperiod. Critical night length for flower development increased (became more restrictive) as temperature increased. However, the night length required for flower initiation decreased (became less restrictive) as temperature increased. This resulted in a greater difference between the critical night length for initiation and flowering as temperature increased. At 50°F (the lowest temperature tested) there was no difference between critical night length for initiation and development of the flower.

Ison and Humphries (1984) reported that for the qualitative SDP *Stylosanthes guianensis* var. *guianensis* cv. Schofield grown at a photoperiod marginal for flowering (12 – 11.75 hrs), floral initiation was promoted by low night temperatures (25/16°C or 25/20°C D/N) temperatures and inhibited by high (35°C) day temperatures. These results are similar to some of the results in chrysanthemum and poinsettia. Several other SDP, namely *Chenopodium*, *Lemna* and *Pharbitis*, also have critical photoperiods which are dependent on temperature (Thomas and Vince-Prue).

Conclusion

According to the evidence presented in this paper, plants can be placed into two general categories: those where temperature seems to affect the perception of light, and those in which critical photoperiod is dependent on temperature. The mechanisms of photoperiodism are not well understood,

despite many years of research on the subject, thus these mechanisms can only be studied by observing plant responses. This complicates any discussion of interactions between the phenomenon of photoperiodism and growing temperature.

Whatever the mechanisms involved, a knowledge of the existence of interactions between temperature and photoperiod can help us to model plant responses, and understand seeming irregularities in plant development. Hopefully this will also lead us to a better understanding of plant physiological processes in general.

Literature Cited

Brøndum, J.J. and R.D. Heins. 1993. Modeling temperature and photoperiod effects on growth and development of dahlia. J. Amer. Soc. Hort. Sci. 118:36-42.

Cathey, H.M. 1957. Chrysanthemum temperature study. F. The effect of temperature upon the critical photoperiod necessary for the initiation and development of flowers of *Chrysanthemum morifolium*. Proc. Amer. Soc. Hort. Sci. 69:485-491.

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

Gur, A. 1985. Rosaceae – deciduous fruit trees, p. 355-389. In: A.H. Halevy (ed). CRC Handbook of Flowering. CRC Press, Inc., Boca Raton.

Healy, W.E and H.F. Wilkins. 1984. Temperature effects on 'Nellie White' flower bud development. HortScience 19:843-844.

Heide, O.M. 1995. Dual induction control of flowering in *Leucanthemum vulgare*. Physiologia Plantarum 95:159-165.

Heins, R.D. 1990. Choosing the best temperature for growth and flowering. Greenhouse Grower.

Hicklenton, P.R., S.M. Newman and L.J. Davies. 1993. Night temperature, photosynthetic photon flux, and long days affect *Gypsophila paniculata* flowering. HortScience 28:888-890.

Ison, R.L. and L.R. Humphries. 1984. Day and night temperature control of floral induction in *Stylosanthes guianensis* var. *Guianensis* cv. Shofield. Annals of Botany 53:207-211.

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

Karlsson, M.G., R.D. Heins, J.E. Erwin, R.D. Berghage, W.H. Carlson and J.A. Biernbaum. 1989. Temperature and photosynthetic photon flux influence chrysanthemum shoot development and flower initiation under short-day conditions. J. Amer. Soc. Hort. Sci. 114:158-163.

Ketellapper, H.J. and A. Barbaro. The role of photoperiod, vernalization and gibberellic acid in floral induction in *Coreopsis grandiflora* Nutt. Phyton. 23(1): 33-41.

Langhans, R.W. and R.O. Miller. 1963. Influence of daylength, temperature, and number of short days on the flowering of poinsettia (*Euphorbia pulcherrima*). Proc. Amer. Soc. Hort. Sci. 75:753-760.

Larsen, R.U. Plant growth modelling [sic] by light and temperature. Acta Hort. 272:235-242.

Milford, G.F.J., T.O. Pocock and J. Reily. 1984. An analysis of leaf growth in sugar beet. I. Leaf appearance and expansion in relation to temperature under controlled conditions. Ann. Appl. Biol. 106, 163-172.

Mirolo, C., M. Bodson, and G. Berner. 1990. Floral Induction of *Xanthium strumarium* in Long
Days. Ann. Bot. 66, 475-477.

Napp-Zinn, K. 1984. Light and vernalization, pp. 75-88. In: D. Vince-Prue, B. Thomas and K.E. Cockshull (eds.). Light and the Flowering Process. Academic Press, London.

Pearson, S., P. Hadley, and A.E. Wheldon. 1993. A reanalysis of the effects of temperature and irradiance on time to flowering in chrysanthemum (*Dendranthema grandiflora*). J. Hort. Sci. 68:89-97.

Roberts, E.H. and R.J. Summerfield. 1987. Measurement and prediction of flowering in annual crops, p. 17-50. In: J. G. Atherton (ed.). Manipulation of Flowering. Butterworths, London.

Runkle, E.S. 1996. The effects of photoperiod and cold treatment on flowering of twenty-five species of herbaceous perennials. MS Thesis, Dept. of Horticulture, Michigan State Univ., East Lansing.

Shlomo, E., R. Shillo, and A. Halevy. 1985. Gibberellin substitution for the high night temperatures required for the long-day promotion of flowering in *Gypsophila paniculata* L. Scientia Hort. 26: 69-76.

Shillo, R. and A.H. Halevy. 1982. Interaction of photoperiod and temperature in flowering-control of *Gypsophila paniculata* L. Scientia Hort. 16:385-393.

Song, C.Y., S.K. Chung, M.S. Roh and R.H. Lawson. 1993. Temperature influences growth and flowering of *Platycodon*. J. Kor. Soc. Hort. Sci. 34(6):446-453.

Thomas, B. and D. Vince-Prue. 1997. Photoperiodism In Plants. Academic Press, San Diego.

Thomas, B. and D. Vince-Prue. 1984. Juvenility, photoperiodism and vernalization. In Advanced Plant Physiology. Wilkins, M. B., ed. Pitman Publ., London. pp. 408-439.

Wang, S., R.D. Heins, W.H. Carlson and A.C. Cameron. 1998. Modeling the effect of temperature on flowering of *Hibiscus moscheutos*. Acta Hort. 456:161-169.

Whitman, C.M., R.D. Heins, A.C. Cameron and W.H. Carlson. 1996. Cold treatments, photoperiod, and forcing temperature influence flowering of *Lavandula angustifolia*. HortScience, 31:1150-1153.

Whitman, C.M., R.D. Heins, A.C. Cameron and W.H. Carlson. 1997. Cold treatment and forcing temperature influence flowering of *Campanula carpatica* 'Blue Clips'. HortScience 32:861-865.

Yuan, M., W.H. Carlson, R.D. Heins and A.C. Cameron. 1998. Effect of forcing temperature on time to flower of *Coreopsis grandiflora*, *Gaillardia ×grandiflora*, *Leucanthemum ×superbum* and *Rudbeckia fulgida*. HortScience 33:663-667.

de Zeeuw, D. 1957. Flowering of *Xanthium* under long day conditions. Nature 180:558.

MODELING TEMPERATURE EFFECTS ON TIME TO FLOWER AND BUD DEVELOPMENT OF *COREOPSIS VERTICILLATA* 'MOONBEAM'

Abstract

Effects of forcing temperature on flowering of *Coreopsis verticillata* L. 'Moonbeam' were recorded. Plants were initially cooled for twelve weeks and then grown under 16-hr long days (4-h night interruption in the first year) in greenhouses set at 17, 20, 23, 26, and 29°C. Flower size, flower number and time to flower decreased as temperature increased. The number of nodes added from the start of forcing to flower was unaffected by temperature. The relationship between flower bud diameter, temperature and time to flower was modeled as a sigmoid logistic function. Models for time from start of long day forcing at each temperature to visible bud (VB), flower (FLW) and from VB to FLW were developed based on a linear function of rate of development. The optimum temperature for time to flower for *C. verticillata* 'Moonbeam' was at least 29°C, although plant quality factors such as flower diameter and flower number were greater at lower temperatures.

Introduction

Accurate scheduling is just as important as a high quality crop in the floriculture industry. Forcing temperature is one of the factors affecting both timing of flowering as well as attributes such as plant height, flower number and flower size which contribute to plant quality (Armitage, 1990; Pearson et. al., 1995; Shvarts et. al. 1997; Whitman et. al., 1996; Yuan et. al., 1998).

Predictive tools such as bud meters and tables can be derived from models to assist growers in precisely timing crops. For example, Easter lilies are commonly timed using temperature models for leaf unfolding and bud development (Karlsson et. al., 1988; Fisher et. al., 1996). Similar models have been developed for plants throughout the horticultural trade for annuals such as *Begonia* (Karlsson 1992), flowering pot crops such as African violet (Faust and Heins, 1993), cut flowers (Criley, 1995) and vegetables (NeSmith, 1997).

Perennials are often sold in a vegetative state. Since selling plants in bloom increases both their value and desirability (Harrison, 1996), there is increased interest in forcing perennials to flower. Scheduling a plant to flower on a particular date requires the proper flower induction environment as well as appropriate temperatures for correct timing. This requires knowledge of the relationship between forcing temperature and time to flower. Some models have been developed relating temperature to time of flowering for perennials, among these are *Campanula*, *Coreopsis*, *Gaillardia*, *Leucanthemum* and *Rudbeckia* (Whitman et. al., 1997; Yuan, 1998). However, few bud development models have been developed for herbaceous perennials.

Temperature responses are generally modeled by first observing times taken to an event, then converting to rates. Rates of development in plants, as for any biological process, will always have some optimum temperature (T_{opt}) where developmental rate reaches a maximum (R_{max}), some base temperature (T_b) below T_{opt} where this rate becomes zero, and some maximum temperature (T_{max}) above T_{opt} where this rate also becomes zero (Larsen, 1990).

Rate is often modeled as a linear function of temperature in the sub-optimal range (Whitman et. al., 1997; Yuan, 1998; Larsen, 1990), and sometimes in the supra-optimal range. The slope of the line in the supra-optimal range may have an equal but opposite slope to the line in the sub-optimal range, creating a "roof" shaped graph (Pearson et. al. 1993), or it may have a different slope, usually steeper. Rate may also be modeled by a quadratic equation (Larsen, 1990) as Wang (1998) did with *Hibiscus moscheutos*. Brøndum and Heins (1993) used an asymmetrical "hoop" shaped curve to describe rates of development to flower in dahlia. Finally, yet another way to model rates above and below T_{opt} is to use a "double exponential" function where one exponential function describes the response below T_{opt}, and one describes the response above T_{opt} (Larsen, 1990). This also allows the model to take into account any asymmetry of the response.

Coreopsis verticillata, also known as Threadleaf Coreopsis, is well known for its outstanding performance in warm sunny areas of the garden. It's fine foliage helps reduce water loss, making it quite drought resistant, and it is hardy over most of the United States, from zones 3-9 (Armitage, 1989; Nau, 1996).

Flowers are 1-2" across, in varying shades of clear yellow, with eight ray florets extending out from a yellow center disk. Most varieties will rebloom sparsely if cut back after the initial flush in June and early July, but 'Moonbeam' will often produce its pale yellow flowers continuously through October (Armitage, 1989). In 1992, 'Moonbeam' was chosen as the Perennial Plant of the Year by the Perennial Plant Association (Nau, 1996). It's popularity, garden performance, and wide range make it an excellent candidate for scheduled forcing.

Hamaker (1998) showed that *Coreopsis verticillata* 'Moonbeam' is an obligate long-day plant for flowering and that a cold treatment increased flower number and hastened flowering. Our objectives were to 1) quantify the influence of temperature on time to VB and time to FLW, 2) develop a model relating bud size and temperature to time to flower, and 3) quantify other effects of forcing temperature on plant quality, including flower number, flower size and plant height for *C. verticillata* 'Moonbeam'.

Materials and Methods

First year. On October 15, 1996, propagules of *Coreopsis verticillata* 'Moonbeam' were received in 70-cell flats from Green Leaf Enterprises (Leola, Pa.). Plants were immediately placed in a growth chamber set at 5° C under a 9-hr photoperiod at ~10 μmol m^{-2} s^{-1} provided by cool white fluorescent bulbs (VHOF96T12: Philips, Bloomfield N.J.) as measured by a LI-COR quantum sensor, model LI-189 (LI-COR, Lincoln, Neb.).

After 12 weeks in the cooler, plants were transplanted into 13-cm square

containers (1.1L), and ten plants per temperature treatment were grown under long days in greenhouses set at 17, 20, 23, 26, and 29°C (actual temperature averages from the start of forcing to average date of FLW for each treatment were 17.3, 19.7, 23.5, 26.1, and 29.3°C respectively). Long days consisted of natural photoperiods plus a 4-hour night interruption from 1000 to 0200 hours, provided by 60-W incandescent lights at 3 to 5 μmol m^{-2} s^{-1} as measured by a quantum sensor (LI-COR).

Temperature in each greenhouse was recorded continually with a CR-10 datalogger (Campbell Scientific, Logan, Utah). Actual average daily temperatures were determined and used in all calculations rather than set point temperature. One representative flower bud was chosen from among those present at the first incidence of visible buds on each plant, and its diameter was measured every three to five days thereafter. Dates of visible bud and anthesis were recorded. At anthesis, plant height, and number of flower buds were recorded.

Second year. On October 2, 1997, propagules of *Coreopsis verticillata* 'Moonbeam' were received in 128-cell flats from Center Greenhouse, Inc. (Denver, Co.). These received the same cold and forcing temperature treatments as in the model-development experiment, but the long-day treatment was delivered using a 16-hr day-extension provided by 400W high-pressure sodium lamps at 50 μmol m^{-2} s^{-1}. These same lights provided 50 μmol m^{-2} s^{-1} supplemental light, when ambient light levels in the greenhouse dropped below 400 μmol m^{-2} s^{-1}. Actual temperature averages from the start of forcing to

average date of FLW in the second year were 17.7, 19.9, 23.0, 26.1, and 29.4°C for the 17, 20, 23, 26, and 29°C treatments, respectively. Vapor pressure deficit (VPD) control was instituted in the second year, and maintained at approximately 0.7 kPa. This was accomplished by monitoring wet and dry bulb temperature, calculating VPD, and activating steam injection when the VPD increased above the threshold. In addition to the data collected in the first year, flower diameter and the number of flowering stalks were also recorded.

Model Theory and Analysis

Rate of progress model. Progress toward a developmental event such as flowering may be modeled as a linear increase with temperature up to a certain point, at which developmental rate levels off at an optimum, and then decreases (Roberts and Summerfield, 1987). In the sub-optimum temperature linear phase, this relationship can be described as follows:

$$\frac{1}{\mathrm{DTE}} = i + sT \qquad [1]$$

where DTE is the days to event (such as days to flowering, days to VB or days from VB to FLW), i and s are constants representing the intercept and slope respectively of a straight line, and T is temperature. Abbreviations and parameters used in models are listed in Table 4. By manipulating Eq. [1], base temperature (T_b) for a given developmental event can be calculated as:

$$T_b = \frac{-i}{s} \qquad [2]$$

and cumulative thermal time (CTT) in degree-days necessary to achieve the

event can be calculated as:

$$CTT = \frac{1}{s} \quad [3]$$

For the analysis, rates were calculated from the number of days from force to VB, VB to FLW and force to FLW (1/DTE) and Eq. [1] was fit to these data points. Model validation DTE were compared with DTE predicted by the model produced from the first-year data.

Bud development model. A sigmoid logistic function was used to describe the increase in bud diameter from visible bud to flower:

$$B = \frac{a}{1 + be^{c(t_f - t)}} \quad [4]$$

where bud diameter (B in mm) at time t (days) depends on the number of days to flowering (at time t_f, in days).

The parameter a defines an asymptote which indicates a theoretical maximum bud diameter just before the expansion of the ray florets, while parameters b and c affect the y-intercept and slope, respectively. To incorporate the temperature response, parameters a, b and c can be replaced by functions of temperature $f_a(T)$, $f_b(T)$ and $f_c(T)$. Thus equation [4] becomes:

$$B = \frac{f_a(T)}{1 + f_b(T)e^{f_c(T)(t_f - t)}} \quad [5]$$

To calibrate the bud development model, the parameters a, b and c in Eq. [4] were estimated independently for each temperature treatment by fitting Eq. [4] to the data set with the nonlinear regression procedure (PROC NLIN) in SAS (SAS Institute, 1990). Actual temperatures from average date of VB to average

date of FLW were used for each treatment.

Parameter *a* was found to vary randomly across the temperature treatments, and for the sake of simplicity, was treated as a constant in this model. Functions $f_b(T)$ and $f_c(T)$ were formulated based on the trends in the values of *b* and *c* values across the range of temperatures (Figure 1). The resultant equation was then fit simultaneously to the entire calibration data set using nonlinear regression to estimate the parameters in $f_b(T)$ and $f_c(T)$ as well as the parameter *a* as a constant across all temperatures. For the final estimation, actual average temperatures from t to t_f for each measurement were used.

To determine the number of days to flower ($t_f - t$) at a given bud diameter (B) and temperature (T), equation [5] (with *a* as a constant) can be algebraically manipulated to produce:

$$\frac{\ln\left(\frac{\frac{a}{B}-1}{f_b(T)}\right)}{f_c(T)} = (t_f - t) \qquad [6]$$

To validate the bud development model, Eq. [6] was used to predict days to flower from given bud diameters and actual temperatures from measurement to flower for the second-year data. These were then compared with the observed days to flower for these measurements and temperatures by fitting a line to the predicted data vs. the observed data.

Other data relating to plant quality such as height, number and size of flowers were analyzed using the general linear models procedure in SAS to determine significance of the main temperature effect and any trends. Data from

the two years were analyzed separately.

Results

Rate of progress model. Rate of progress from force to FLW and from VB to FLW increased linearly as temperature increased. Time from force to VB increased from 17 to 23°C and leveled off at temperatures ≥23°C (Figure 2). Taking this into account, the linear regression for force to VB was fit only to data points from temperatures ≤23°C.

In the validation experiment, where actual average times to a given event were compared with times predicted from the first year model, the average deviation in time from force to VB was 4.0 days with a maximum deviation of 6.4 days at 20.5 °C. The average deviation for VB to FLW was 0.9 days with a maximum deviation of 1.9 days at 29.3 °C and the average deviation for force to FLW was 4.9 with a maximum deviation of 7.1 days at 19.9 °C.

Bud development model calibration. The rate of expansion of buds increased with temperature from 17 to 29°C; parameters *b* and *c* increased similarly (Figure 1). An exponential function was fit to the estimated *b* values, and a linear function was fit to the estimated *c* values. These functions $f_b(T)$ and $f_c(T)$ were then incorporated into Eq. [5] resulting in the following equation:

$$B = \frac{a}{1 + (b_1 e^{b_2 T}) e^{(c_1 + c_2 T)(t_f - t)}} \qquad [7]$$

where a, b_1, b_2, c_1, and c_2 are constants. When Eq. [7] was fit to the entire data set, the resulting model (Table 5) closely fit the observed bud diameters for the

calibration experiment (R^2 = 0.945)(Figure 3). When predicted days to flower using Eq. [6] were compared to actual days to flower, data highly correlated (R^2 = 0.89) (Figure 4, a-e).

Bud development model validation. When predicted time to flower in the second year was compared with actual time to flower, there was a consistent bias in both the slope and the intercept such that the model was most accurate at the middle temperatures, ranging from 20-26°C (Figure 5). Largest deviation was seen in the model at the 17°C treatment, very close to time of flowering (Figure 4, f-j).

Other plant qualities. There was no significant effect of temperature on the number of flowers the first year, but the number of flowers per plant decreased markedly as temperature increased the second year. This decrease in flower number with increased temperatures was due to the significant trend in the number of flowers per stalk, as there was no effect on the number of stalks per plant (Table 6). Heights were lower on the average in the second year, but in both years the lowest average plant height was achieved at 23°C. Diameter of open flowers decreased significantly from 47mm to 25mm as temperatures increased from 17 to 29°C (Figure 6). The number of nodes formed from the start of forcing to flower initiation was not affected by temperature, and was very similar for both years, averaging about 8 nodes.

Discussion

In the sub-optimum temperature range, rate of progress toward a given developmental event can be described by a linear function. The first year data on which the time to flower model was based clearly fit a linear pattern for days to FLW and days from VB to FLW, but for days to VB, the pattern was linear only at temperatures $\leq$23 °C. For days to FLW and days from VB to FLW the optimum must be at least 29 °C. For time to VB, the rate of development started to level off as temperatures increased, which indicates that perhaps 29 °C is near the optimum for this species.

Overall, times to VB and FLW were lower in the second year than in the first. This may have been due to several factors which were different in the second year experiment, namely the long day treatment by day extension with high-pressure sodium lights vs. night interruption with incandescent lights the first year, and the addition of VPD control in the second year. Faust and Heins (1997) found that high pressure sodium lights (HPS) can significantly increase the temperature of the shoot tip, reducing time to flower. The additional radiation from the day-extension treatment in the second year may have heated the meristem sufficiently to have accelerated flowering. The VPD control instituted in the second year may also have reduced the cooling effects of transpiration, resulting in warmer plants and faster flowering.

The time from VB to FLW was practically unchanged from the first to the second year, which indicates that differences in time to FLW the second year were due almost entirely to effects on time to VB.

Coreopsis verticillata 'Moonbeam' bud development was sigmoid which contrasts with bud-development models on other species. Increase in diameter of buds of *Hibiscus moscheutos*, another commonly grown herbaceous perennial, was found to follow an exponential curve (Wang 1998), as did increase in length of Easter lily buds (Fisher et. al., 1996).

Although *C. verticillata* 'Moonbeam' could be flowered sooner at higher temperatures, flower number and flower diameter decreased as temperatures increased. This reduction in flower size with increasing temperature concurs with similar research results for other plants such as petunias (Shvarts et. al., 1997), pansies (Pearson et. al., 1995) Impatiens (Lee et. al., 1990) and chrysanthemum (Karlsson, 1998). Pearson et al. suggest that the smaller flower size at higher temperatures may be due to a reduction in the duration of bud development.

It was observed that stem strength was weaker at higher temperatures, probably due to a reduction in stem diameter, although no data were taken to substantiate this observation. Similar results for tweedia (*Oxypetalum caeruleum*) showed that stem diameter decreased linearly with increasing temperature from 14 to 30°C (Armitage, 1990).

The models developed in the current study may be used by growers to schedule flowering of plants grown at different temperatures, estimate time to flower at a given bud diameter, or to adjust temperature settings to achieve flowering of *C. verticillata* 'Moonbeam' on a given date for commercial production (Table 7). While higher temperatures caused faster blooming, flower size and

number was reduced. Thus the advantages of a reduction in time to flower must be weighed against a corresponding reduction in plant quality.

Literature Cited

Armitage, A.M. 1989. Herbaceous perennial plants; A treatise on their identification, culture, and garden attributes. Varsity Press, Athens, GA.

Armitage, A.M., N.G. Seager, I.J. Warrington D.H. Greer and J. Reyngoud. Response of *Oxypetalum caeruleum* to irradiance, temperature and photoperiod. 1990. J. Amer. Soc. Hort. Sci. 115(6):910-914.

Brøndum, J.J. and R.D. Heins. 1993. Modeling temperature and photoperiod effects on growth and development of dahlia. J. Am. Soc. Hort. Sci. 118(1):36-42.

Criley, R.A. 1995. Temperature influences flowering of Palakana (*Telosma cordata* Merrill) under long days. HortScience 30(3):482-483.

Faust, J.E. and R.D. Heins. 1993. Modeling leaf development of the African violet (*Saintpaulia ionantha* Wend.). J. Amer. Soc. Hort. Sci. 118(6):747-751).

Faust, J.E. and R.D. Heins. 1997. Quantifying the influence of high-pressure sodium lighting on shoot-tip temperature. Acta Hort. 418:85-91.

Fisher, P.R., J.H. Lieth and R.D. Heins. 1996. Modeling flower bud elongation in Easter lily (*Lilium longiflorum* Thunb.) in response to temperature. HortScience 31(3):349-352.

Hamaker, C.K. 1998. Influence of photoperiod and temperature on flowering of *Asclepias tuberosa*, *Campanula carpatica*, 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', *Coreopsis verticillata* 'Moonbeam', *Lavandula angustifolia* 'Munstead', and *Physostegia virginiana* 'Alba'. MS Thesis, Dept. of Horticulture, Michigan State Univ., East Lansing.

Harrison, D. 1996. Colour is the key in selling perennials. Greenhouse Canada Sept 1996, 32-33.

Karlsson, M.G. 1992. Leaf unfolding rate in *Begonia* ×*hiemalis*. HortScience 27(2):109-110.

Karlsson, M.G., R.D. Heins and J.E. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113(1):70-74.

Karlsson, M.G., R.D. Heins, J.E Erwin, R.D. Berghage, W.H. Carlson and J.A. Biernbaum. 1989. Irradiance and temperature effects on time of development and flower size in chrysanthemum. Scientia Hort. 39:257-267.

Larsen, R.U. 1990. Plant growth modelling by light and temperature. Acta Hort. 272:235-242.

Lee, W., J.E. Barrett and T.A. Nell. 1990. High temperature effects on the growth and flowering of *Impatiens wallerana* cultivars. Acta Hort. 272:121-127.

Nau, J. 1996. Ball perennial manual; Propagation and production. Ball Publishing, Batavia, IL.

NeSmith, D.S. 1997. Summer squash (*Cucurbita pepo* L.) Leaf number as influenced by thermal time. Scientia Hort. 68(1997) 219-225.

Pearson, S., P. Headley, and A.E. Wheldon. 1993. A reanalysis of the effects of temperature and irradience on time to flowering in chrysanthemum (*Dendranthema grandiflora*). J. Hort. Sci. 68:89-97.

Pearson, S., A. Parker, S.R. Adams, P. Hadley and D.R. May. 1995. The effects of temperature on the flower size of pansy (*Viola ×wittrockiana* Gams.) J. Amer. Soc. Hort. Sci. 70(2)183-190).

Roberts, E.H. and R.J. Summerfield. 1987. Measurement and prediction of flowering in annual crops, pp.17-50. In: J.G. Atherton (ed.). Manipulation of flowering. Butterworths, London.

SAS Institute. 1990. SAS/STAT users guide, release 6.12 ed. SAS Inst., Cary, NC.

Shvarts, M., D. Weiss and A. Borochov. 1997. Temperature effects on growth, pigmentation and post-harvest longevity of petunia flowers. Sciencia Horticulturae 69(1997) 217-227.

Whitman, C.M., R.D. Heins, A.C. Cameron and W.H. Carlson. 1997. Cold treatment and forcing temperature influence flowering of *Campanula carpatica* 'Blue Clips'. HortScience 32(5):861-865.

Wang, S., R.D. Heins, W.H. Carlson and A.C. Cameron. 1998. Modeling the effect of temperature on flowering of *Hibiscus moscheutos*. Acta Hort. 456:161-169.

Yuan, M., W.H. Carlson, R.D. Heins and A.C. Cameron. 1998. Effect of forcing temperature on time to flower of *Coreopsis grandiflora*, *Gaillardia ×grandiflora*, *Leucanthemum ×superbum* and *Rudbeckia fulgida*. HortScience 33(4):663-667.

Table 4. List of abbreviations and parameters.

Symbol	Description	Units
a	Parameter in bud development model	mm
B	Flower bud diameter	mm
b	Parameter in bud development model	dimensionless
b_1	Parameter in $f_b(T)$	dimensionless
b_2	Parameter in $f_b(T)$	$°C^{-1}$
c	Parameter in bud development model	$days^{-1}$
c_1	Parameter in $f_c(T)$	$days^{-1}$
c_2	Parameter in $f_c(T)$	$°C^{-1} \cdot days^{-1}$
CTT	Cumulative thermal time	°C • days
DTE	Days to event	days
FLW	Flower (expansion of ray florets)	—
i	Parameter in linear timing model (intercept)	event • $days^{-1}$
s	Parameter in linear timing model (slope)	event • $°C^{-1}$ • $days^{-1}$
t	Time of bud measurement	days
t_f	Time of flower	days
T	Average air temperature	°C
T_b	Base temperature	°C
VB	Visible bud	—
VPD	Vapor pressure deficit	—

Table 5. Nonlinear regression results from fitting Eq. [4] to the full calibration data set using actual temperature data for each measurement. The number of observations in the data set was 421, and the R^2 was .945.

Parameter	Estimate	Asymptotic standard error	Asymptotic 95% confidence interval	
			Lower	Upper
a	5.70	0.118	5.46	5.93
b_1	0.00897	0.00481	-0.000511	0.0184
b_2	0.0854	0.0147	0.0563	0.114
c_1	0.0283	0.0159	-0.00298	0.0596
c_2	0.00550	0.000678	0.00417	0.00684

Table 6. Significance of effect of temperature on height at flower, number of nodes added in forcing, flower diameter, number of visible buds at first flower, number of stalks, and number of visible buds per stalk at first flower for *Coreopsis verticillata* 'Moonbeam'.

Characteristic	year	main temperature effect	trends	
			linear	quadratic
height at first flower	1	***	***	***
	2	***	NS	***
number of nodes added	1	NS	NS	NS
	2	NS	NS	NS
flower diameter	2	***	***	***
total number of visible buds at first flower	1	NS	NS	NS
	2	***	***	*
number of stalks	2	NS	NS	NS
number of visible buds per stalk at first flower	2	***	***	**

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

Table 7. Relationship between bud diameter, temperature, and time to flower for *Coreopsis verticillata* 'Moonbeam' according to Eq. 6.

Bud diameter (mm)	Number of days to flower at indicated temperature in °C:												
	17	18	19	20	21	22	23	24	25	26	27	28	29
1	39	39	38	37	37	36	35	35	34	33	32	32	31
1.5	35	34	34	33	32	32	31	30	30	29	28	27	27
2	32	31	30	30	29	28	28	27	26	25	25	24	23
2.5	29	28	27	27	26	25	25	24	23	22	22	21	20
3	26	25	24	24	23	22	22	21	20	20	19	18	17
3.5	23	22	22	21	20	19	19	18	17	17	16	15	15
4	20	19	18	18	17	16	16	15	14	13	13	12	11
4.5	16	15	14	14	13	12	12	11	10	10	9	8	7
5	11	10	9	8	8	7	6	6	5	4	4	3	2

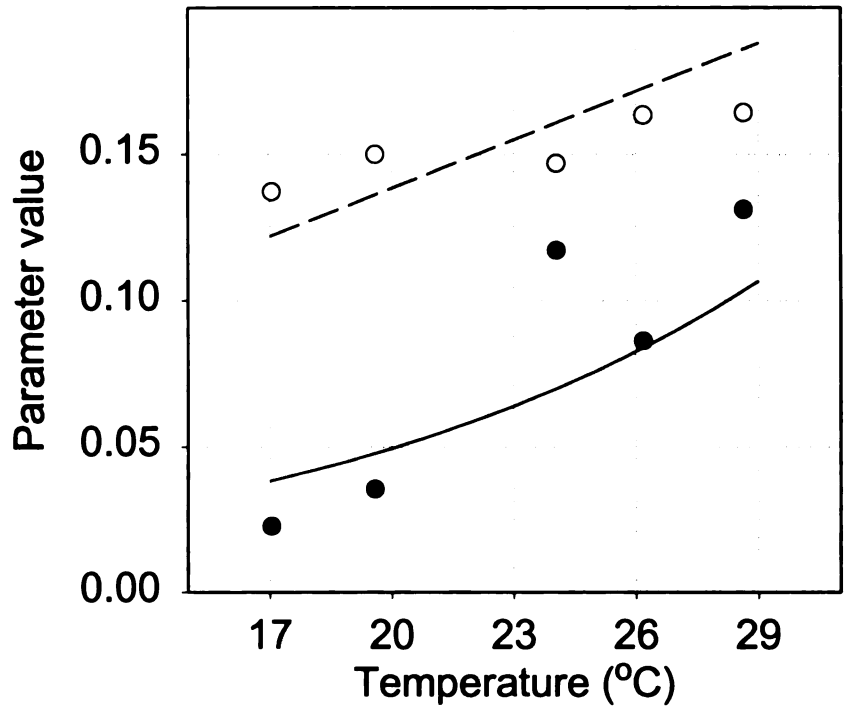

Figure 1. Parameters as fit to each temperature treatment individually, and the lines fit to them using Eq. [7] fit to the whole data set. Parameter *b* is indicated by closed circles and exponential function shown as a solid line, while parameter *c* is indicated by open circles and straight dashed line.

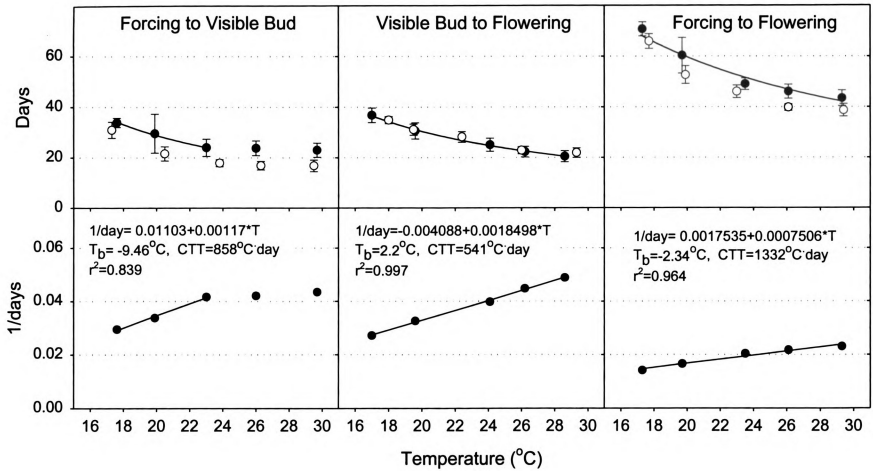

Figure 2. Influence of forcing temperature on time and rate toward flowering for *Coreopsis verticillata* 'Moonbeam'. Solid lines represent predicted values from the regression equations calculated from the first year data (filled circles). Second year data is represented by open circles, and all error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

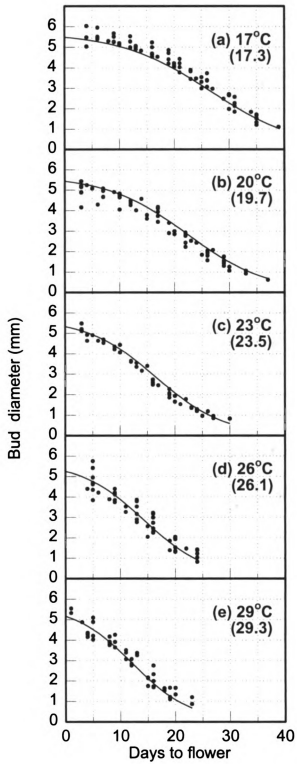

Figure 3. Observed bud diameters at various times before flower for each temperature treatment from the calibration data set for *C. verticillata* 'Moonbeam'. Line indicates bud diameter as modeled according to Eq. [7]. R^2 = .945.

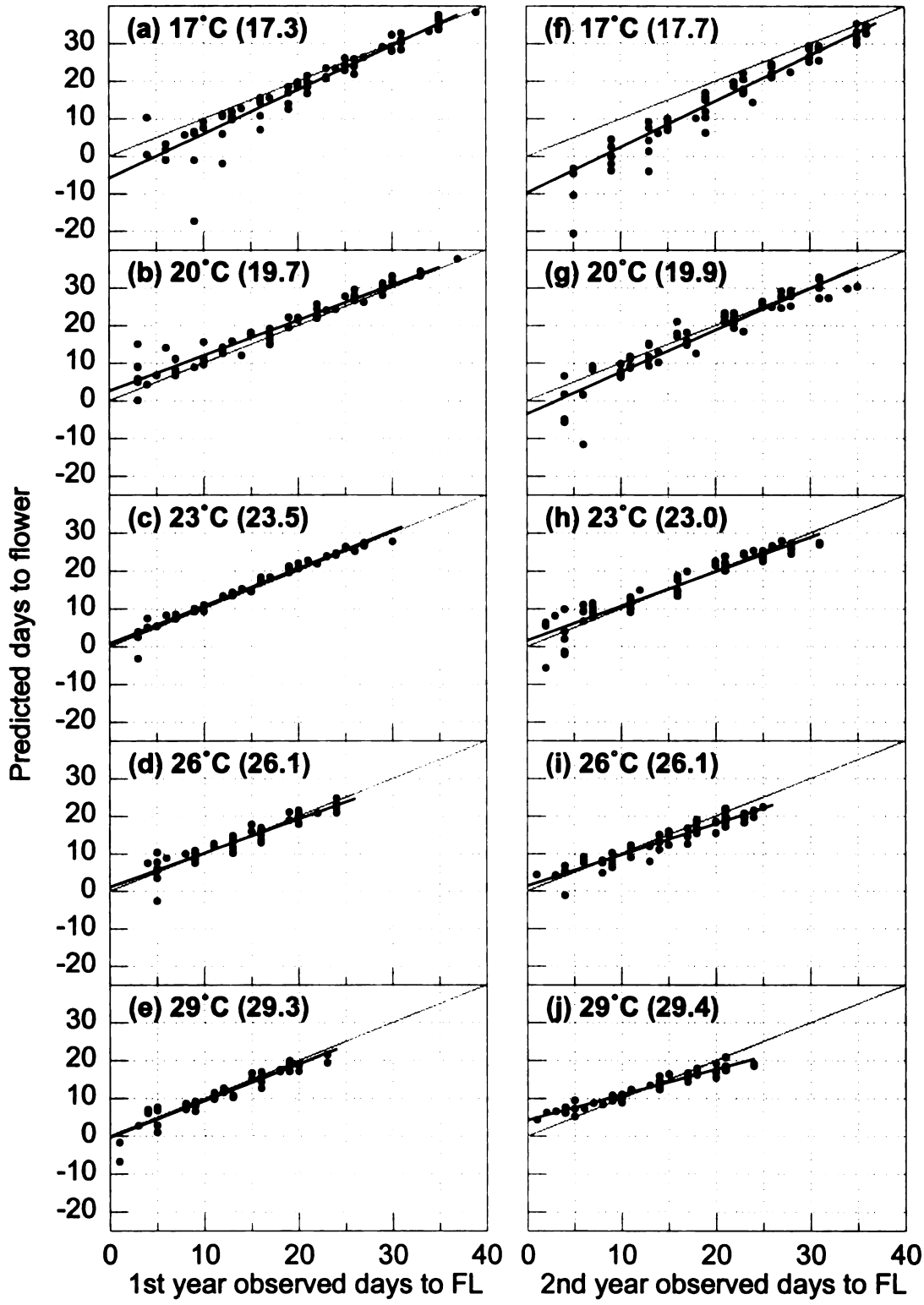

Figure 4. Predicted days to flower for *C. verticillata* 'Moonbeam' from a given bud diameter based on Eq. [6] vs. observed days to flower from a given bud diameter from the validation data set. Black line shows regression fitted to data points. Gray line represents 1:1 relationship.

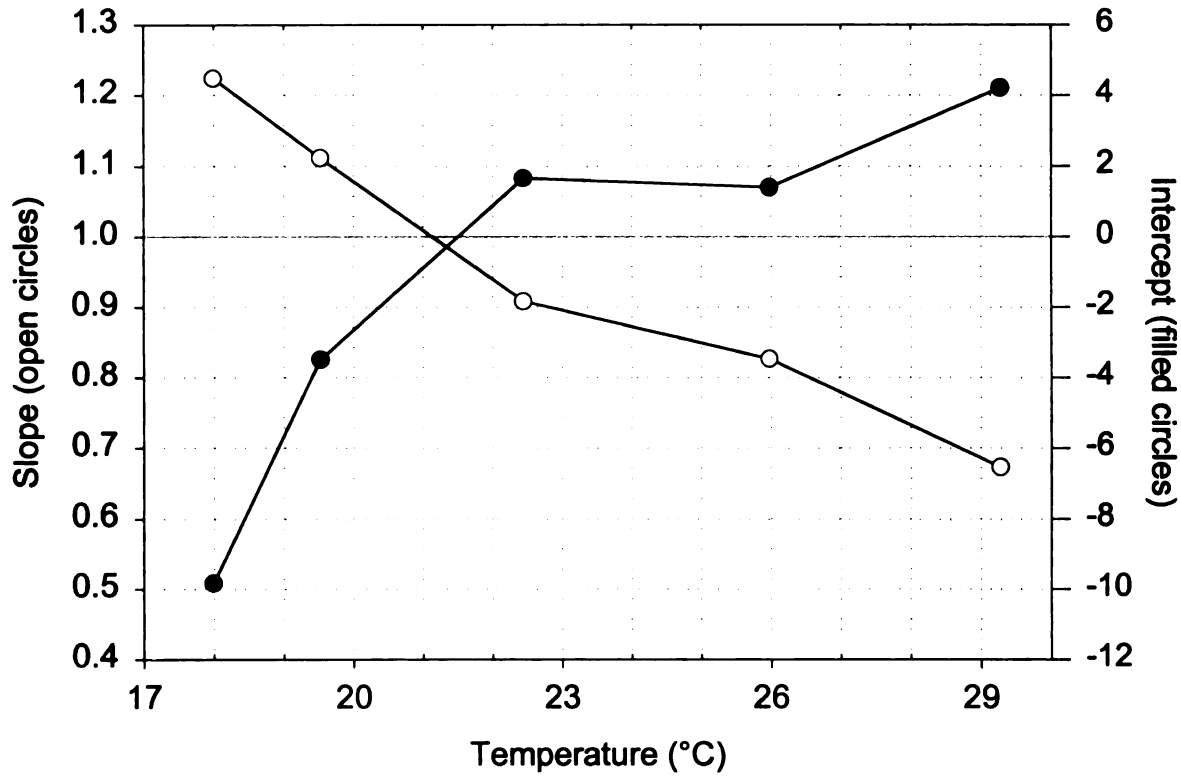

Figure 5. Slope and intercept of regression lines fit to predicted vs. observed second year data. Actual average temperatures from average date of visible bud to average date of flower were used. Slope is indicated by open circles and corresponds to the axis on the left, while intercept is indicated by closed circles and corresponds to the axis on the right. The gray line indicates where slope and intercept would be for a 1:1 line.

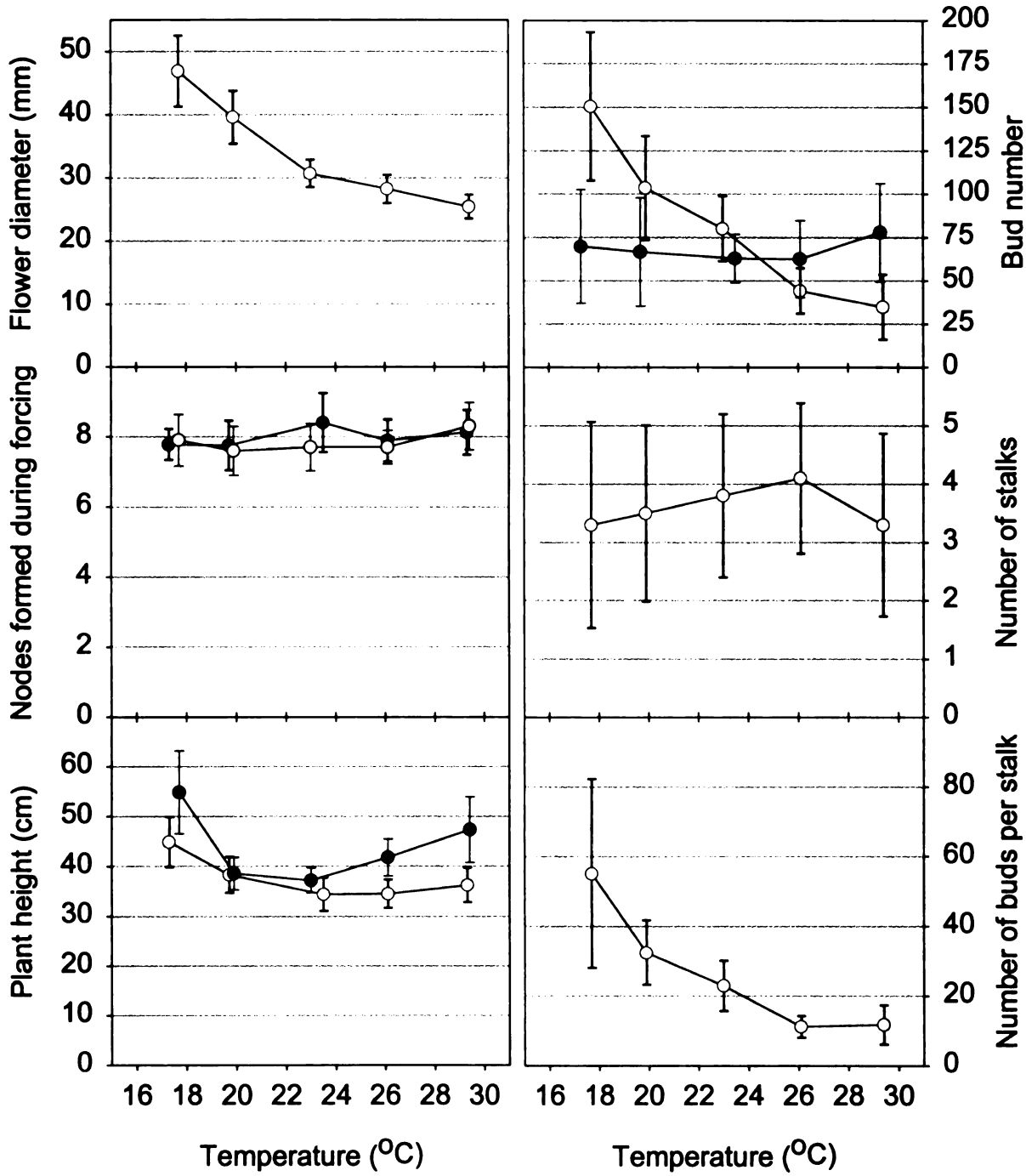

Figure 6. Influence of forcing temperature on plant height, number of nodes formed during forcing, diameter of open flowers, number of flowers, number of stalks per plant, and number of flowers per stalk for *Coreopsis verticillata* 'Moonbeam'. Filled circles represent first year data, open circles represent second year data. Error bars show standard deviation.

THE RESPONSE OF LONG-DAY HERBACEOUS PERENNIALS TO A NIGHT-INTERRUPTION AT LOW NIGHT TEMPERATURES

Abstract

The effectiveness of a four-hour night interruption (NI) to induce flowering in the long-day herbaceous perennials, *Achillea* L. 'Anthea', *Campanula carpatica* Jacq. 'White Clips', *Coreopsis grandiflora* Hogg ex Sweet 'Early Sunrise', *C. grandiflora* 'Sunray', *C. verticillata* L. 'Moonbeam', *Oenothera missouriensis* Sims, *O. speciosa* Nutt., and *Rudbeckia fulgida* Ait. 'Goldsturm' was tested at six different night temperatures. Plants were grown under natural short days (9:03 hrs to 11:35 hrs) December through March, augmented with a four-hour NI from 2200 to 200 hours provided by 60-W incandescent lights at 3 to 5 μmol m^{-2} s^{-1}. Night temperature setpoints were 2.5, 5, 10, 15, 20, and 25 °C with a day temperature setpoint of 25 °C for all treatments (actual average temperatures during the 4-h NI varied from 3.4 to 24.7°C).

Flower induction occurred in most species at all night temperatures. Flowering percentage for *O. missouriensis*, *O. speciosa* and *C.* 'Sunray' varied widely among treatments in the first year. An increase in the number of nodes developed prior to flower induction and a lower flowering percentage at temperatures above 20° C indicated some heat delay in *O. speciosa*, *A.* 'Anthea', and in smaller, second-year material of *C.* 'Early Sunrise'.

Night temperatures as low as 3.4° C did not inhibit flowering of any species. Therefore the species tested in this experiment perceived long days delivered by a 4-h night-interruption at night temperatures from 3.4 to 24.7 °C with day temperatures of ~25°C.

Introduction

A four-hour night interruption (NI) is an effective way to promote flowering in many long-day herbaceous perennials under natural short-day conditions (Runkle et al., 1998). Some perennials are commercially grown outdoors in the early spring and are, under normal temperature conditions, exposed to low night temperatures. To accelerate flower induction in early spring when natural photoperiods are too short, commercial growers often provide NI lighting. Under low-temperature conditions, Shillo and Halevy (1985) found that flowering percentage for *Gypsophila paniculata* 'Bristol Fairy' was severely reduced under long days delivered by day lengthening (additional hours of light in both morning and evening) when night temperatures were $\leq$17°C. Hicklenton et al. (1993), obtained similar results with a 18-h day-extension lighting on the same cultivar. It is not known whether other long-day herbaceous perennials might be affected similarly when subjected to NI lighting at low night temperatures.

Our objective was to determine the effectiveness of NI long-day lighting treatments in promoting flowering of several long-day herbaceous perennials when delivered at different night temperatures.

As the main interest was whether the plants would flower, and if so, whether there was any delay in initiation, data were taken as to whether the plant differentiated a flower bud or not, and at what node with respect to the start of forcing.

Materials and Methods

1st year. In early December 1996, five species of perennials were received from commercial growers. Species studied, plug size and exact numbers and dates regarding plant material are presented in Table 7. Plants were transplanted into 13-cm square containers (1.1L) at the start of treatments (unless otherwise noted in Table 7). Long days consisted of natural days (9:03 hrs to 11:35 hrs) December through March, plus a 4-hour night interruption from 2200 to 0200 hours at 3 to 5 μmol m^{-2} s^{-1} as measured by a LI-COR quantum sensor model LI-189 (LI-COR, Lincoln, Neb.) provided by 60-W incandescent lights.

Day temperature (from 800-1800 HR) was set at 25°C for all treatments, while night temperature (NT) was set at 25, 20, 15, 10, 5 or 2.5°C. On some nights when prevailing outside temperatures were not low enough, it was not possible to maintain the coolest night temperature set points. Actual average daily temperatures for each treatment, and average temperatures during the NI lighting period for each treatment presented in Table 8. Temperature in each greenhouse was recorded continually with a CR-10 datalogger (Campbell Scientific, Logan, Utah).

After 11 weeks of NI treatment, plants that had not reached visible bud were dissected under a stereoscope to determine if flower buds were present. Data recorded were: number of nodes at the start of forcing, presence or absence of a terminal flower bud, and number of nodes developed from the start of treatments to the first flower bud or inflorescence.

2nd year. The same procedures were followed the second year for six perennial species, except that at the end of treatment (Feb 15 for NT treatments 10-25°C, or March 8 for 2.5-5°C treatments), plants which had not reached visible bud were moved to natural short days at 20°C and held until approximately March 31, 1998. As well, 400W high-pressure sodium lamps were added to provide 50 μmol m^{-2} s^{-1} supplemental light. The lights were turned on when photosynthetic photon flux (ppf) levels in the greenhouse dropped below 200 μmol m^{-2} s^{-1}, and turned off when ppf exceeded 400 μmol m^{-2} s^{-1}. A control group was also added, which was held at a constant 20°C set temperature and natural short days for the duration of the experiment.

Flowering percentage and average number of nodes formed during forcing were determined for each treatment. New-node data was tested for significant linear and quadratic trends using the general linear models procedure (PROC GLM) in SAS (SAS Institute, 1990).

Results and Discussion

Percentage flower initiation. Most plants of *A.* 'Anthea', *C. verticillata*, *R. fulgida*, *C. carpatica*, and *C. grandiflora* 'Early Sunrise' initiated flowers in all treatments. All *O. missouriensis* plants initiated flowers the second year, while only about 60% did so the first year. In the first year, *O. speciosa* and *C. grandiflora* 'Sunray' demonstrated an incomplete and variable pattern of initiation over the temperature treatments. None of the plants in the control group in the second year initiated flowers. There was no evidence that night temperatures as low as 3.4°C affected the ability of these eight herbaceous perennials to initiate

flowers (Figures 6,7).

Nodes formed prior to initiation. The number of nodes formed prior to flower initiation from the start of long days indicates whether any treatment had delayed flower induction. With the exception of *R. fulgida* and *C. grandiflora* 'Sunray', the number of nodes formed prior to flower initiation was either not affected or was increased by increasing night temperature (figures 6, 7). Flower initiation was strongly delayed in *A.* 'Anthea' and *O. speciosa* as night temperature increased above 15°C (Figure 6).

In the second year *C. grandiflora* 'Early Sunrise' also showed an increase in the number of nodes added during forcing above 15°C night temperatures, as well as a slight decrease in the percentage of plants flowering, which would indicate heat delay. This trend was not evident in the first year, perhaps because the plant material in the first year was larger (first year material averaged ~16 nodes , while second year material averaged ~13 nodes). While cold night temperatures did not cause any adverse effects on flowering for this species, night temperatures above approximately 15°C may delay initiation in plants with 13 or fewer nodes (Figure 7).

For *C. grandiflora* 'Sunray' flowering percentage varied widely across treatments, and no treatment achieved 100% flowering (Figure 7). *Coreopsis* 'Sunray' normally requires vernalization before long day treatment in order to flower, but short days may substitute for this cold requirement (Runkle, 1996). It is possible that these plants did not receive enough short days before the start of treatments to ensure 100% flowering.

On the other hand, *O. missouriensis*, which also showed irregular flowering in the first year, had 100% flowering in all treatments in the second year, which suggests that perhaps the addition of supplemental lighting may have affected flowering responses. Thus, it may have been low light levels (lack of supplemental lighting) which was the cause of variable flowering percentages across treatments in *C. grandiflora* 'Sunray', *O. missouriensis* and *O. speciosa* in the first year.

While low night temperatures did not inhibit initiation of flowers in any of the species tested, a low night temperature does contribute to an overall lowering of average daily temperature (see Table 8), which slows developmental rates in general (Roberts and Summerfield, 1987; Wang, 1998; Yuan, 1998). On the other hand, many of the species tested showed evidence of heat delay as night temperatures increased above approximately 15-20°C. As all treatments experienced relatively high day temperatures of ~25°C, this delay may have been due to high average daily temperature, or it may have been due specifically to high night temperatures. While the species tested in this experiment perceived long days delivered by a 4-h night-interruption at night temperatures from 3.4 to 24.7°C, growers should take into account other possible effects of night temperature on timing, such as heat delay or delay due to a low average daily temperature.

Literature Cited

Hicklenton, P.R., S.M. Newman and L. J. Davies. 1993. Night temperature, photosynthetic photon flux, and long days affect *Gypsophila paniculata* flowering. HortScience 28(9):888-890.

Roberts, E.H. and R.J. Summerfield. 1987. Measurement and prediction of flowering in annual crops, pp.17-50. In: J.G. Atherton (ed.). Manipulation of flowering. Butterworths, London.

Runkle, E.S. 1996. The effects of photoperiod and cold treatment on flowering of twenty-five species of herbaceous perennials. MS Thesis, Dept. of Horticulture, Michigan State Univ., East Lansing.

Runkle E.S, R.D. Heins, A.C. Cameron, and W.H. Carlson. 1998. Flowering of herbaceous perennials under various night interruption and cyclic lighting treatments. HortScience 33(4):672-677.

SAS Institute. 1990. SAS/STAT users guide, release 6.12 ed. SAS Inst., Cary, NC.

Shillo, R. and A.H. Halevy. 1982. Interaction of photoperiod and temperature in flowering-control of *Gypsophila paniculata* L. Scientia Hort. 16:385-393.

Wang, S., R.D. Heins, W.H. Carlson and A.C. Cameron. 1998. Modeling the effect of temperature on flowering of *Hibiscus moscheutos*. Acta Hort. 456:161-169.

Yuan, M., W.H. Carlson, R.D. Heins and A.C. Cameron. 1998. Effect of forcing temperature on time to flower of *Coreopsis grandiflora*, *Gaillardia ×grandiflora*, *Leucanthemum ×superbum* and *Rudbeckia fulgida*. HortScience 33(4):663-667.

Table 7. Species used each year, number of plants per replicate, plug size at arrival[a], average number of nodes at the start of forcing, dates of arrival, start of treatment and end of treatment. Plants were held under 9-h SD in between arrival and start of treatments.

Species	Year	plants per treatment	Starting size		Date of arrival	Start of treatment	End of treatment
			plug[a]	# nodes			
Achillea 'Anthea'	2	10	50	26	29 Oct 1997	21 Dec 1997	15 Feb 1998[c]
Campanula carpatica	1	20	128	6	6 Dec 1996	11 Dec 1996	24 Feb 1997
'White Clips'	2	10	128	6	27 Nov 1997	22 Dec 1997	15 Feb 1998[c]
Coreopsis grandiflora	1	10	50	8	Nov 1996[b]	11 Dec 1996	24 Feb 1997
'Early Sunrise'	2	10	128	6	27 Nov 1997	20 Dec 1997	15 Feb 1998[c]
C. grandiflora 'Sunray'	1	10	50	8	Nov 1996[b]	11 Dec 1996	24 Feb 1997
C. verticillata 'Moonbeam'	2	10	128	cut back	8 Nov 1997	31 Dec 1997	15 Feb 1998[c]
Oenothera missouriensis	1	40	128	4	6 Dec 1996	11 Dec 1996	24 Feb 1997
	2	10	128	6	27 Nov 1997	20 Dec 1997	15 Feb 1998[c]
Oenothera speciosa	1	40	128	13	6 Dec 1996	11 Dec 1996	24 Feb 1997
Rudbeckia fulgida 'Goldsturm'	2	10	2½"	19	13 Oct 1997	18 Dec 1997	15 Feb 1998[c]

[a]Volume of plug sizes is as follows:
128-cell: 10 ml; 50-cell: 85 ml; 2½" pots: 350 ml.

[b]Coreopsis 'Early Sunrise' and C. 'Sunray' arrived in early November and were potted into 11-cm square pots and bulked under 9-h SD at 20 °C from November 9 until December 11 when they were placed into treatments.

[c]Two coolest night temperature treatments ended 8 Mar 1998.

Table 8. Average daily temperatures and temperature during 4-h night interruption (NI) for each treatment in the first and second year.

Set temperature day/**night** °C	Year 1 temperatures		Year 2 temperatures	
	avg. daily	NI	avg. daily	NI
25/**25**	24.7	24.7	24.5	24.6
25/**20**	21.9	19.5	22.2	19.8
25/**15**	19.5	14.9	19.3	14.6
25/**10**	17.3	10.5	16.8	10.4
25/**5**	14.2	5.5	16.2	7.0
25/**2.5**	13.7	3.4	15.5	4.9

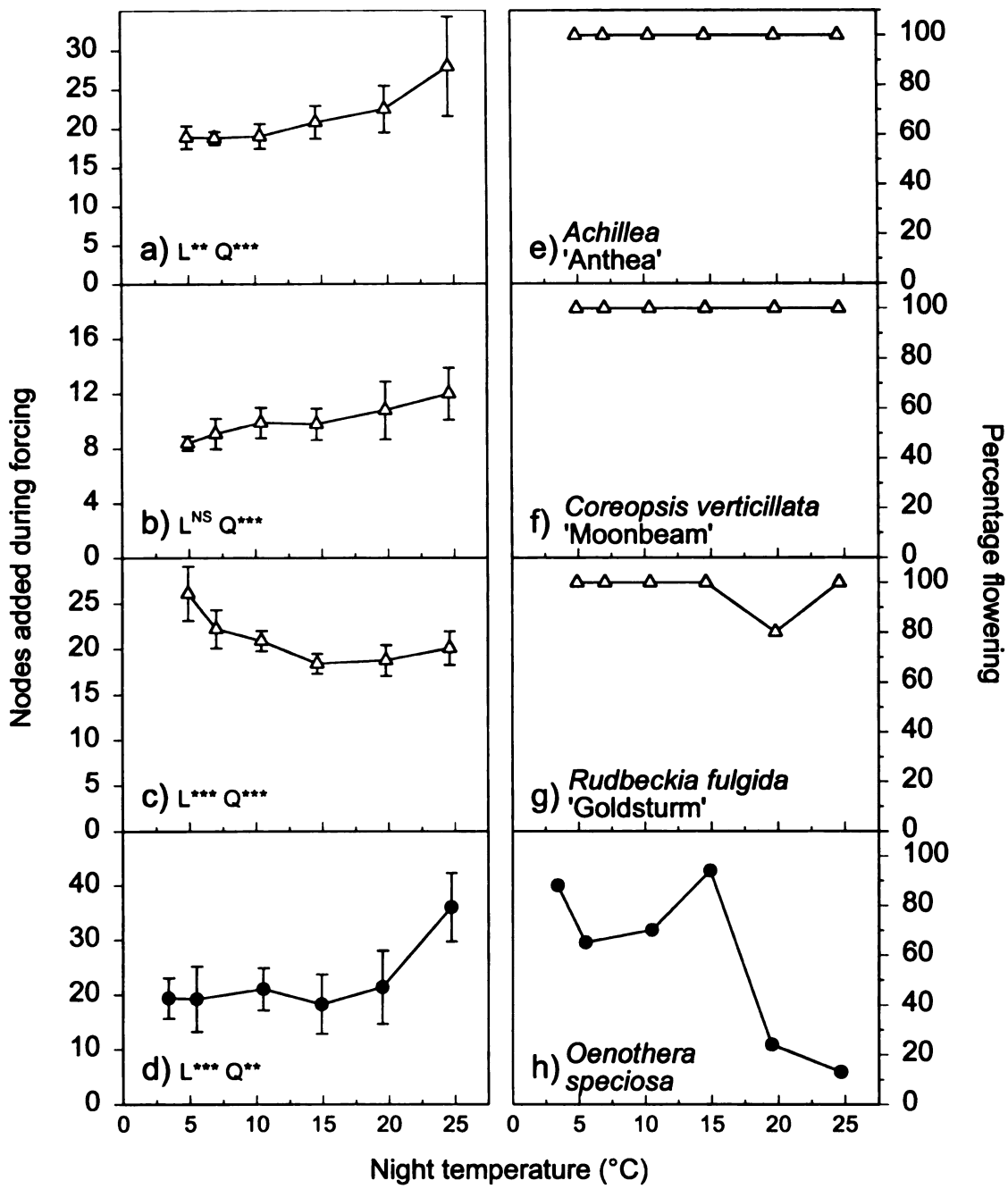

Figure 7. Graphs a-d show average number of nodes added from the start of treatments to the first flower bud. Error bars show 95% confidence interval. Graphs e-h show flowering percentage. Closed circles represent data taken the first year, while open triangles represent data taken the second year. Linear trend (L) or quadratic trend (Q) nonsignificant (^{NS}), or significant at P=0.05 (*), 0.01 (**), or 0.001 (***).

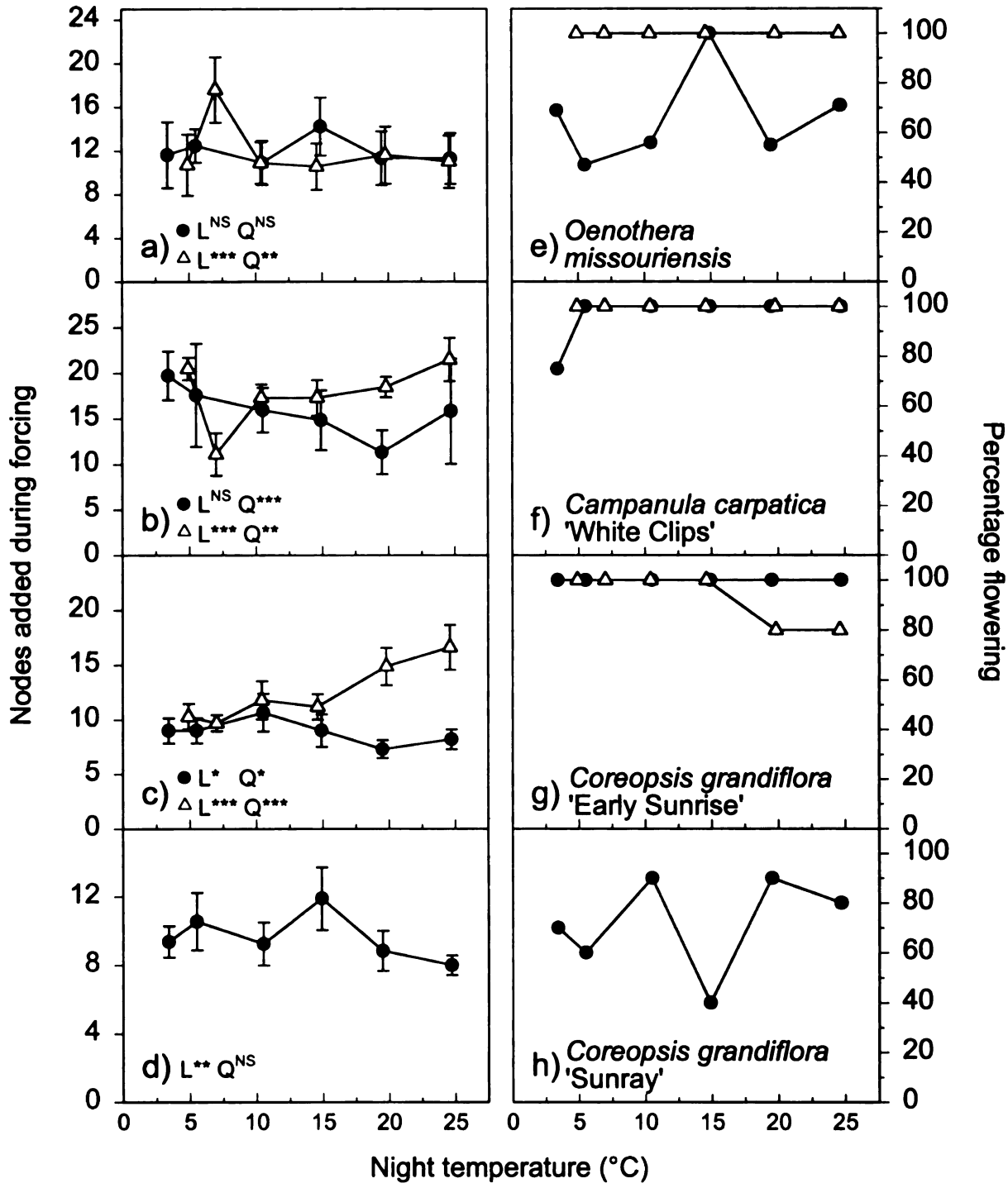

Figure 8. Graphs a-d show average number of nodes added from the start of treatments to the first flower bud. Error bars show 95% confidence interval. Graphs e-h show flowering percentage. Closed circles represent data taken the first year, while open triangles represent data taken the second year. Linear trend (L) or quadratic trend (Q) nonsignificant (^{NS}), or significant at P=0.05 (*), 0.01 (**), or 0.001 (***).

APPENDIX A:

NEW SPECIES SCREEN

INTRODUCTION

As perennials have become more popular, the demand for growers to produce them has increased. Since selling plants in bloom increases both their value and desirability, recent research has focused on how to bring perennials into flower on demand. As a preliminary step in the research process, species new to the MSU perennial program are put through a simple experiment designed to elucidate the basics of their requirements to flower.

To determine whether they require cold to flower, they are given either 15 weeks of cold treatment at 5°C, or no cold treatment. These plants are then divided into short day treatments (9-h) or long day treatments (9-h with a 4-h night interruption) to find out what photoperiod they require to bloom. In addition to noting whether and when the plants flower, measurements such as height and number of flowers are recorded. Informal observations are made as to the potential of each species as a flowering potted plant.

The new species screen provides an information base from which to choose species which have promise for the grower based on appearance and ease of production. Those plants which show potential are then studied in more detail. The data taken in the new species screen helps the researcher to know what to expect from the plant, and to design experiments to pinpoint cold, photoperiod and temperature responses.

PROTOCOL

OBJECTIVE: To screen various species for flowering response under long and short days and before and after cold treatment.

EXPERIMENTAL DESIGN:

Plant Material: See table 9

Photoperiods:

1) 9 hours (0800 - 1700)
2) Night interruption from 2200 to 0200 HR with incandescent lamps

Cold Treatments:

1) No cold treatment
2) 15 weeks at 5°C (9-h photoperiod from cool-white fluorescent light)

Plant Requirements:

10 plants x 2 photoperiods x 2 cold treatments = 40 plants/species

RESEARCH PROTOCOL:

Half of the plants of each species will be planted into 5" square pots and put under the indicated photoperiods upon arrival; the other half will be put into a 5°C cooler for 15 weeks and then potted up and put under photoperiod treatments. Greenhouse forcing temperatures will be set at a constant 20°C.

Data collected will include:

1) Initial leaf count
2) Date of visible bud/inflorescence
3) Date of flowering
4) Final leaf number at date of flowering
5) Number of flower buds/inflorescences at date of flowering
6) Height of plant/inflorescence at date of flowering

Table 9. New species screens 1997-1999. Production information, including rating as a potted plant, cold and photoperiod recommendations, based on the treatments given in this screen, and approximate weeks to flower at 20°C.

Species/Cultivar	rating as pot plant	15 weeks cold?	provide NI?	wks to FL at 20°C	Comments
Achillea 'Anthea'	☆☆☆	yes	yes	7	Lots of long lasting flowers
Achillea ptarmica 'The Pearl'	☆	rec.	yes	5	very susceptible to powdery mildew
Agastache 'Pink Panther'	☆☆	rec.	no	6	very long bloom time some PGR work needed
Ajuga reptans 'Bronze Beauty'	☆☆☆	yes	no	3	nice with or without flowers – and easy
Anemone hupehensis	☆☆☆	yes	yes	14	a nice show of pink flowers
Anemone sylvestris	☆	?	?	2	Inconsistent flowering and short lived blooms
Anemone vitifolia 'Robustissima'	☆☆☆	yes	yes	14	very similar to *A. hupehensis*
Aster alpinus 'Goliath'	☆	yes	?	5	nice flowers, but flowering was inconsistent
Aster dumosis 'Purple Dome'	☆☆	yes	no	8	needs work with PGRs
Aubrieta 'Whitewell Gem'	☆☆	yes	no	3	easy. nice flowers but scraggly
Campanula portenschlagiana	☆☆☆	yes	no	5	good but not as nice as 'Birch Hybrid'
Clematis montana 'John Paul II'	☆☆☆	yes	yes	12	a nice show if you can contain it.
Clethra alnifolia 'Rosea'	☆	yes	not neces.	15	inconsistent flowering
Coreopsis auriculata 'Nana'	☆☆	no	?	4	short & cute, but needs photoperiod work
Coreopsis rosea	☆☆☆	rec.	yes	7	like pink C. verticillata – great, but may need staking
Dianthus deltoides 'Shrimp'	☆	yes	no	8	few flowers – also needs juvenility work

☆☆☆ = excellent, ready for pot culture
☆☆ = consistent, not ready for pot culture
☆ = not suited for pot culture at this time

rec. = recommended
prob. = probably
not neces. = not necessary
PGR's = plant growth regulators

Table 9 (cont'd)

Species/Cultivar	rating as pot plant	15 weeks cold?	provide NI?	wks to FL at 20°C	Comments
Dianthus deltoides 'Canta Libre'	☆	prob.	prob. not	—	no flowers from plugs– needs juvenility work
Dicentra eximia 'Luxuriant'	☆☆	yes	no	6	could be nice but needs cultural work
Echinacea purpurea 'Magnus'	☆☆	rec.	yes	15	needs work with PGRs or other height reduction
Geranium 'Johnson's Blue'	☆☆	rec.	no	6	long bloomer – needs work with PGRs
Geum 'Mrs. Bradshaw'	☆☆	yes	not neces.	8	needs work with PGRs otherwise v. nice
Gypsophila paniculata 'Happy Festival'	☆☆☆	yes	yes	11.5	needs PGRs, as recommended by breeder
Helenium 'Bruno'	☆☆	yes	yes	10	needs work with PGRs
Helenium autumnale 'Red & gold Hybrid'	☆☆	yes	yes	14	needs work with PGRs
Hemerocallis 'Rocket City'	☆☆☆	not neces.	yes if no cold	15	needs a gallon pot
Iris 'Sambo'	☆	?	yes	3	flowers extrememly short-lived
Lewisia cotyledon	☆☆	rec.	no	12	beautiful show, but inconsistent flowering
Lychnis coronaria 'Angel Blush'	☆	yes	?	8	inconsistent flowering – needs juvenility & PGR work
Oenothera fruticosa 'Youngii-Lapsley'	☆☆☆	yes	not neces.	6	a great display!
Pennisetum alopecuroides 'Little Bunny'	☆	?	?	—	did not flower under any treatment
Polygonum affine 'Dimity'	☆☆	yes	yes	13	not very showy
Potentilla atrosanguinea 'Miss Willmott'	☆	yes	?	7	inconsistent flowering – needs juvenility & PGR work
Sidalcea 'Party Girls'	☆☆	not neces.	no	10	very nice but too tall – needs work with PGRs

☆☆☆ = excellent, ready for pot culture
☆☆ = consistent, not ready for pot culture
☆ = not suited for pot culture at this time

rec. = recommended
prob. = probably
not neces. = not necessary
PGR's = plant growth regulators

Table 9 (cont'd)

Species/Cultivar	rating as pot plant	15 weeks cold?	provide NI?	wks to FL at 20°C	Comments
Stokesia laevis 'Klaus Jellito'	☆☆☆	yes	no	11	fills out a 5" pot very nicely
Tanacetum 'Robinson Dk Crimson'	☆	rec.	yes	15	low flowering % – needs juvenility work
Thalictrum aquilegifolium	☆	yes	?	8	inconsistent and not very showy
Tiarella wherryi	☆☆☆	no	not neces.	4	very easy to flower. Long lasting display
Tricyrtis hirta 'Miyazaki'	☆	yes	yes	16	sparse flowering, long force time
Trollius ledebourii 'Golden Queen'	☆☆	rec.	no	>15	nice flowers, but long force time – juvenility?
Veronica longifolia 'Icicle' (veg)	☆☆☆	yes	not neces.	9	fills out a 5" pot nicely — tall white spikes
Veronica longifolia 'Red Fox'	☆☆☆	yes	not neces.	7	fills out a 5" pot — smaller pink spikes

☆☆☆ = excellent, ready for pot culture
☆☆ = consistent, not ready for pot culture
☆ = not suited for pot culture at this time

rec. = recommended
prob. = probably
not neces. = not necessary
PGR's = plant growth regulators

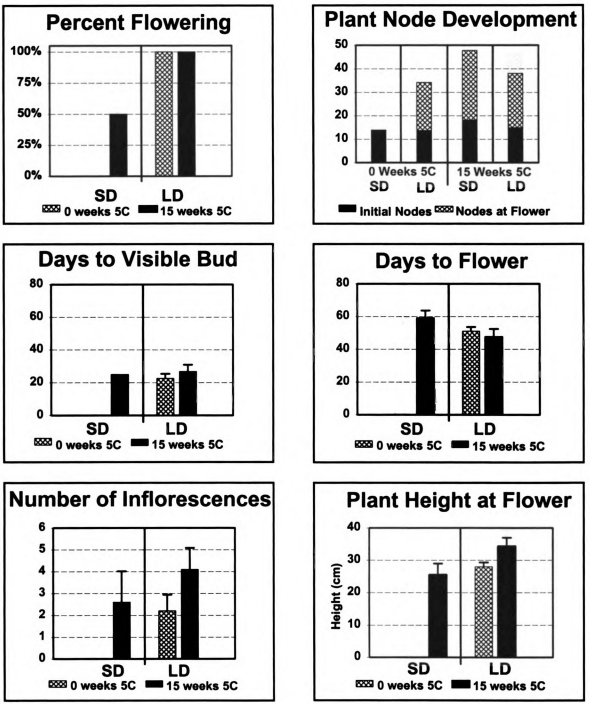

Figure 9. Effects of photoperiod and cold treatment on *Achillea* 'Anthea' as indicated. Error bars show 95% confidence intervals.

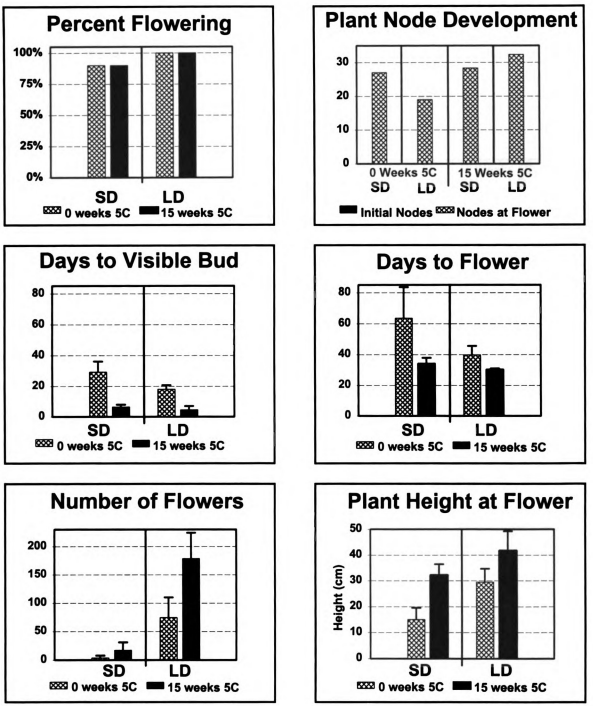

Figure 10. Effects of photoperiod and cold treatment on *Achillea ptarmica* 'The Pearl' as indicated. Error bars show 95% confidence intervals.

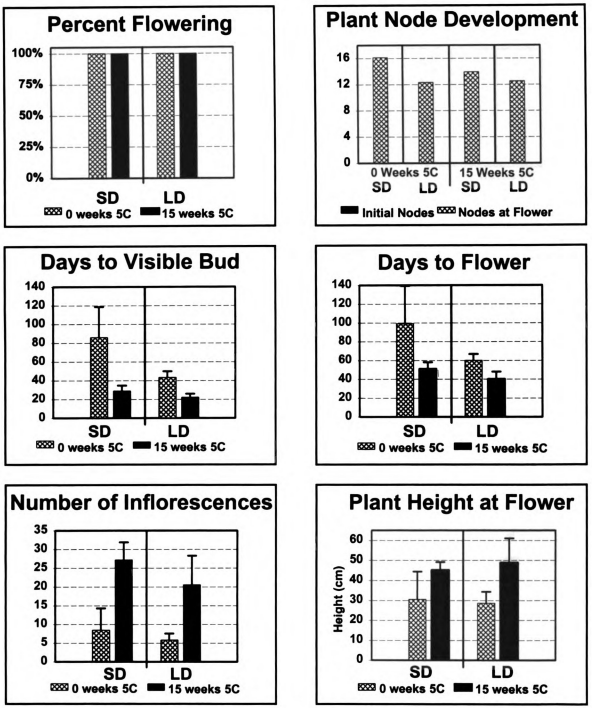

Figure 11. Effects of photoperiod and cold treatment on *Agastache* 'Pink Panther' as indicated. Error bars show 95% confidence intervals.

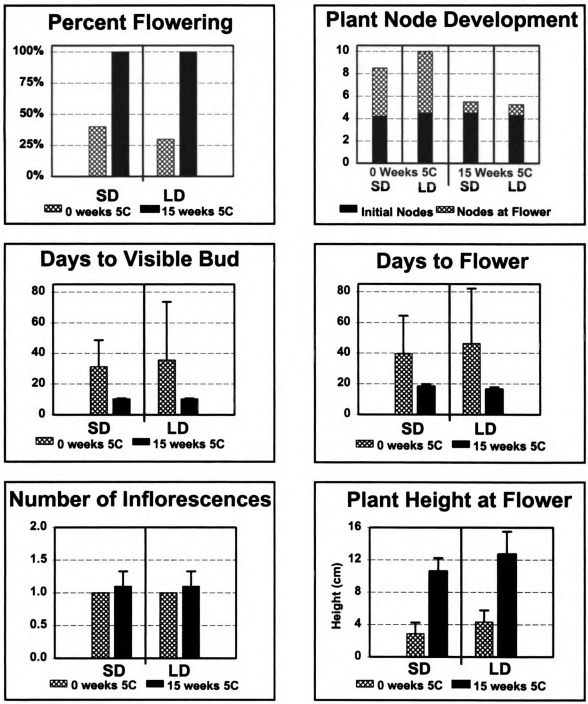

Figure 12. Effects of photoperiod and cold treatment on *Ajuga reptans* 'Bronze Beauty' as indicated. Error bars indicate 95% confidence intervals.

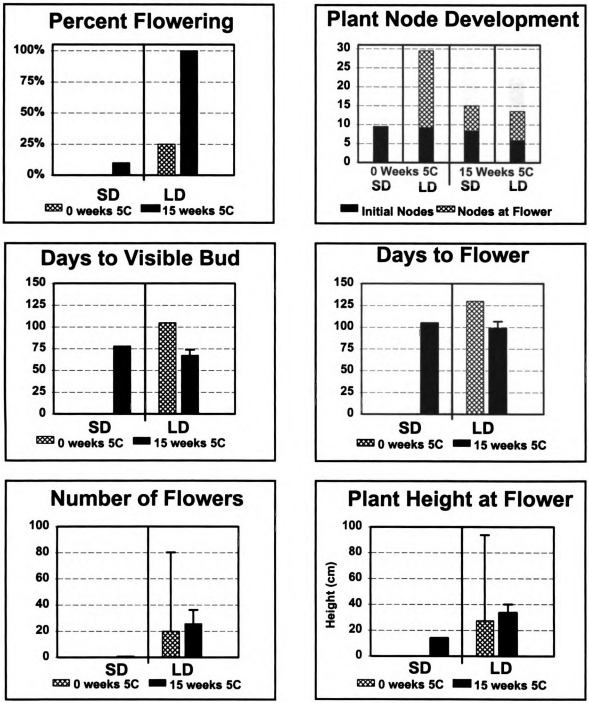

Figure 13. Effects of photoperiod and cold treatment on *Anemone hupehensis* as indicated. Error bars show 95% confidence intervals.

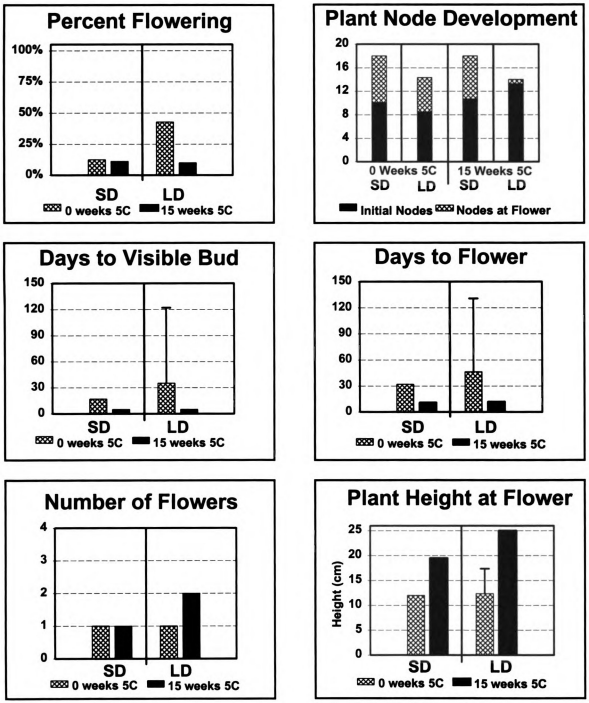

Figure 14. Effects of photoperiod and cold treatment on *Anemone sylvestris* as indicated. Error bars show 95% confidence intervals.

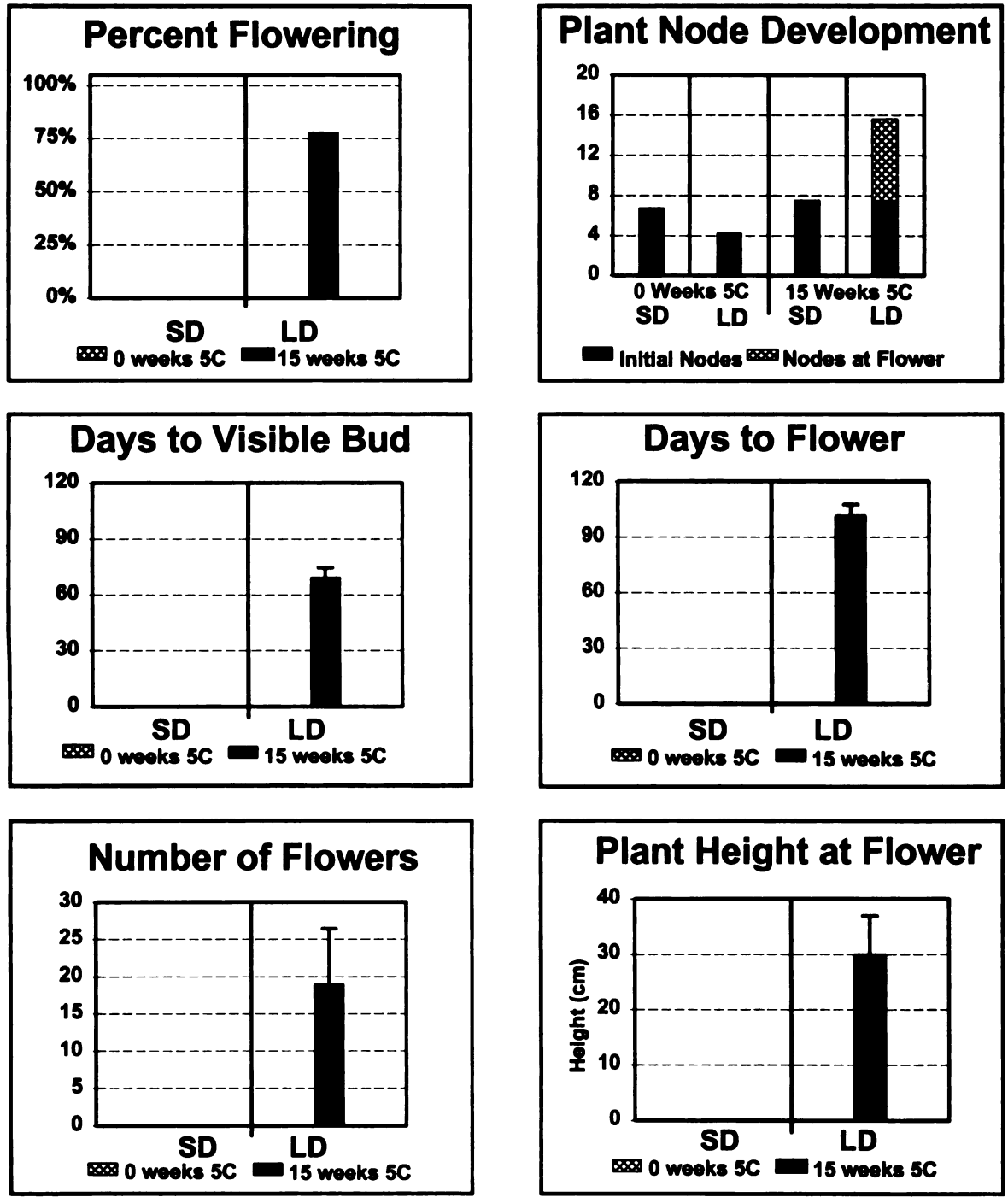

Figure 15. Effects of photoperiod and cold treatment on *Anemone vitifolia* 'Robustissima' as indicated. Error bars show 95% confidence intervals.

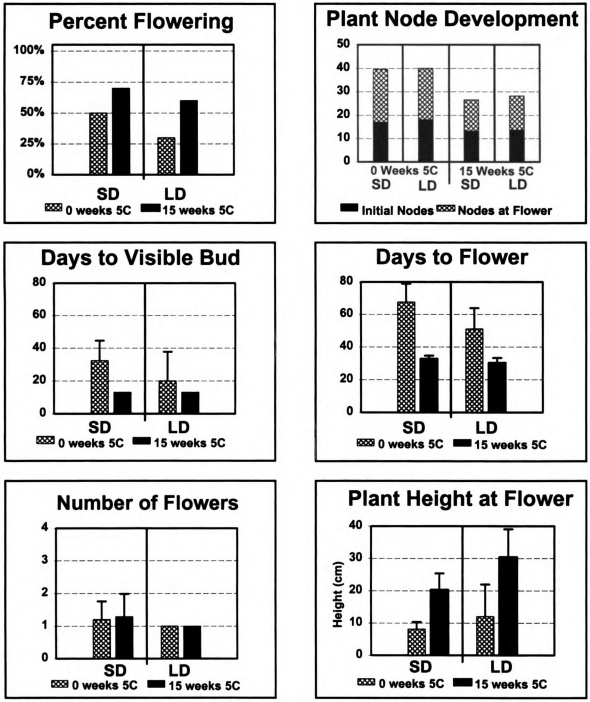

Figure 16. Effects of photoperiod and cold treatment on *Aster alpinus* 'Goliath' as indicated. Error bars show 95% confidence intervals.

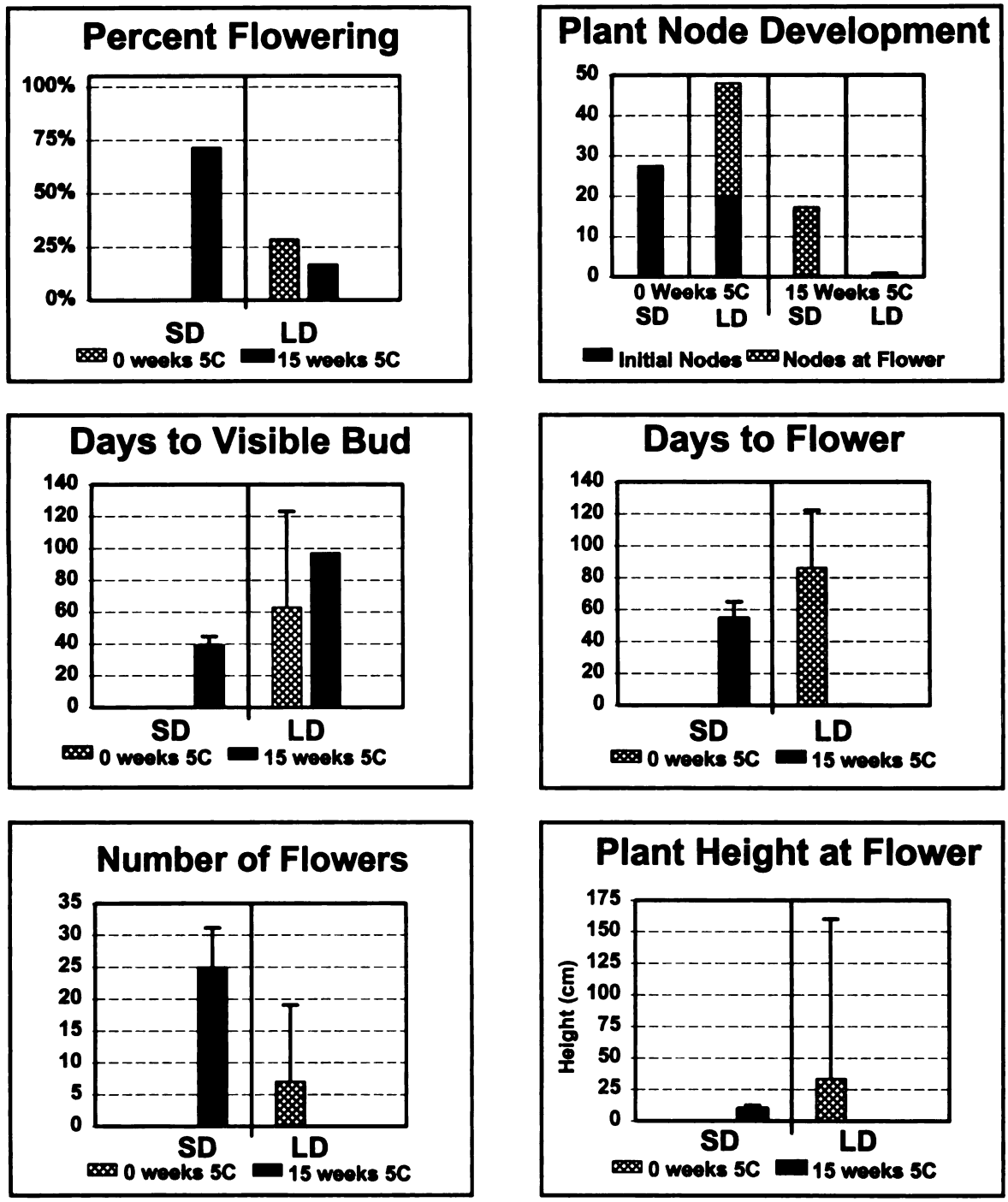

Figure 17. Effects of photoperiod and cold treatment on *Aster dumosus* as indicated. Error bars show 95% confidence intervals.

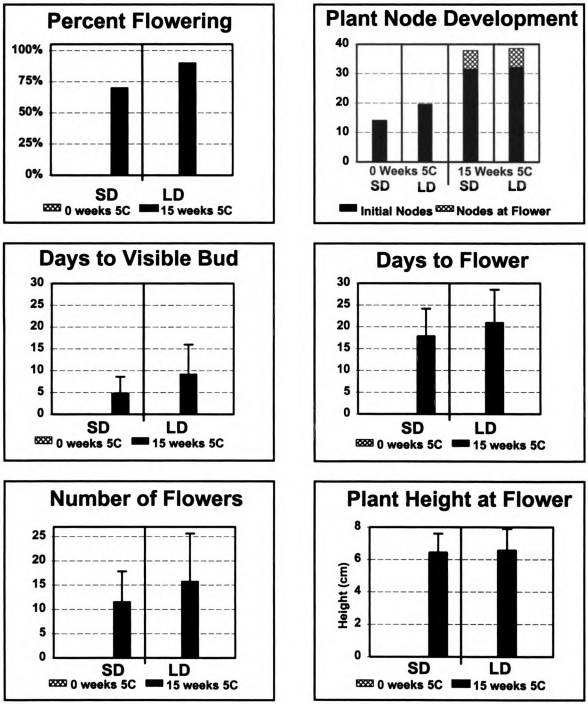

Figure 18. Effects of photoperiod and cold treatment on *Aubrieta* 'Whitewell Gem' as indicated. Error bars show 95% confidence intervals.

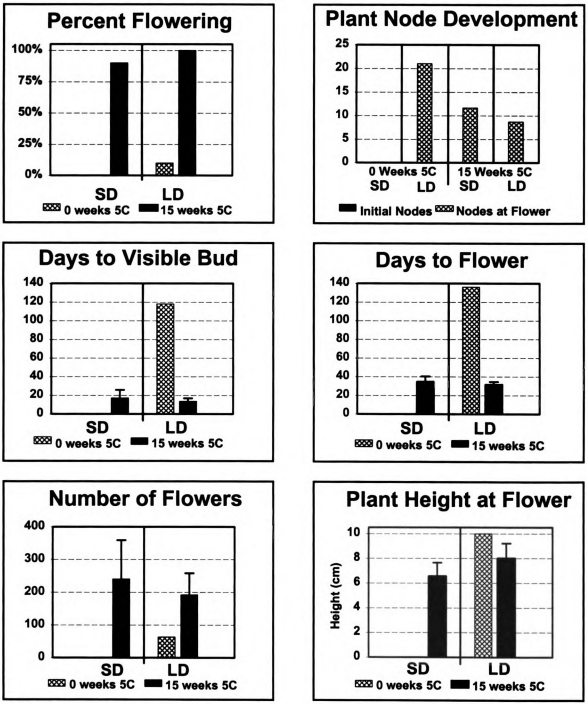

Figure 19. Effects of photoperiod and cold treatment on *Campanula portenschlagiana* as indicated. Error bars show 95% confidence intervals.

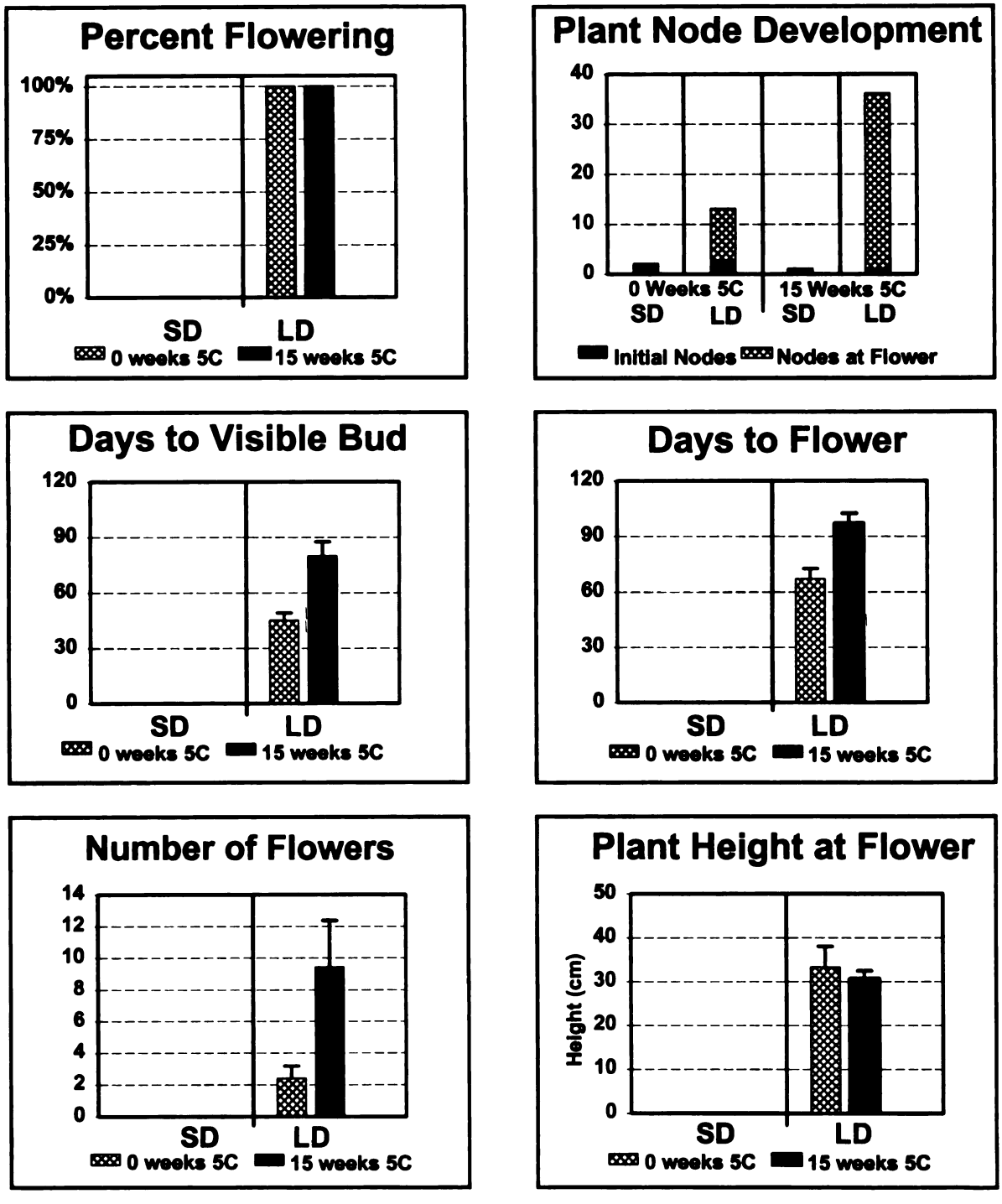

Figure 20. Effects of photoperiod and cold treatment on *Clematis montana* 'John Paul II' as indicated. Error bars show 95% confidence intervals.

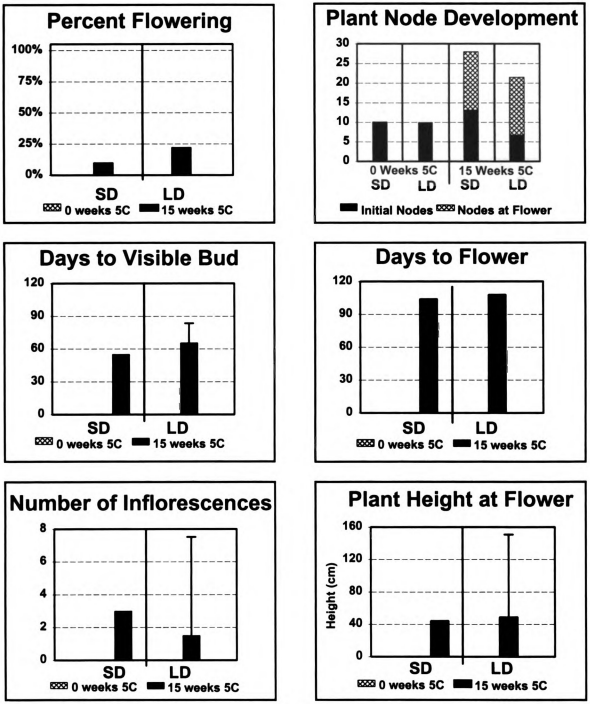

Figure 21. Effects of photoperiod and cold treatment on *Clethra alnifolia* 'Rosea' as indicated. Error bars show 95% confidence intervals.

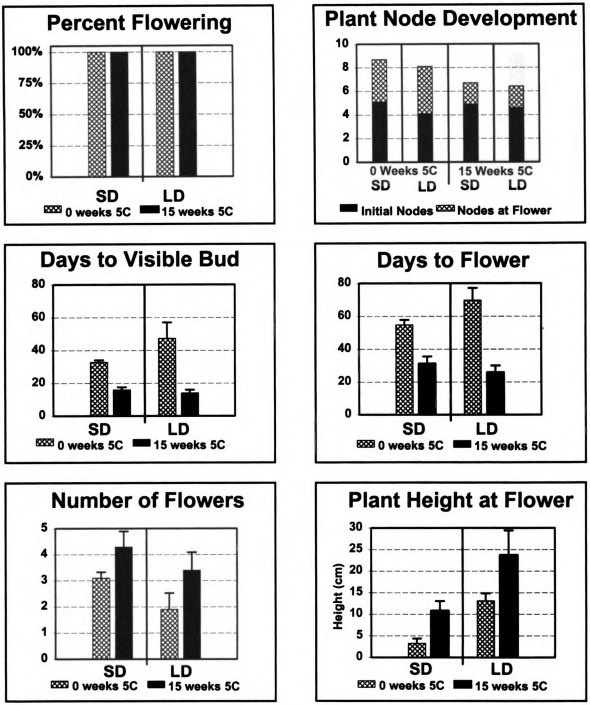

Figure 22. Effects of photoperiod and cold treatment on *Coreopsis auriculata* 'Nana' as indicated. Error bars show 95% confidence intervals.

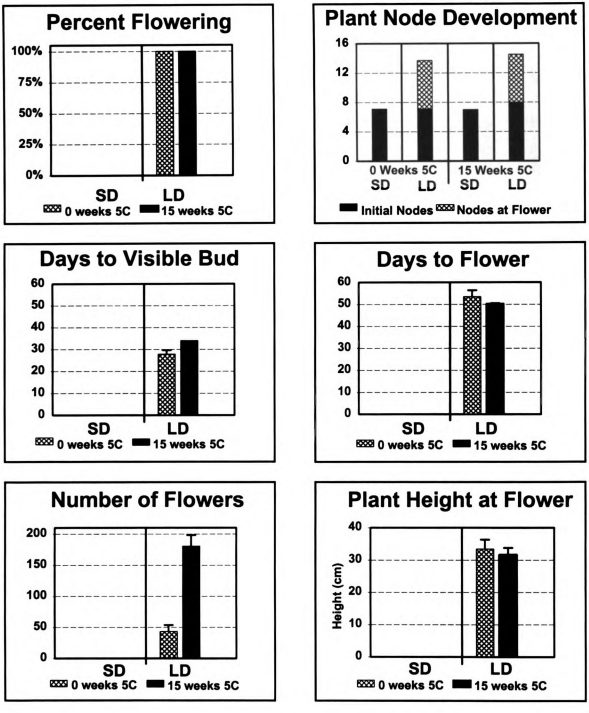

Figure 23. Effects of photoperiod and cold treatment on *Coreopsis rosea* as indicated. Error bars show 95% confidence intervals.

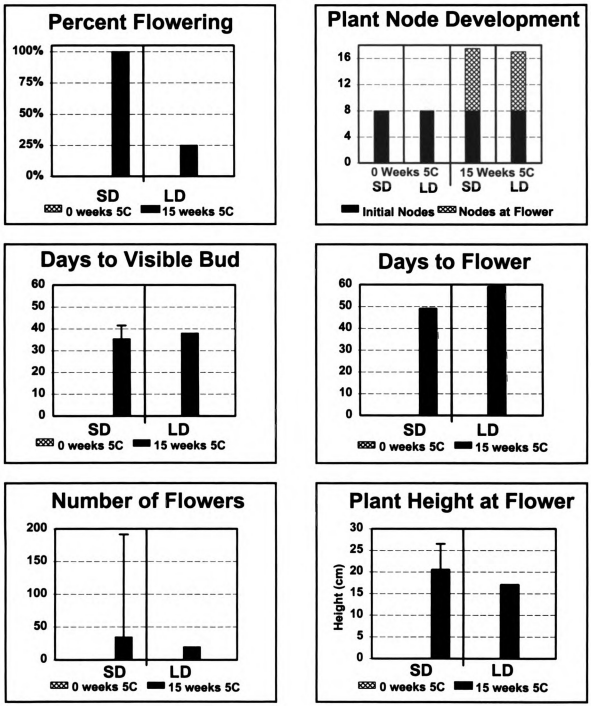

Figure 24. Effects of photoperiod and cold treatment on *Dianthus deltoides* 'Shrimp' as indicated. Error bars show 95% confidence intervals.

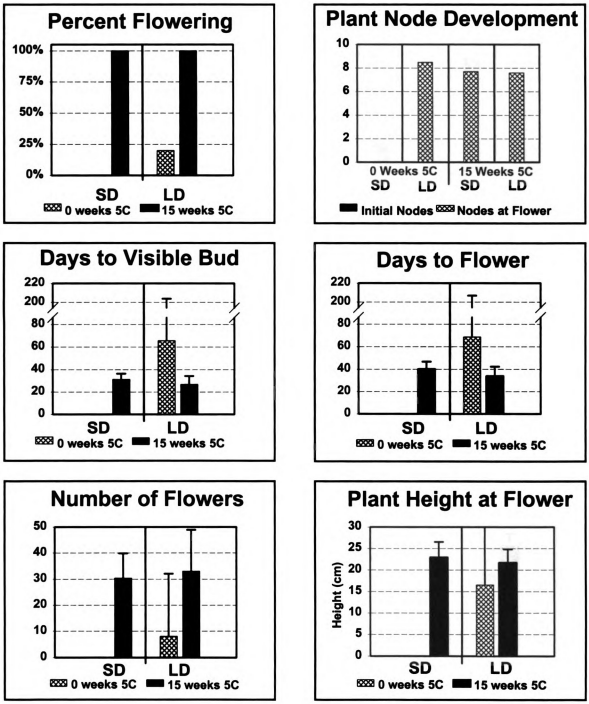

Figure 25. Effects of photoperiod and cold treatment on *Dicentra eximia* 'Luxuriant' as indicated. Error bars show 95% confidence intervals.

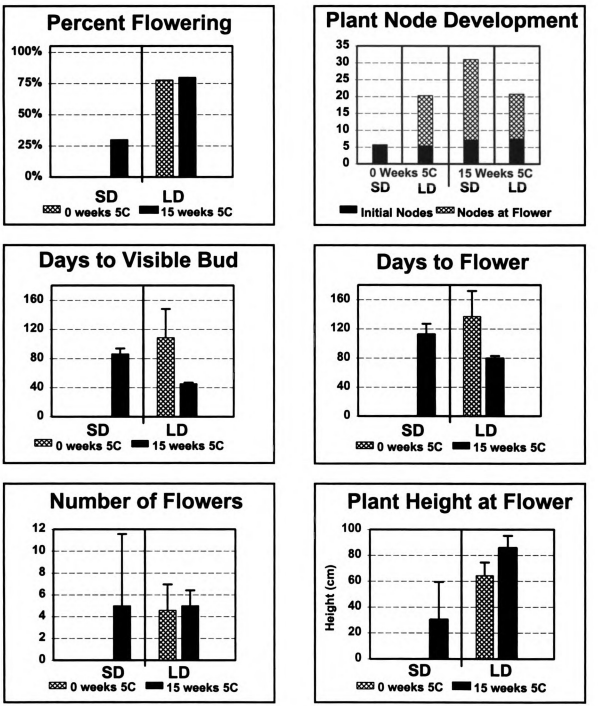

Figure 26. Effects of photoperiod and cold treatment on *Echinacea purpurea* 'Magnus' as indicated. Error bars show 95% confidence intervals.

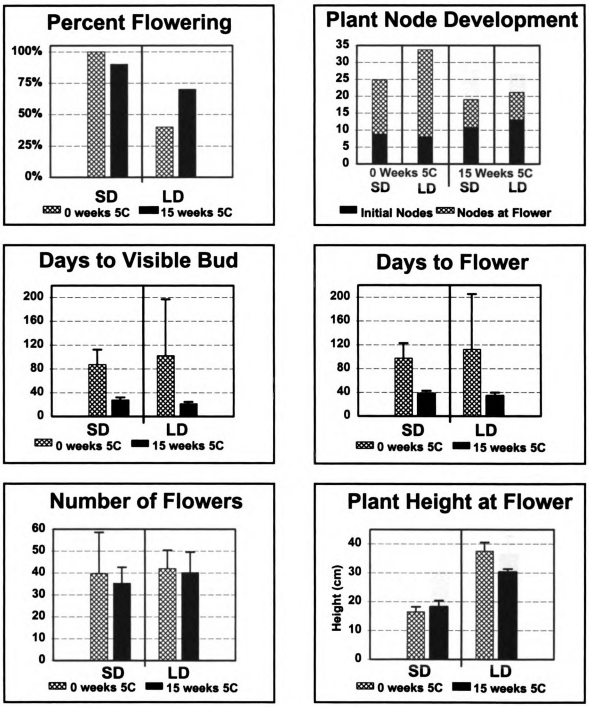

Figure 27. Effects of photoperiod and cold treatment on *Geranium* 'Johnson's Blue' as indicated. Error bars show 95% confidence intervals.

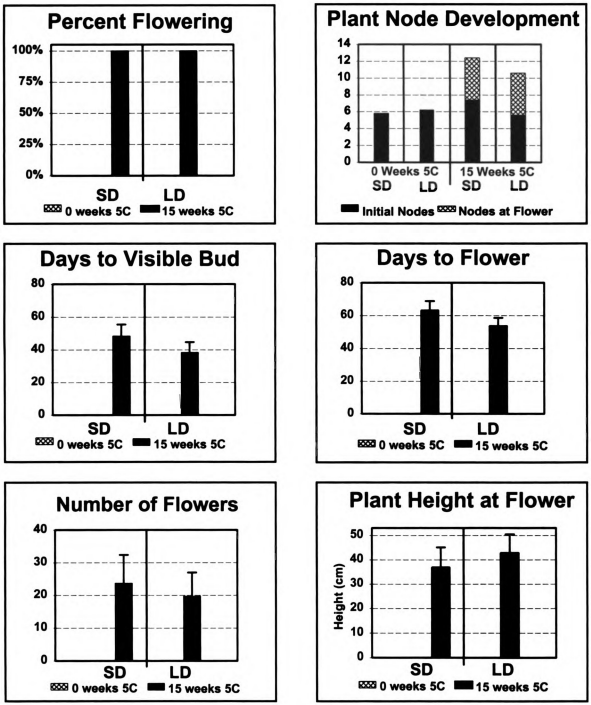

Figure 28. Effects of photoperiod and cold treatment on *Geum* 'Mrs. Bradshaw' as indicated. Error bars show 95% confidence intervals.

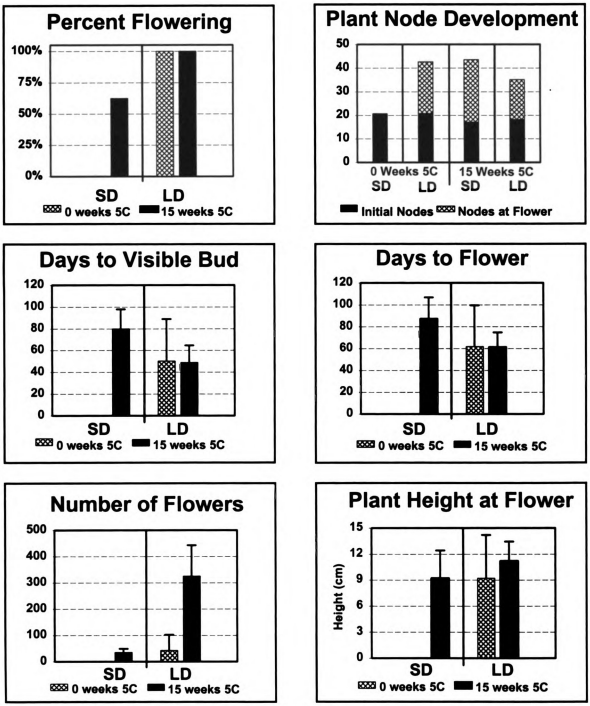

Figure 29. Effects of photoperiod and cold treatment on *Gypsophila paniculata* 'Happy Festival' as indicated. Error bars show 95% confidence intervals.

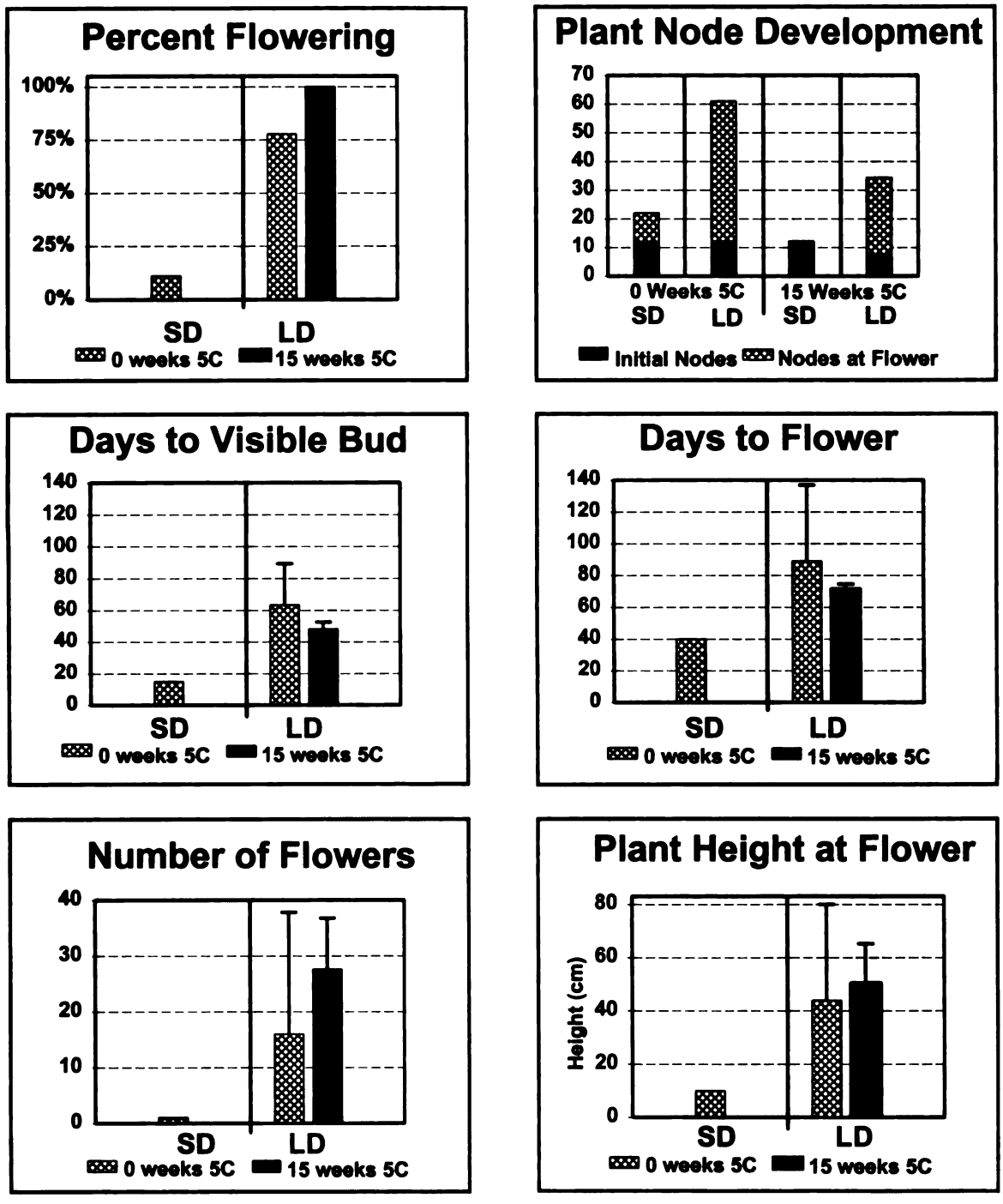

Figure 30. Effects of photoperiod and cold treatment on *Helenium* 'Bruno' as indicated. Error bars show 95% confidence intervals.

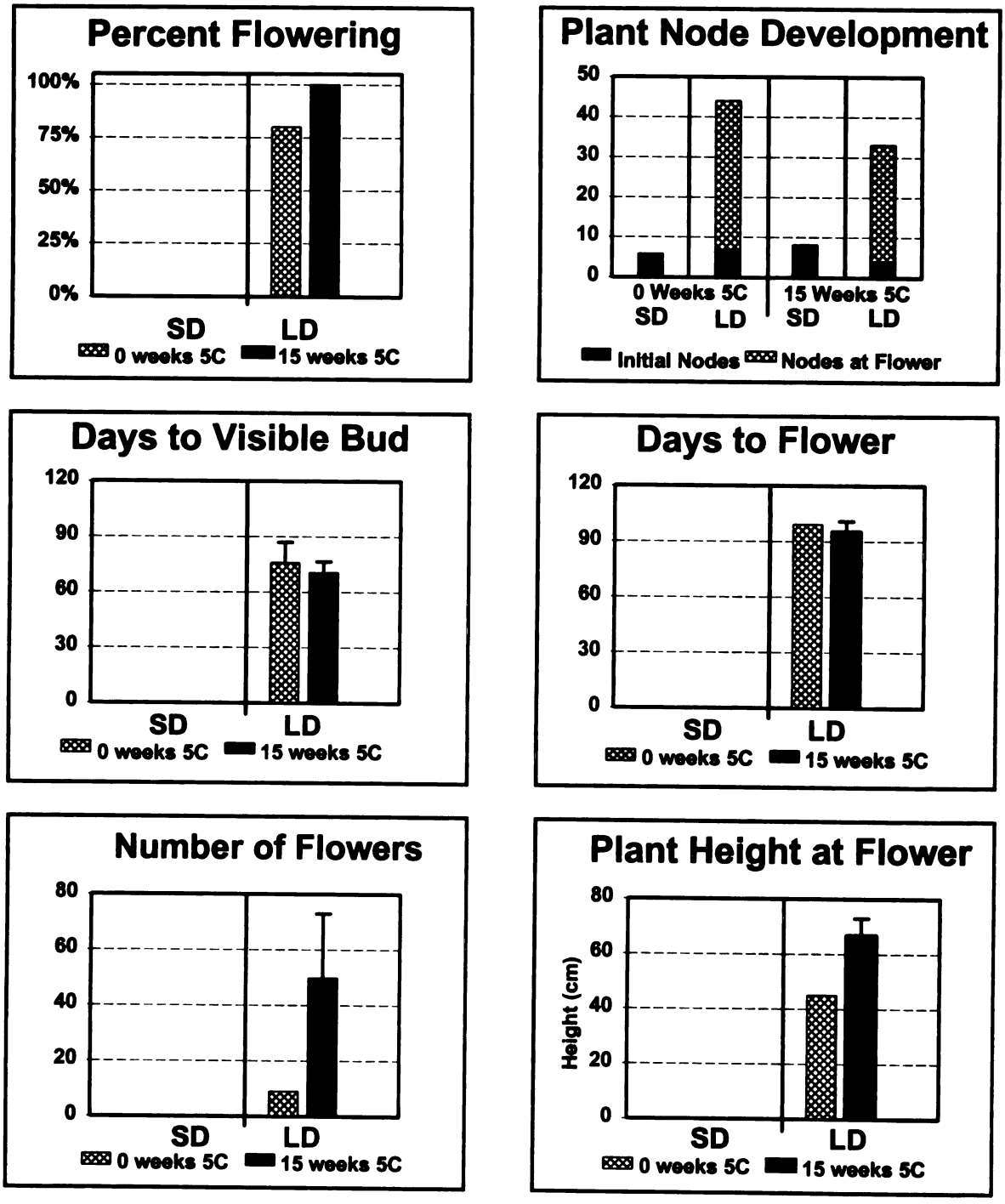

Figure 31. Effects of photoperiod and cold treatment on *Helenium* 'Red and Gold Hybrid' as indicated. Error bars show 95% confidence intervals.

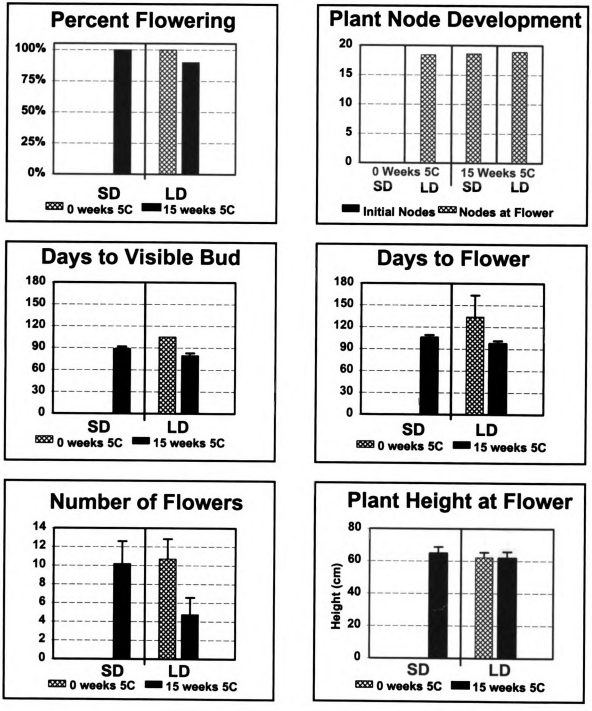

Figure 32. Effects of photoperiod and cold treatment on *Hemerocallis* 'Rocket City' as indicated. Error bars show 95% confidence intervals.

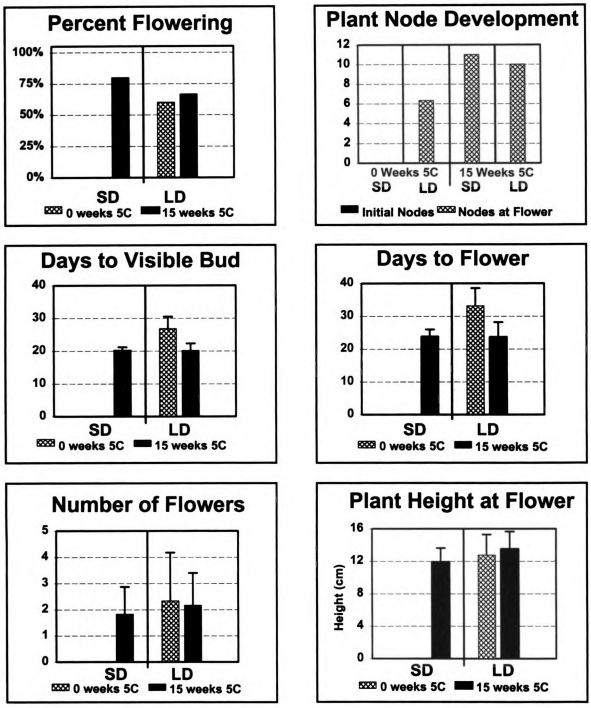

Figure 33. Effects of photoperiod and cold treatment on *Iris* 'Sambo' as indicated. Error bars show 95% confidence intervals.

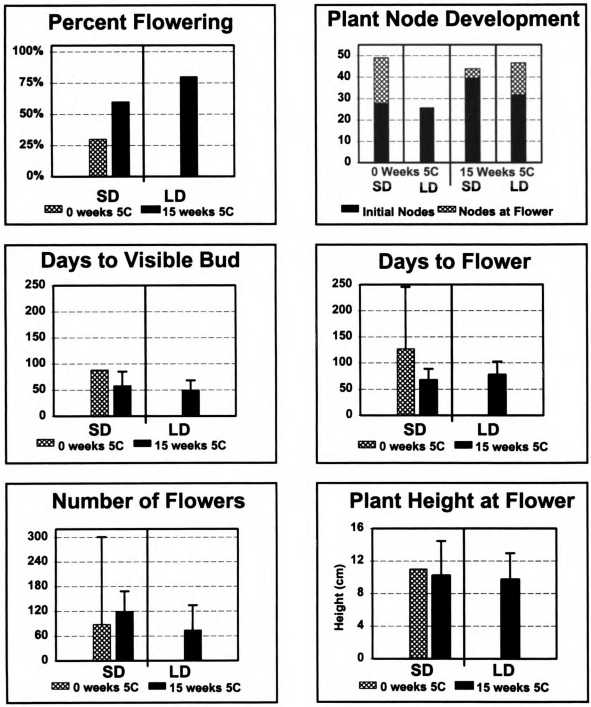

Figure 34. Effects of photoperiod and cold treatment on *Lewisia cotyledon* as indicated. Error bars show 95% confidence intervals.

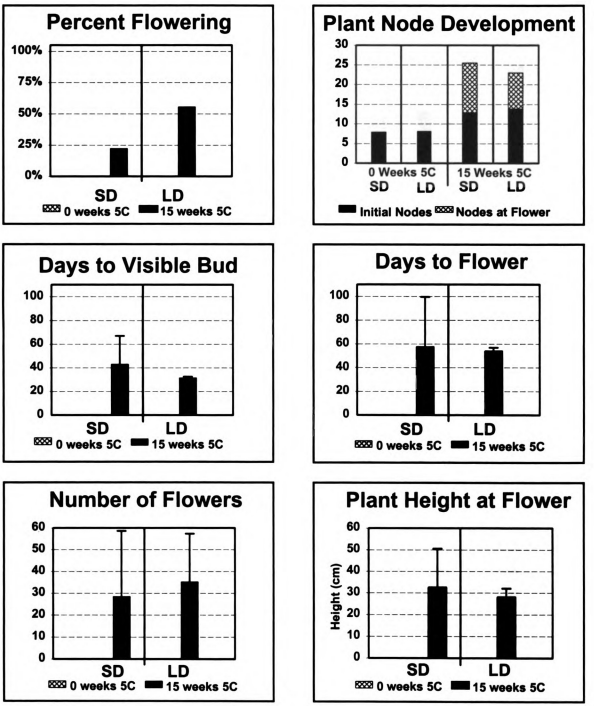

Figure 35. Effects of photoperiod and cold treatment on *Lychnis coronaria* 'Angel Blush' as indicated. Error bars show 95% confidence intervals.

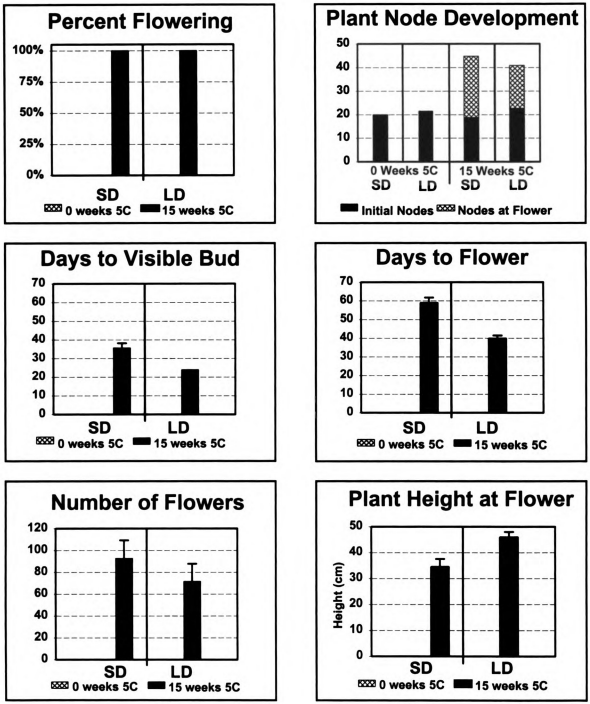

Figure 36. Effects of photoperiod and cold treatment on *Oenothera fruticosa* 'Youngii-Lapsley' as indicated. Error bars show 95% confidence intervals.

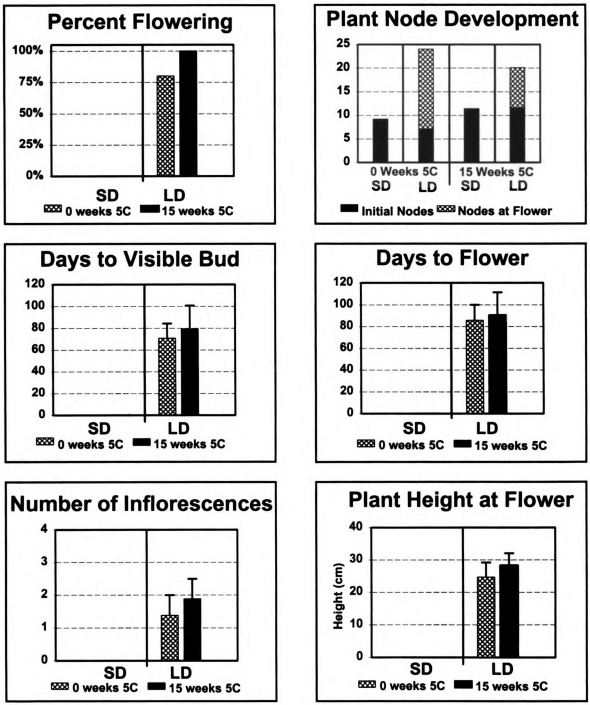

Figure 37. Effects of photoperiod and cold treatment on *Polygonum affine* 'Dimity' as indicated. Error bars show 95% confidence intervals.

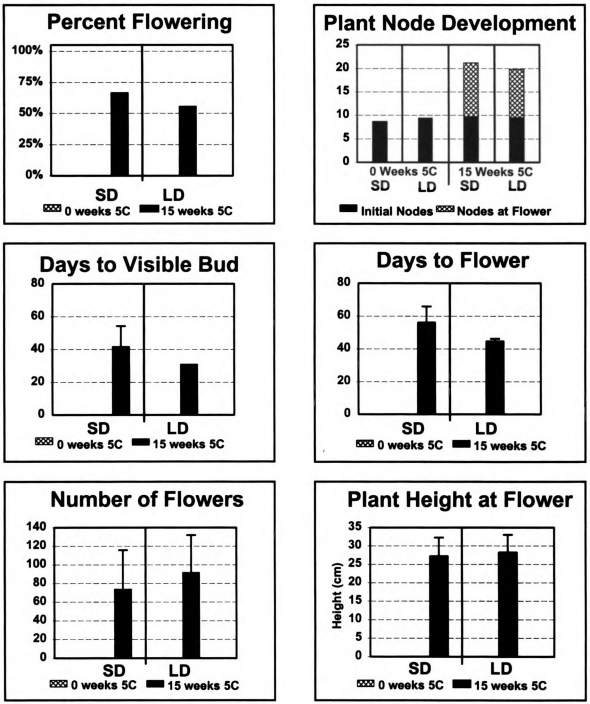

Figure 38. Effects of photoperiod and cold treatment on *Potentilla atrosanguinea* 'Miss Willmott' as indicated. Error bars show 95% confidence intervals.

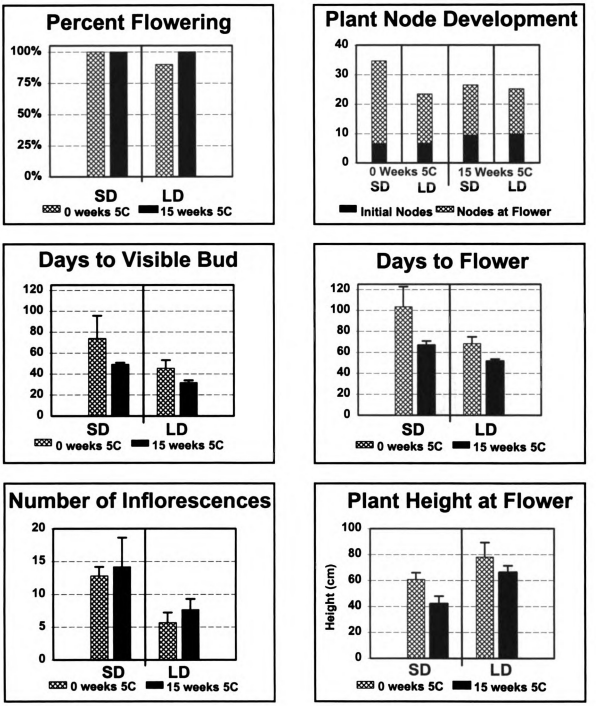

Figure 39. Effects of photoperiod and cold treatment on *Sidalcea* 'Party Girls' as indicated. Error bars show 95% confidence intervals.

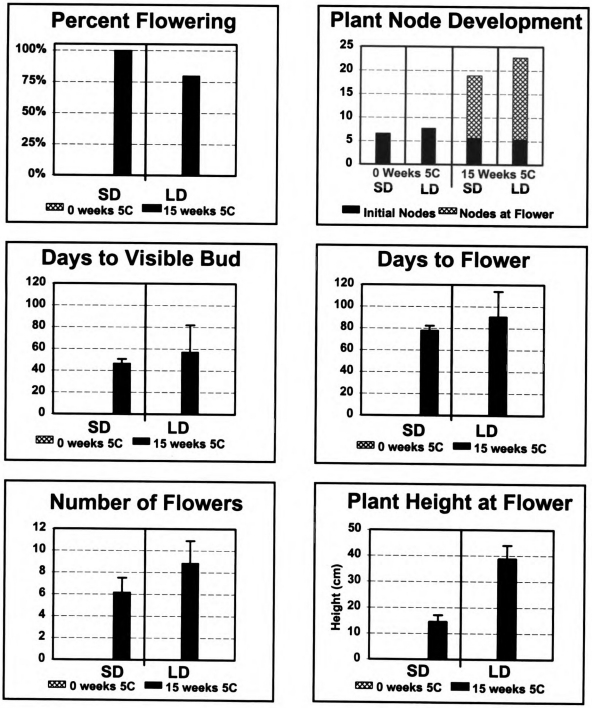

Figure 40. Effects of photoperiod and cold treatment on *Stokesia laevis* 'Klaus Jellito' as indicated. Error bars show 95% confidence intervals.

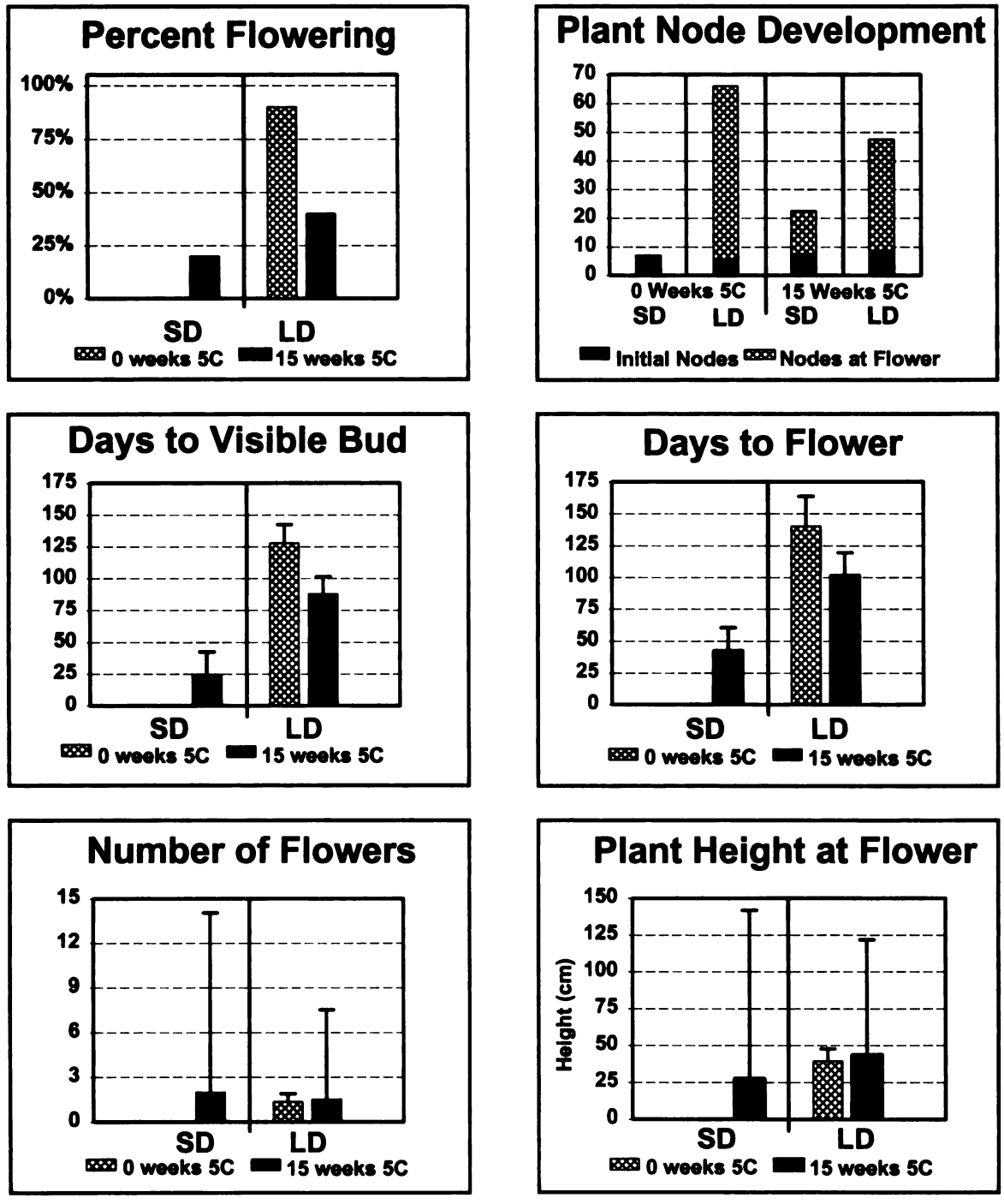

Figure 41. Effects of photoperiod and cold treatment on *Tanacetum* 'Robinson's Dark Crimson' as indicated. Error bars show 95% confidence intervals.

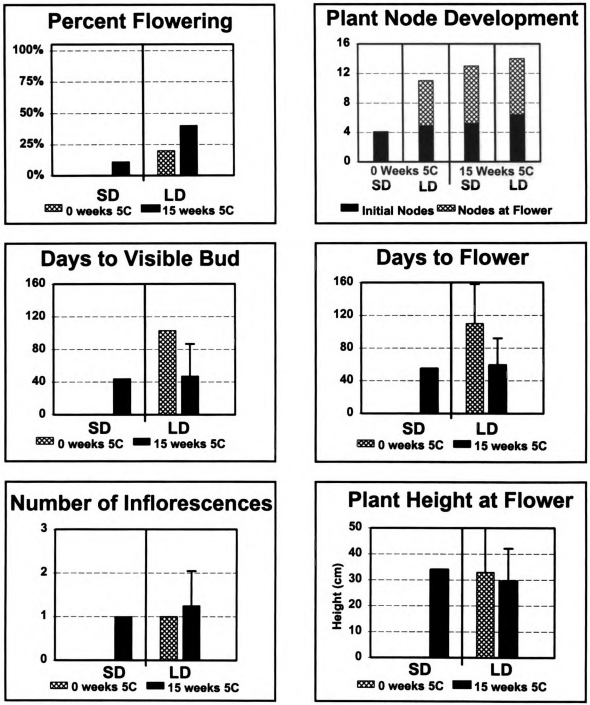

Figure 42. Effects of photoperiod and cold treatment on *Thalictrum aquilegifolium* as indicated. Error bars show 95% confidence intervals.

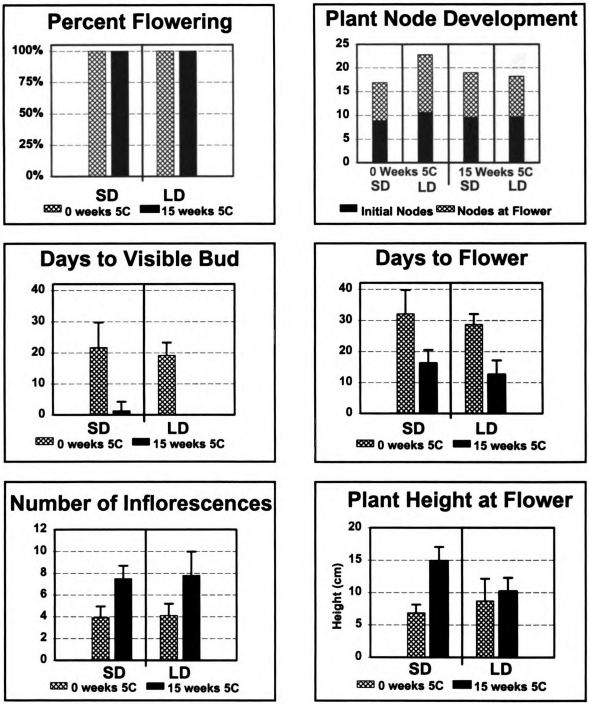

Figure 43. Effects of photoperiod and cold treatment on *Tiarella wherryi* as indicated. Error bars show 95% confidence intervals.

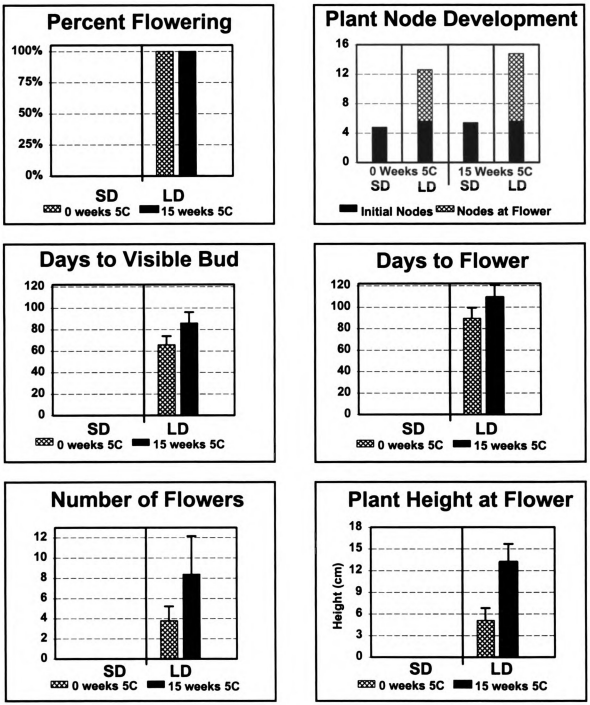

Figure 44. Effects of photoperiod and cold treatment on *Tricyrtis hirta* 'Miyazaki' as indicated. Error bars show 95% confidence intervals.

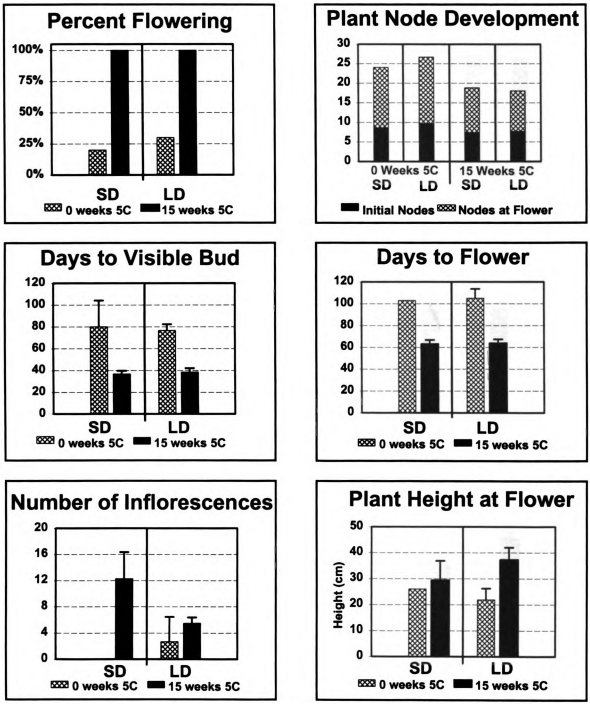

Figure 45. Effects of photoperiod and cold treatment on *Veronica longifolia* 'Icicle' as indicated. Error bars show 95% confidence intervals.

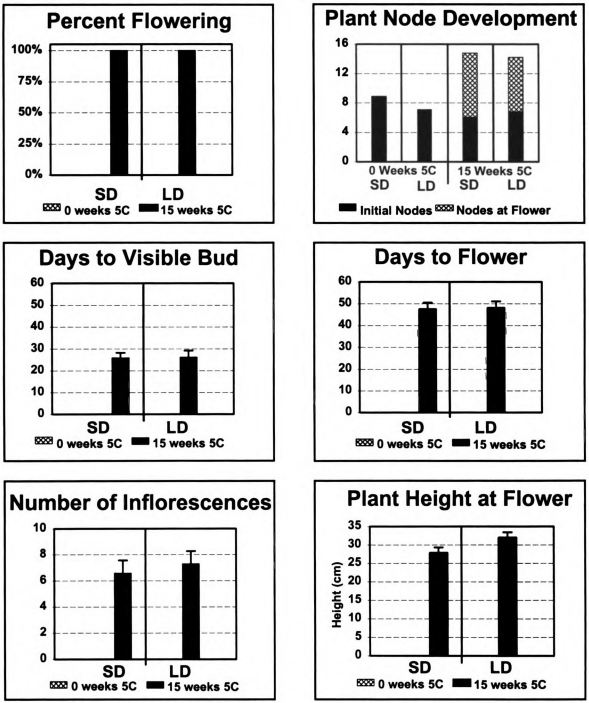

Figure 46. Effects of photoperiod and cold treatment on *Veronica longifolia* 'Red Fox' as indicated. Error bars show 95% confidence intervals.

APPENDIX B:

EFFECTS OF FORCING TEMPERATURE

INTRODUCTION

Timing is just as important as a high quality crop in the floriculture industry. As most commercial growers must produce their crop on a strict schedule, knowing how long it takes for a plant to reach a saleable stage is crucial. Temperature is known to affect both the quality and the rate of development in plants, and is the most commonly used method of regulating timing in greenhouse crops. By testing today's popular new herbaceous perennials for their responses to different forcing temperatures, we can make recommendations as to what temperatures will produce the highest quality crop in the fastest time.

As most of the species we work with require or benefit from a cold treatment, species in the temperature experiment spend ~12 weeks in the cooler at 5°C. They are then potted up and placed in greenhouses at five different temperatures ranging from 17-29°C. Data taken includes such standard information as date of visible bud and flower, height at bloom, and the number and size of flowers. Buds are measured every 3-4 days as they expand to provide a yardstick for flower development. General health and appeal of the plants under different temperatures is also noted.

The temperature experiment provides basic timing information for growers new to a crop, or those wishing to improve plant quality. Bud measurements help growers to gauge the progress of plants towards flower, so they can adjust temperatures to meet scheduling requirements. Researchers also use this information as a reference in planning other experiments using these species.

PROTOCOL

OBJECTIVE: To quantify the influence of forcing temperature on plant quality and time to visible bud and flower.

EXPERIMENTAL DESIGN:

Plant Material: See Table 10

Cold treatment prior to forcing:
12 weeks at 5°C (9-h photoperiod from cool-white fluorescent light)

Forcing environment:
1) Photoperiod:
NI from 2200 to 0200 HR with incandescent lamps (1st year)
16-hr day extension with high-pressure sodium lamps (2nd year)
2) Temperature:
17, 20, 23, 26 or 29°C

Plant Requirements:
10 plants x 5 temperatures =50 plants/species

RESEARCH PROTOCOL:

Plants will be cooled for 12 weeks before being potted into 5" square pots. Cooled plants will be placed in the above temperature treatments and forced under long days, provided either by day extension to 16 hrs, or a 4-h night interruption. Data collected will include:

1) Initial leaf count
2) Date of visible bud/inflorescence
3) Bud length or diameter every three to five days, where appropriate
4) Date of flowering
5) Final leaf number at date of flowering
6) Number of flower buds/inflorescences at date of flowering
7) Height of plant/inflorescence at date of flowering
8) Flower diameter at anthesis, where appropriate
9) Date of first color, where appropriate
10) Number of flowering stalks, where appropriate

Table 10. Effects of Forcing Temperature. Production information, including year included in experiment, weeks of cold given, approximate weeks to flower at 17-29°C, and comments on plant quality and other observations. Recommended temperature range represented by bold numbers in the weeks to flower columns.

Species/Cultivar	year	wks cold	weeks to flower at:					Comments
			17	20	23	26	29	
Astilbe chinensis pumila	1st 2nd	18 12	**14** **12**	**12** **11**	11 10	10 11	10 11	prefers cooler to mid-range temps, flowering% very low at 29°C
Campanula 'Birch Hybrid'	1st 2nd	16 12	**5.1** **7.4**	**4.2** **5.6**	4.0 4.7	3.6 5.0	6.4 7.3	prefers cooler temps; flower size and number was best at 17°C
Coreopsis verticillata 'Moonbeam'	1st 2nd	12 12	**10** **9**	**9** **8**	**7** **7**	**7** **6**	6 6	tolerates high temps, sturdier w/ larger & more flowers at low temps
Delphinium grandiflorum 'Blue Mirror'	1st	16	**9.2**	**8.2**	7.6	7.7	8.4	taller but sturdier, with larger flowers at low temperatures
Geranium xdalmaticum	1st 2nd	16 12	**6.9** **8.3**	**5.9** **6.5**	4.8 5.7	4.6 5.7	4.9 8.4	cooler temperatures result in fuller plants with more flowers
Hemerocallis 'Stella de Oro'	2nd	12	**11**	**8**	**7**	7	8	little effect on flower size; more flowers at lower temperatures
Hibiscus ×hybrida 'Disco Belle Mix'	1st	0	14	14	**9**	**8**	**7**	prefers higher temps; plant quality very low at 17°C
Monarda didyma 'Gardenview Scarlet'	2nd	12	**10**	**9**	**9**	8	10	cooler temps produce a taller, but much sturdier plant with more flowers
Phlox paniculata 'Eva Cullum'	1st 2nd	19 12	**11** **13**	**10** **12**	9 11	8 11	8 10	stems sturdier and plants more branched at cooler temperatures
Phlox subulata 'Emerald Blue'	2nd	12	**2.5**	**2.2**	**1.7**	**1.5**	1.5	bud development in the cooler; very little effect of forcing temperature
Sedum 'Autumn Joy'	1st 2nd	16 12	**13** **13**	**12** **12**	**11** **12**	**11** **13**	13 14	temp had little effect on plant quality; a bit sparse looking at 29°C

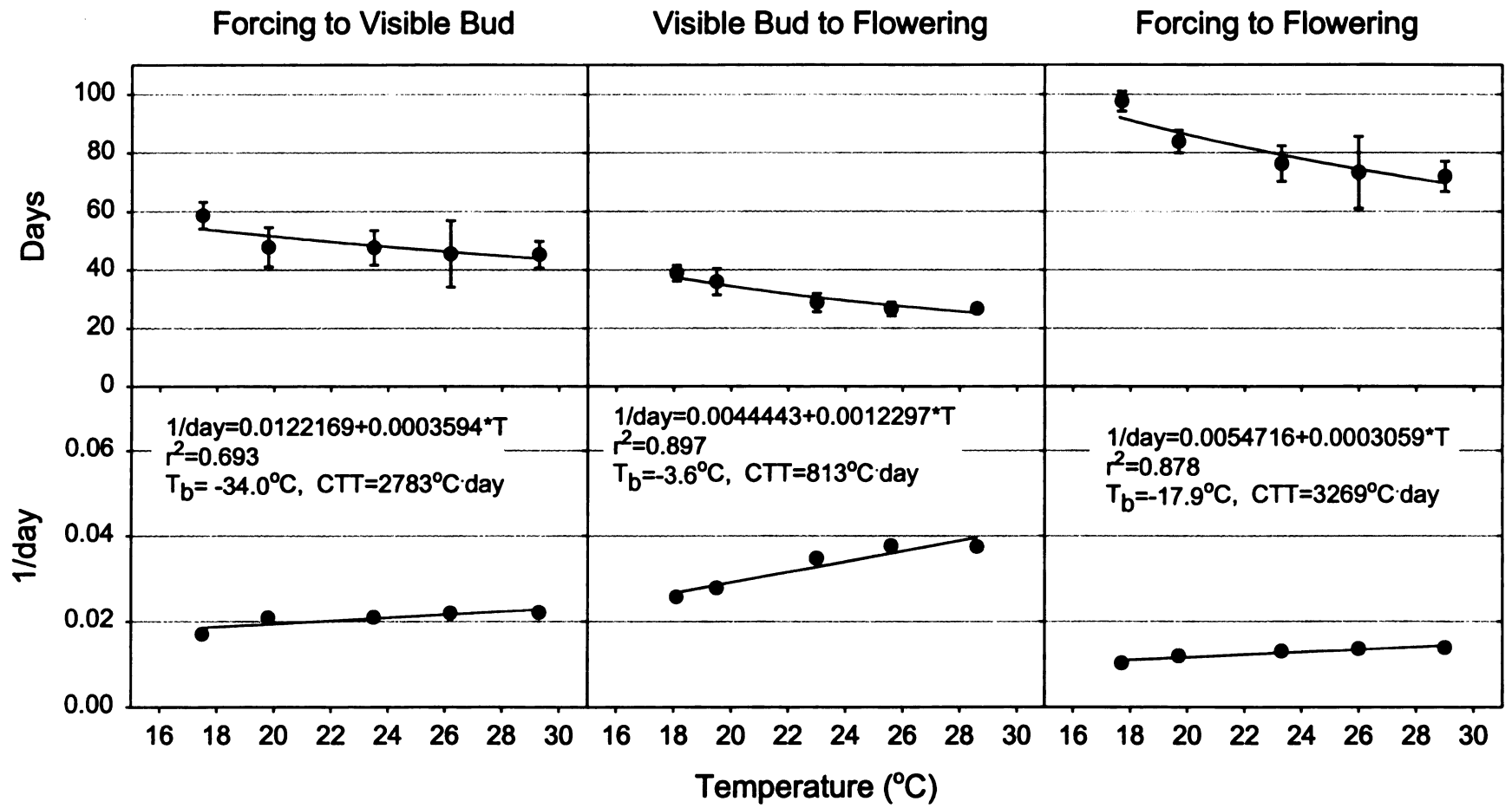

Figure 47. Influence of forcing temperature on time and rate toward flowering for *Astilbe chinensis pumila* in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

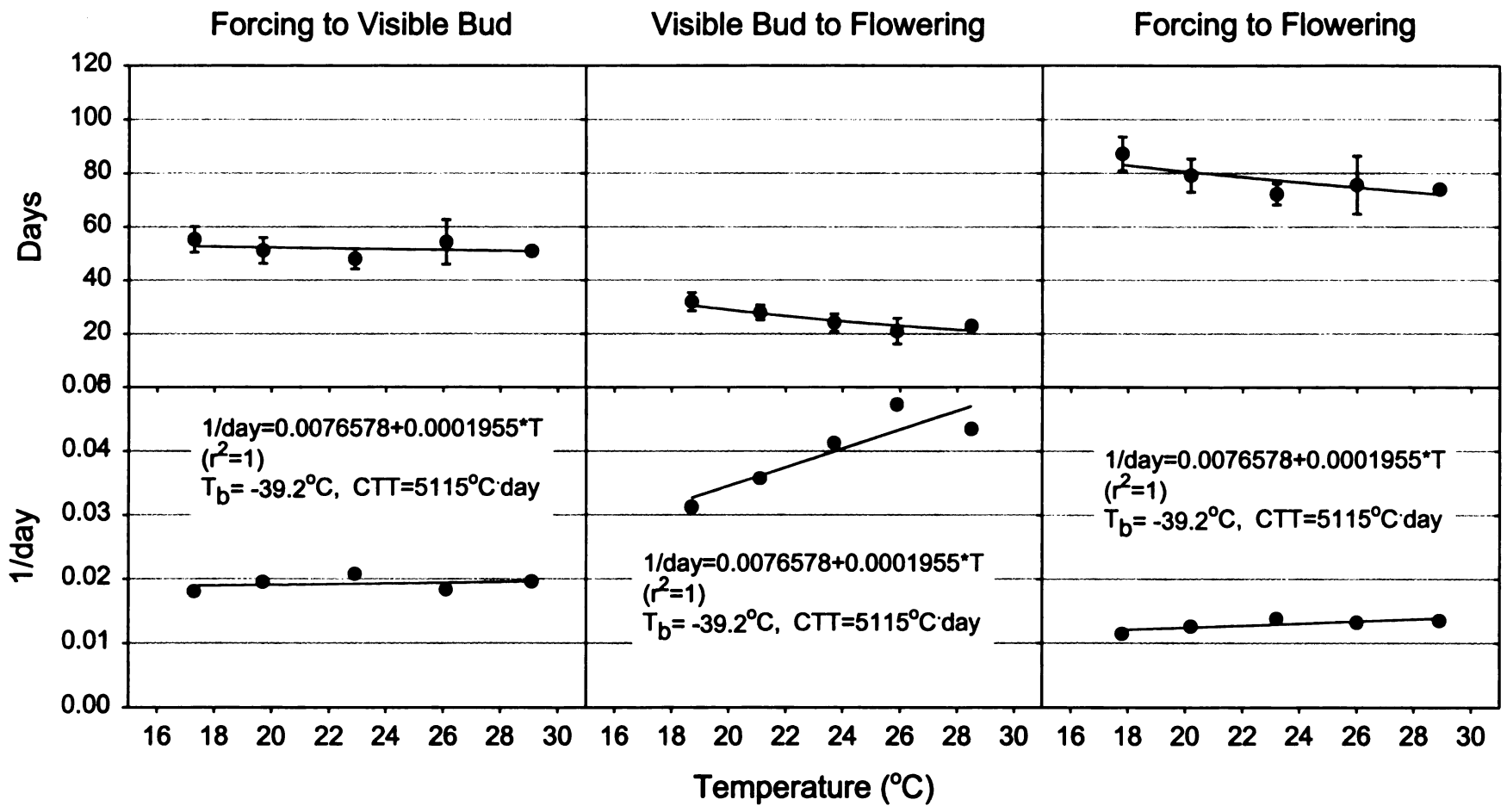

Figure 48. Influence of forcing temperature on time and rate toward flowering for *Astilbe chinensis pumila* in year 2. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

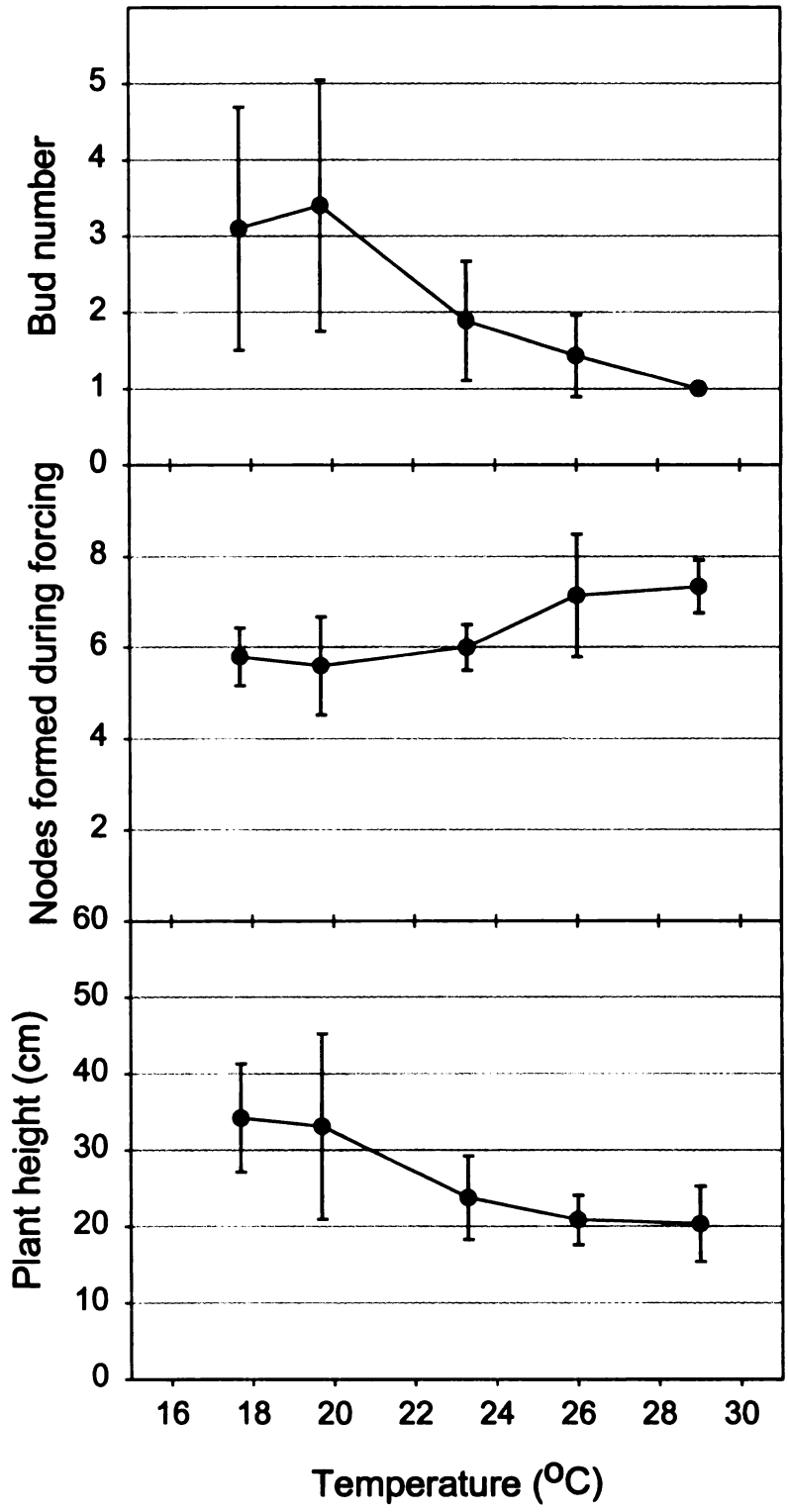

Figure 49. Influence of forcing temperature on number of flower buds, number of nodes formed during forcing, and plant height measured at first flower for *Astilbe chinensis pumila* in year 1. Error bars show standard deviation.

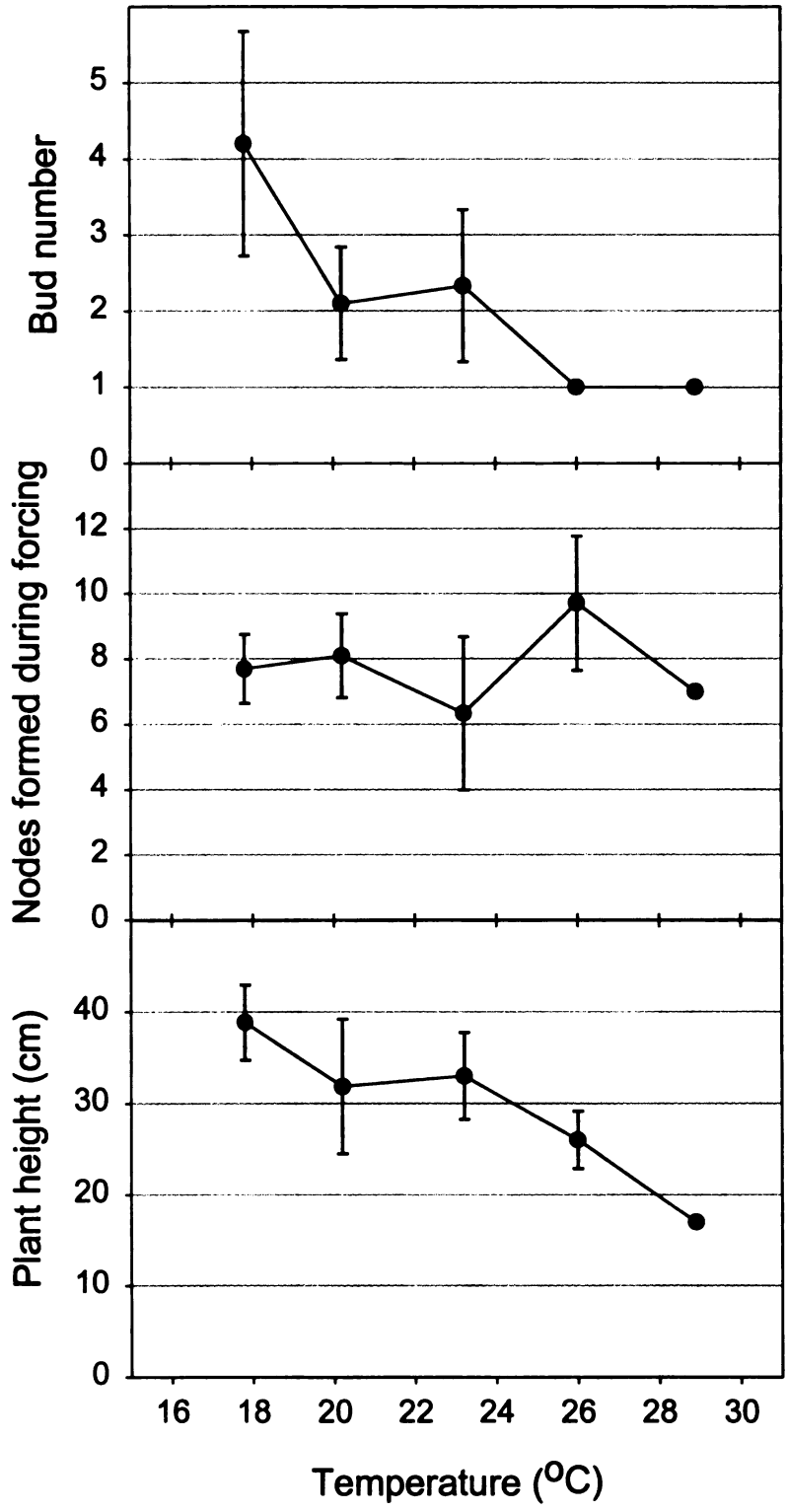

Figure 50. Influence of forcing temperature on number of flower buds, number of nodes formed during forcing, and plant height measured at first flower for *Astilbe chinensis pumila* in year 2. Error bars show standard deviation.

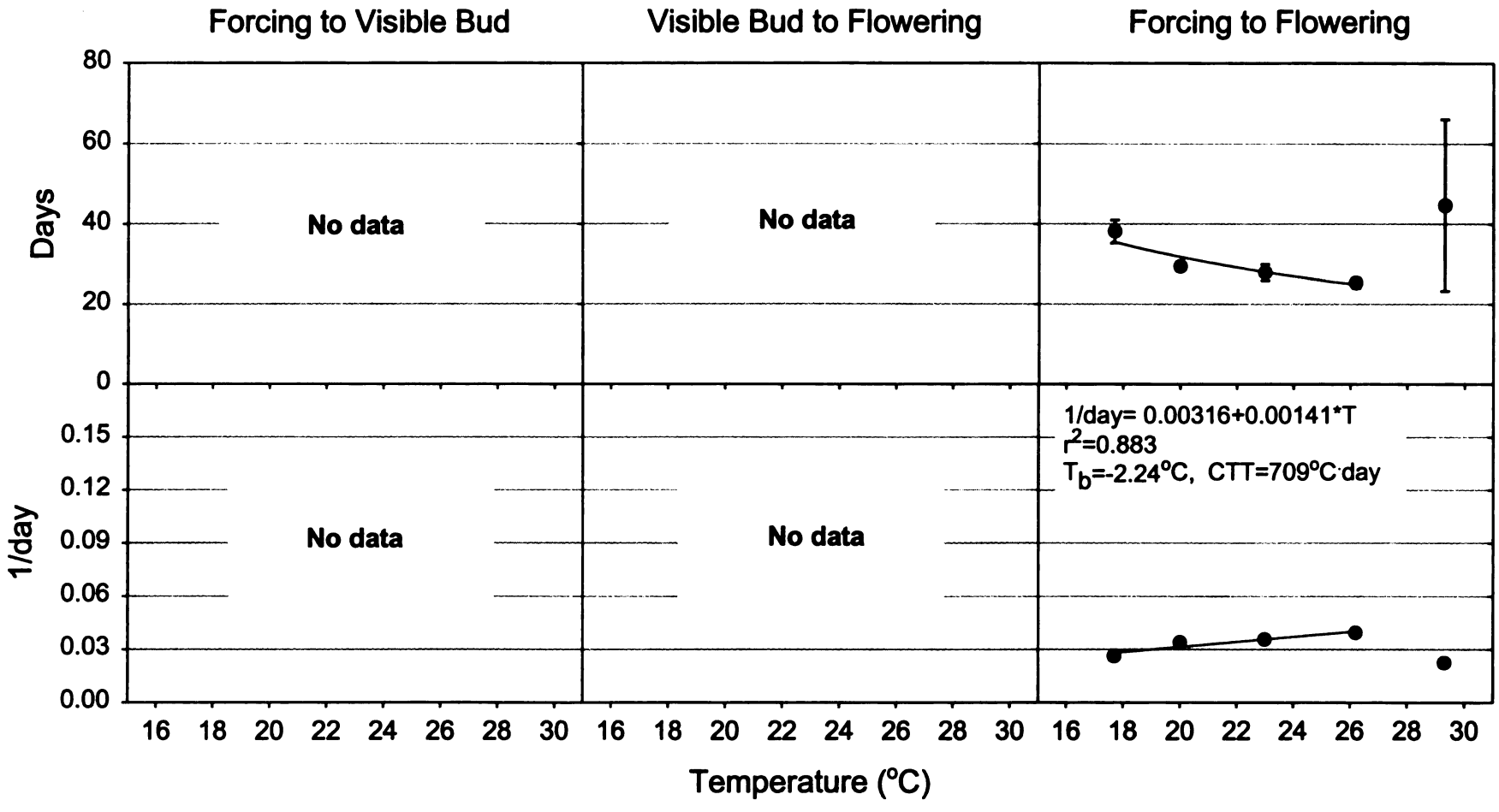

Figure 51. Influence of forcing temperature on time and rate toward flowering for *Campanula* 'Birch Hybrid' in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

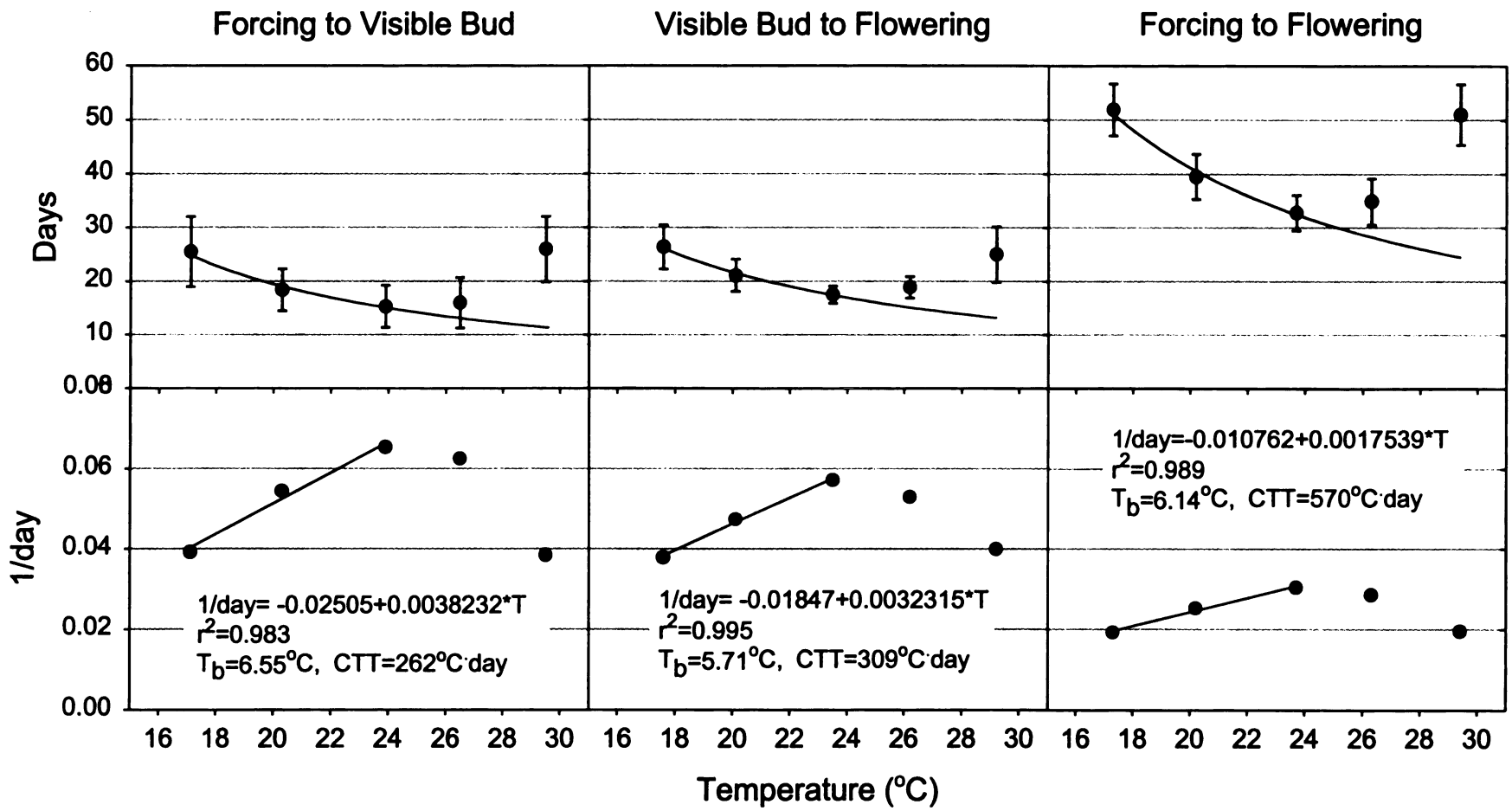

Figure 52. Influence of forcing temperature on time and rate toward flowering for *Campanula* 'Birch Hybrid' in year 2. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

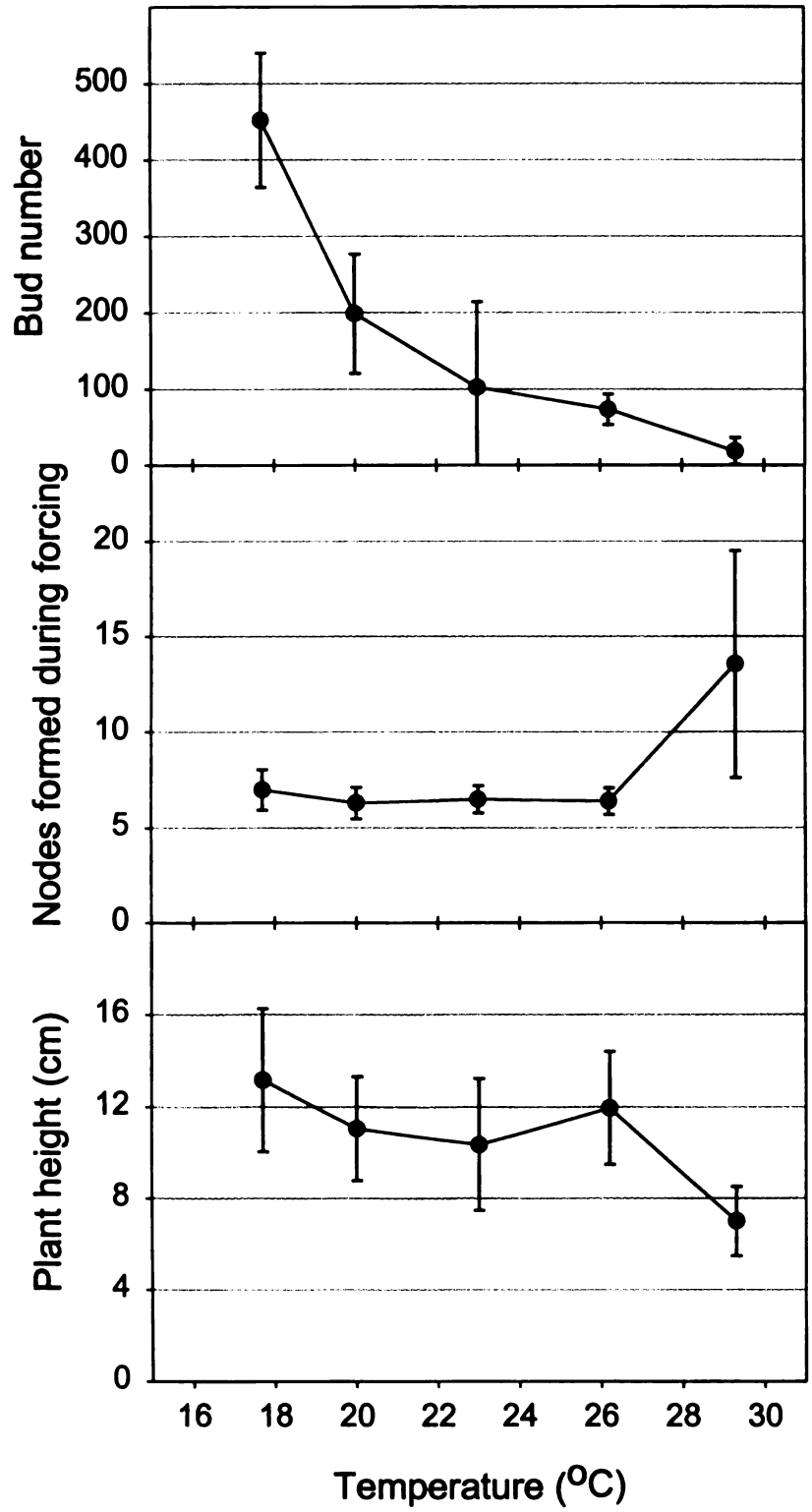

Figure 53. Influence of forcing temperature on number of flower buds, number of nodes formed during forcing, and plant height measured at first flower for *Campanula* 'Birch Hybrid' in year 1. Error bars show standard deviation.

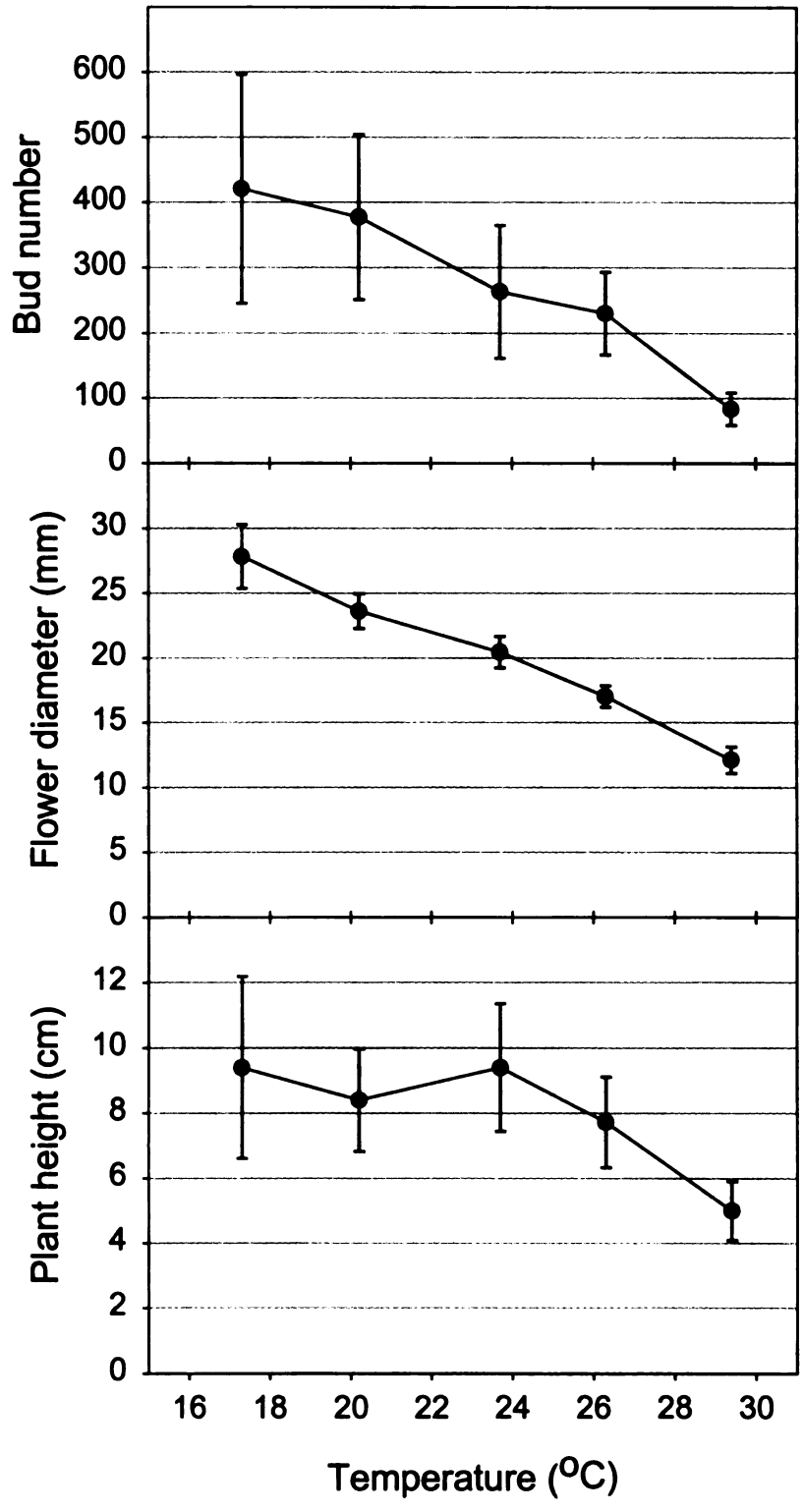

Figure 54. Influence of forcing temperature on number of flower buds, flower diameter, and plant height measured at first flower for *Campanula* 'Birch Hybrid' in year 2. Error bars show standard deviation.

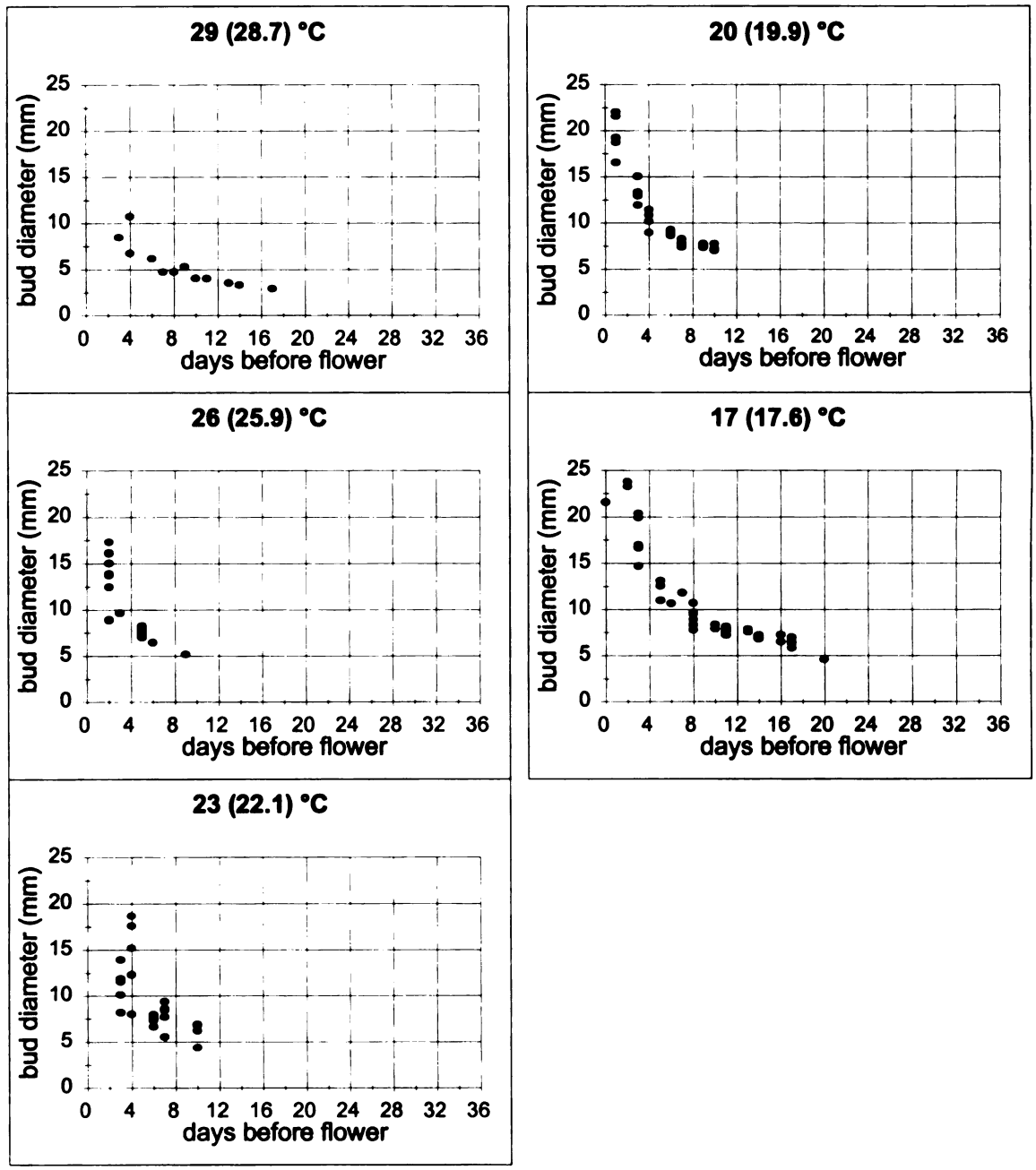

Figure 55. Relationship between bud diameter and number of days before flower for *Campanula* 'Birch Hybrid' in year 1. Actual temperatures for the indicated treatments are from average date of visible bud to average date of flower.

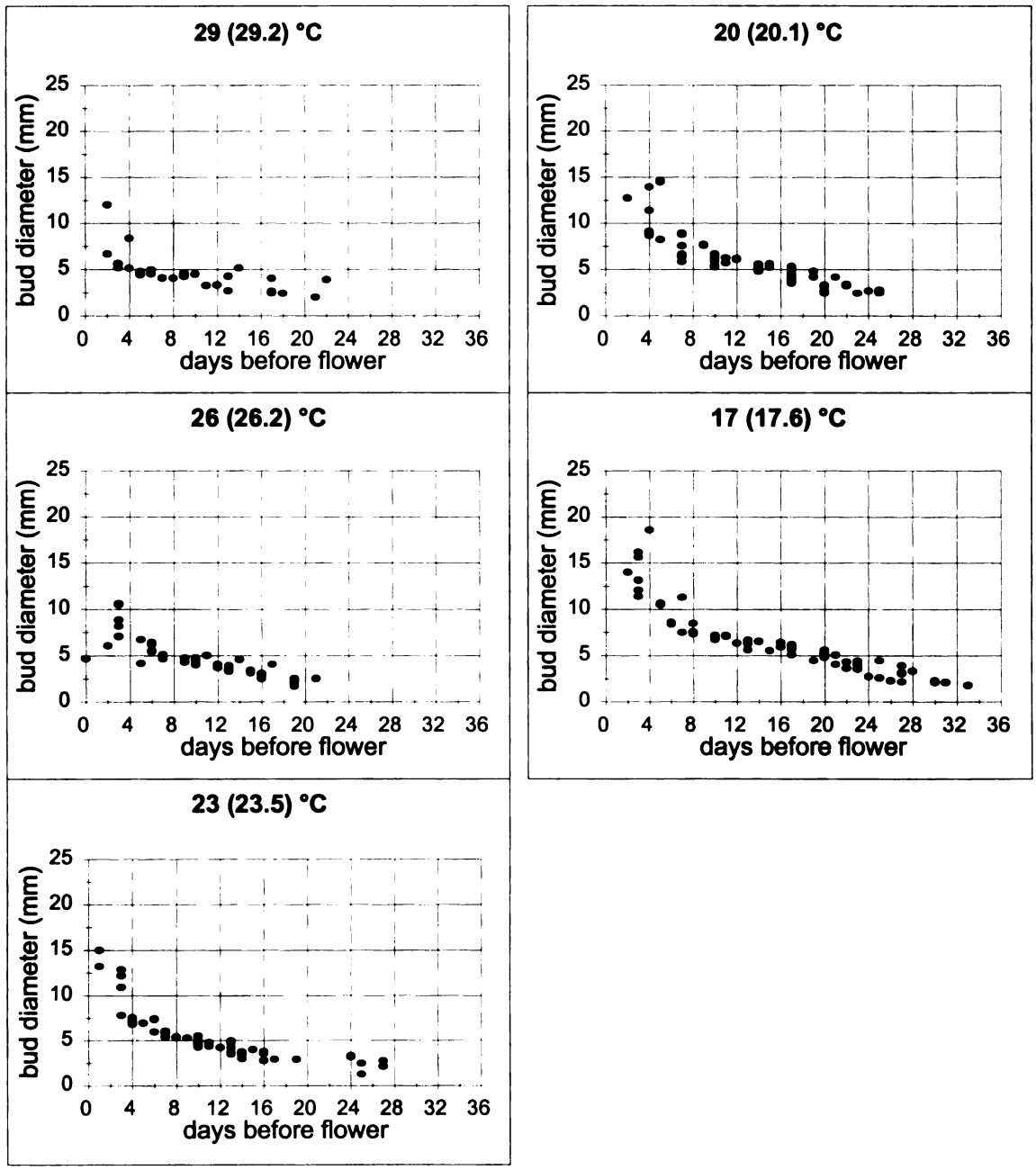

Figure 56. Relationship between bud diameter and number of days before flower for *Campanula* 'Birch Hybrid' in year 2. Actual temperatures for the indicated treatments are from average date of visible bud to average date of flower.

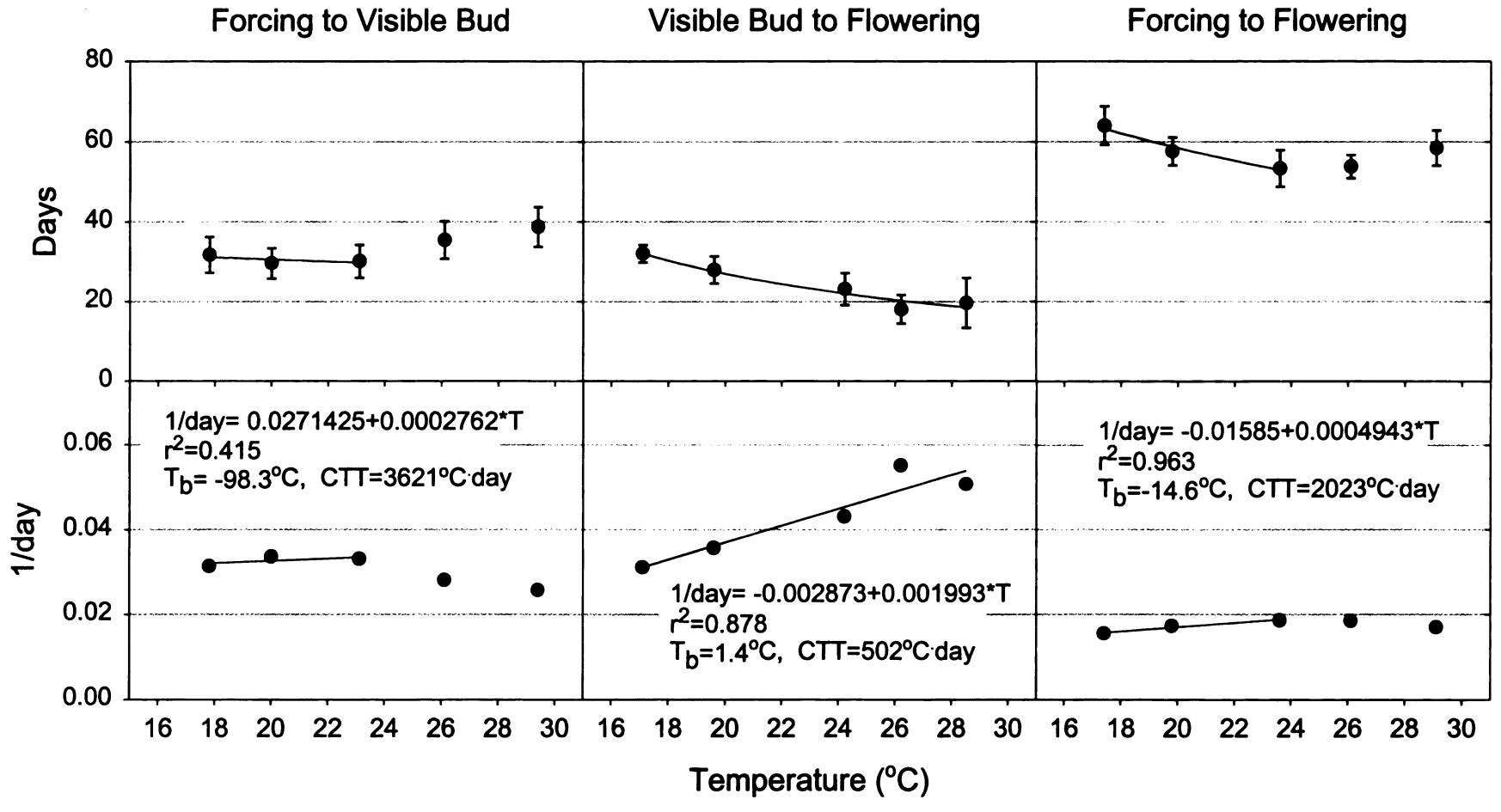

Figure 57. Influence of forcing temperature on time and rate toward flowering for *Delphinium grandiflorum* 'Blue Mirror' in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

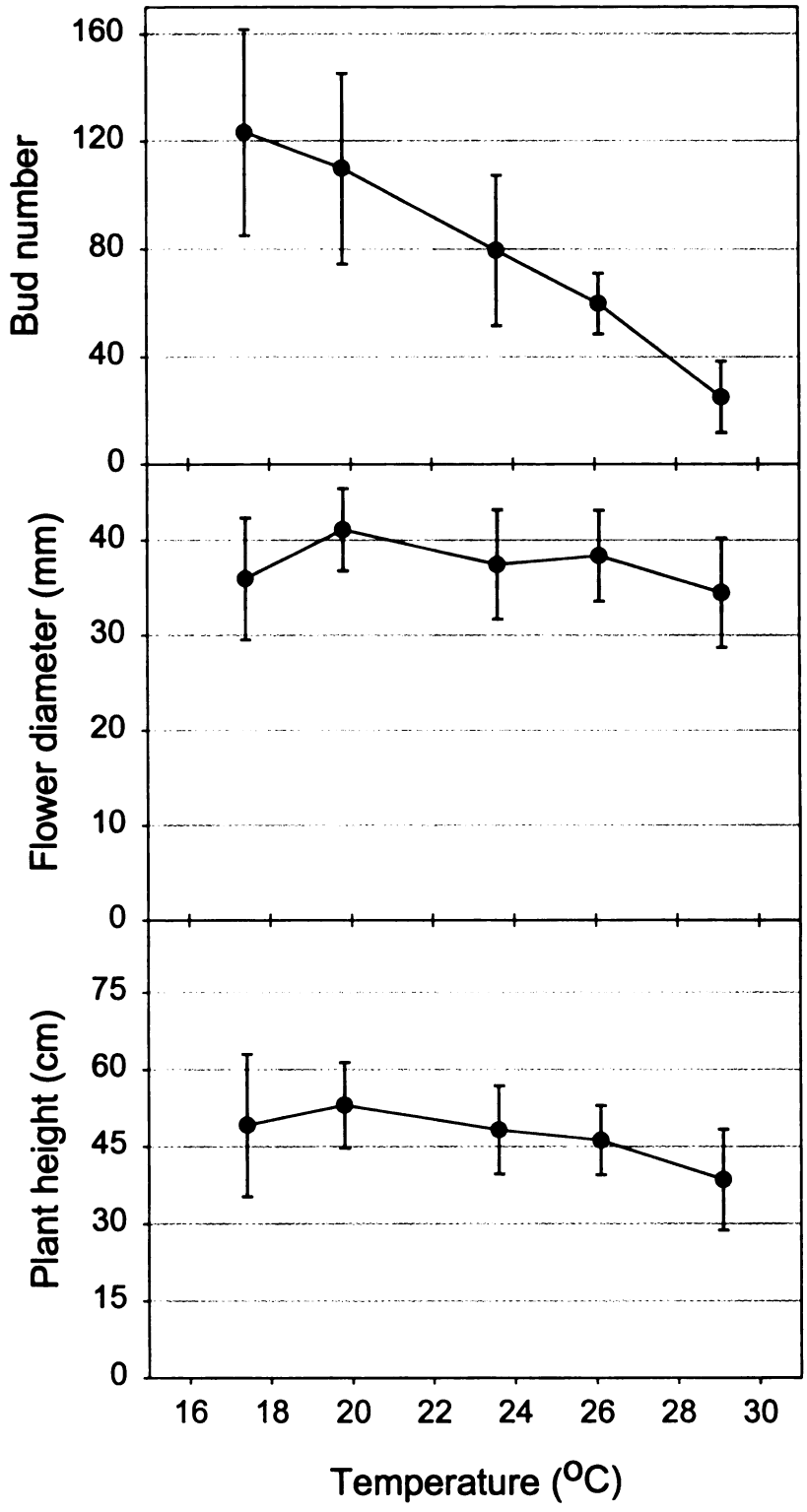

Figure 58. Influence of forcing temperature on number of flower buds, flower diameter, and plant height measured at first flower for *Delphinium grandiflora* 'Blue Mirror' in year 1. Error bars show standard deviation.

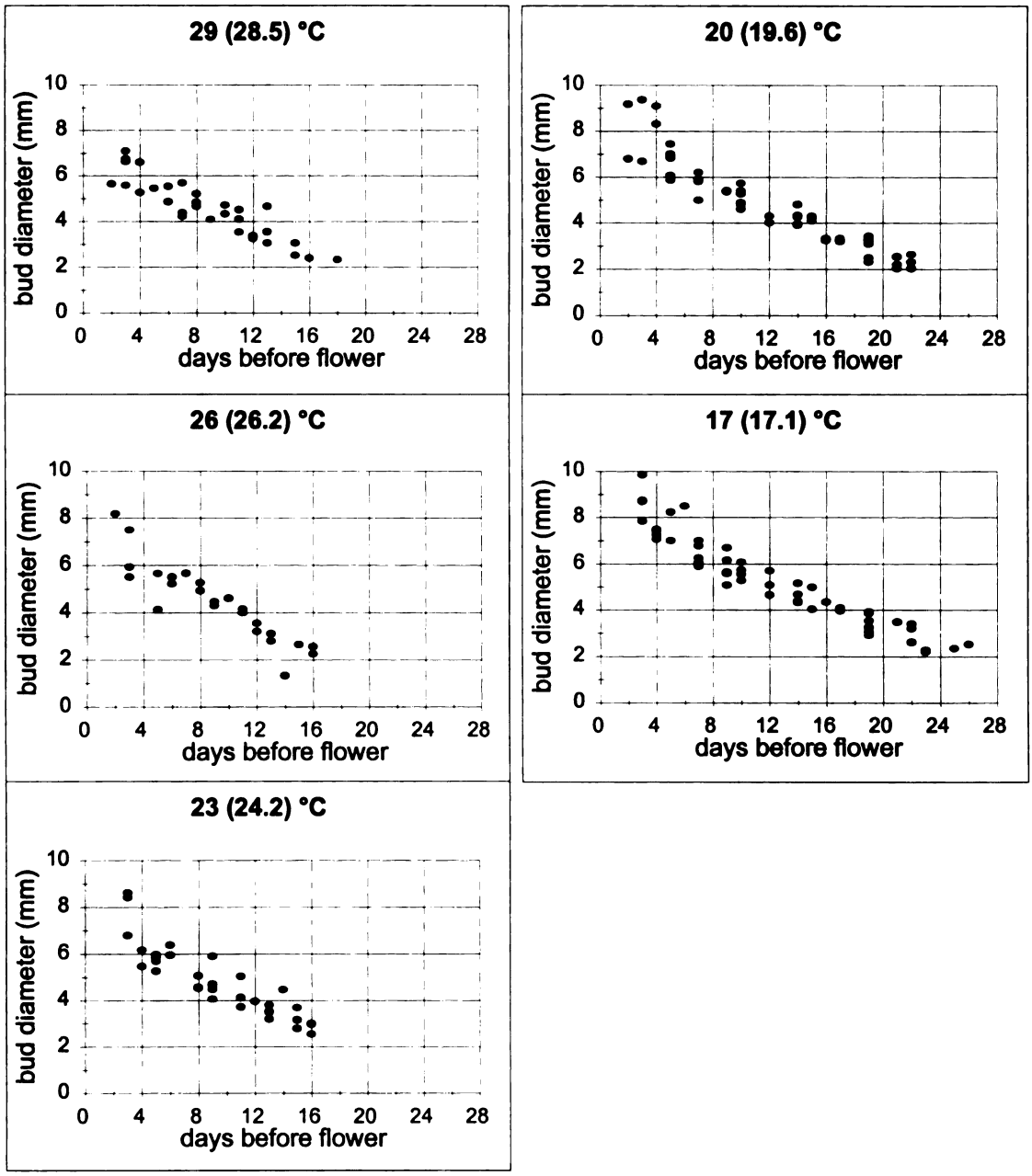

Figure 59. Relationship between bud diameter and number of days before flower for *Delphinium grandiflora* 'Blue Mirror' in year 1. Actual temperatures for the indicated treatments are from average date of visible bud to average date of flowe

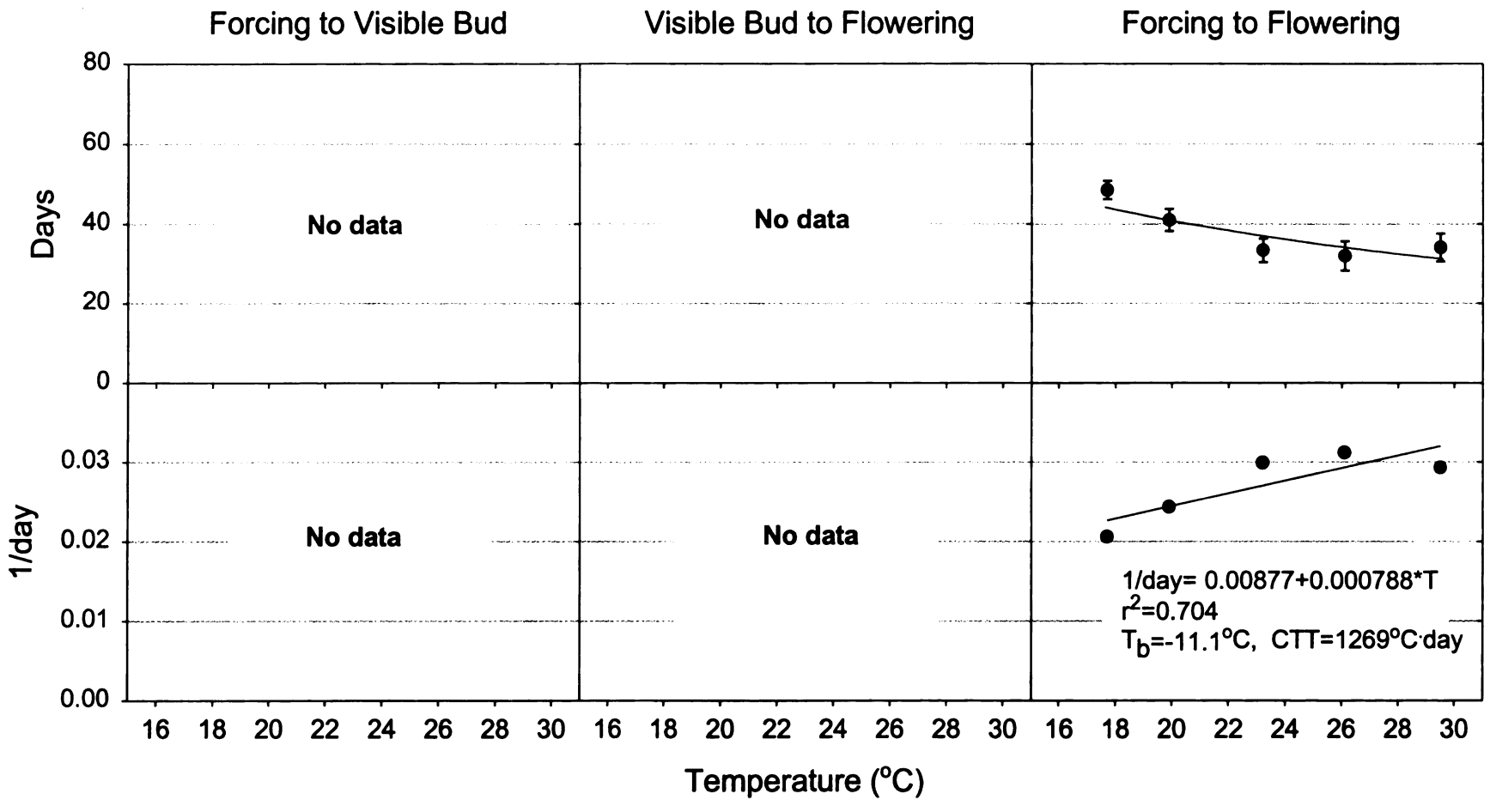

Figure 60. Influence of forcing temperature on time and rate toward flowering for *Geranium dalmaticum* in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

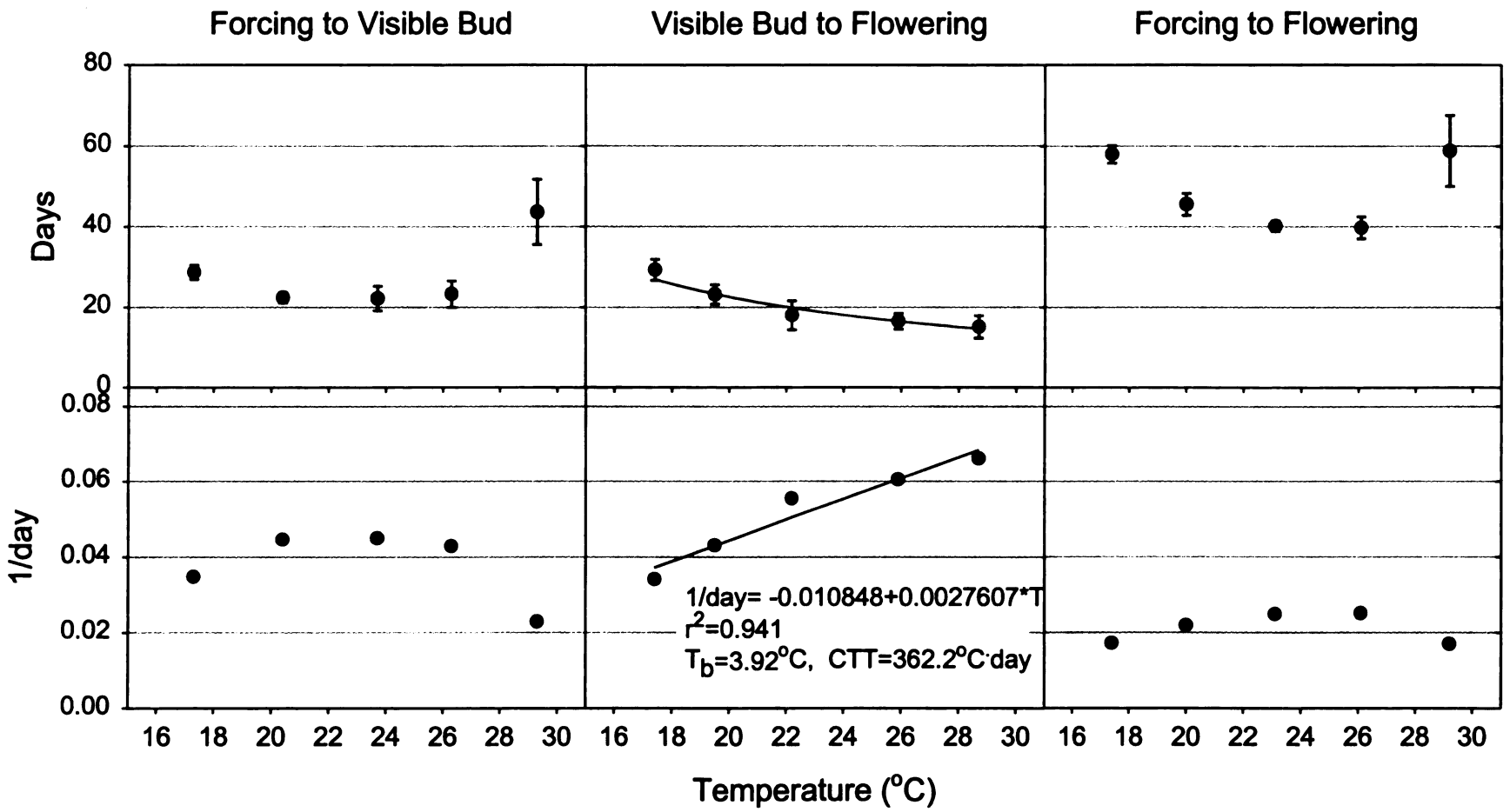

Figure 61. Influence of forcing temperature on time and rate toward flowering for *Geranium dalmaticum* in year 2. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

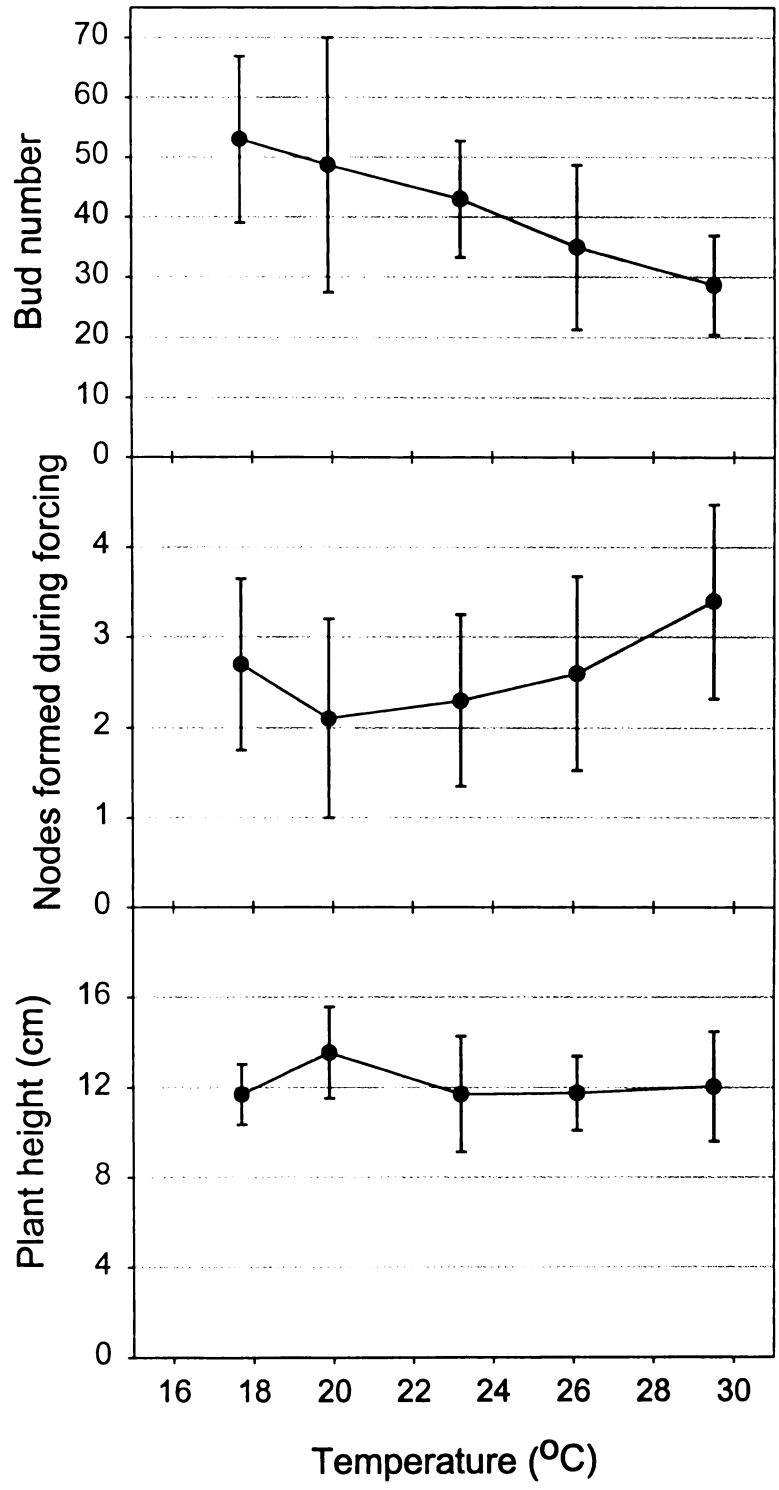

Figure 62. Influence of forcing temperature on number of flower buds, number of nodes formed during forcing, and plant height measured at first flower for *Geranium dalmaticum* in year 1. Error bars show standard deviation.

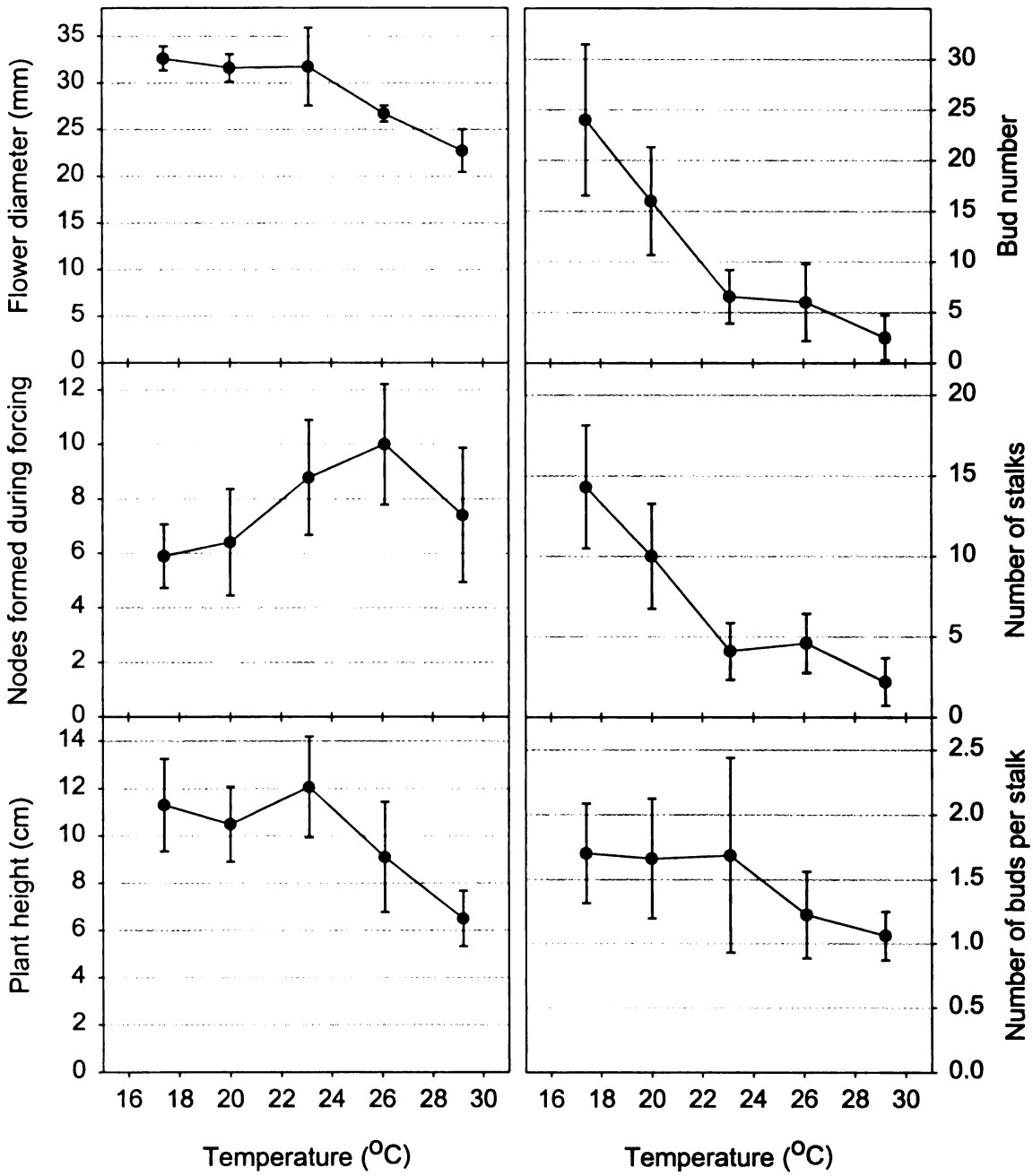

Figure 63. Influence of forcing temperature on plant height, number of nodes formed during forcing, diameter of open flowers, number of flowers, number of stalks per plant, and number of flowers per stalk for *Geranium dalmaticum* in year 2. Error bars show standard deviation.

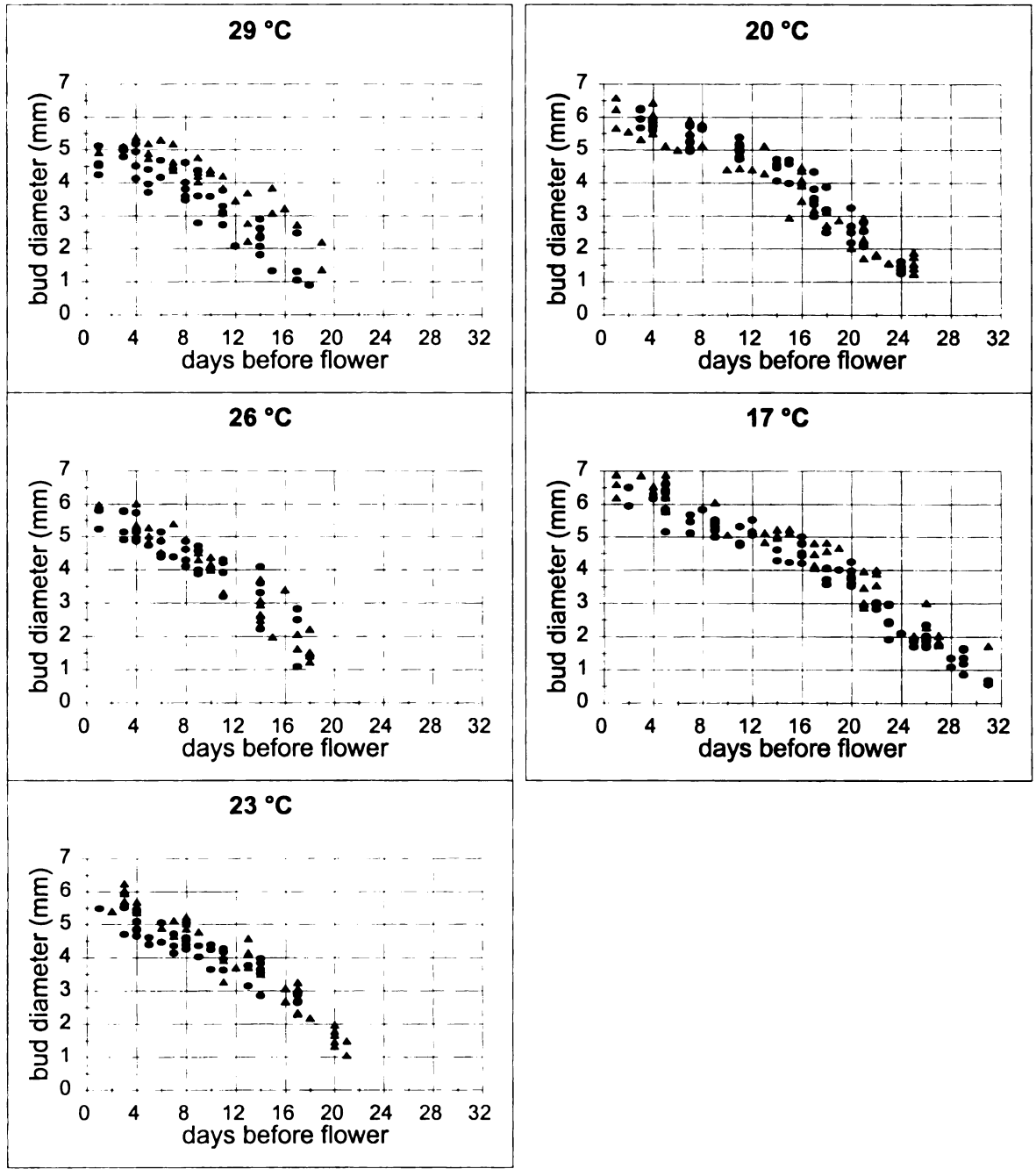

Figure 64. Relationship between bud diameter and number of days before flower for *Geranium dalmaticum*. First year data represented by circles, second year data represented by triangles. Actual temperatures for the indicated treatments from average date of visible bud to average date of flower were 29.4, 25.8, 23.1, 19.9, and 17.6°C for the first year and 28.7, 25.9, 22.2, 19.5, and 17.4°C for the second year.

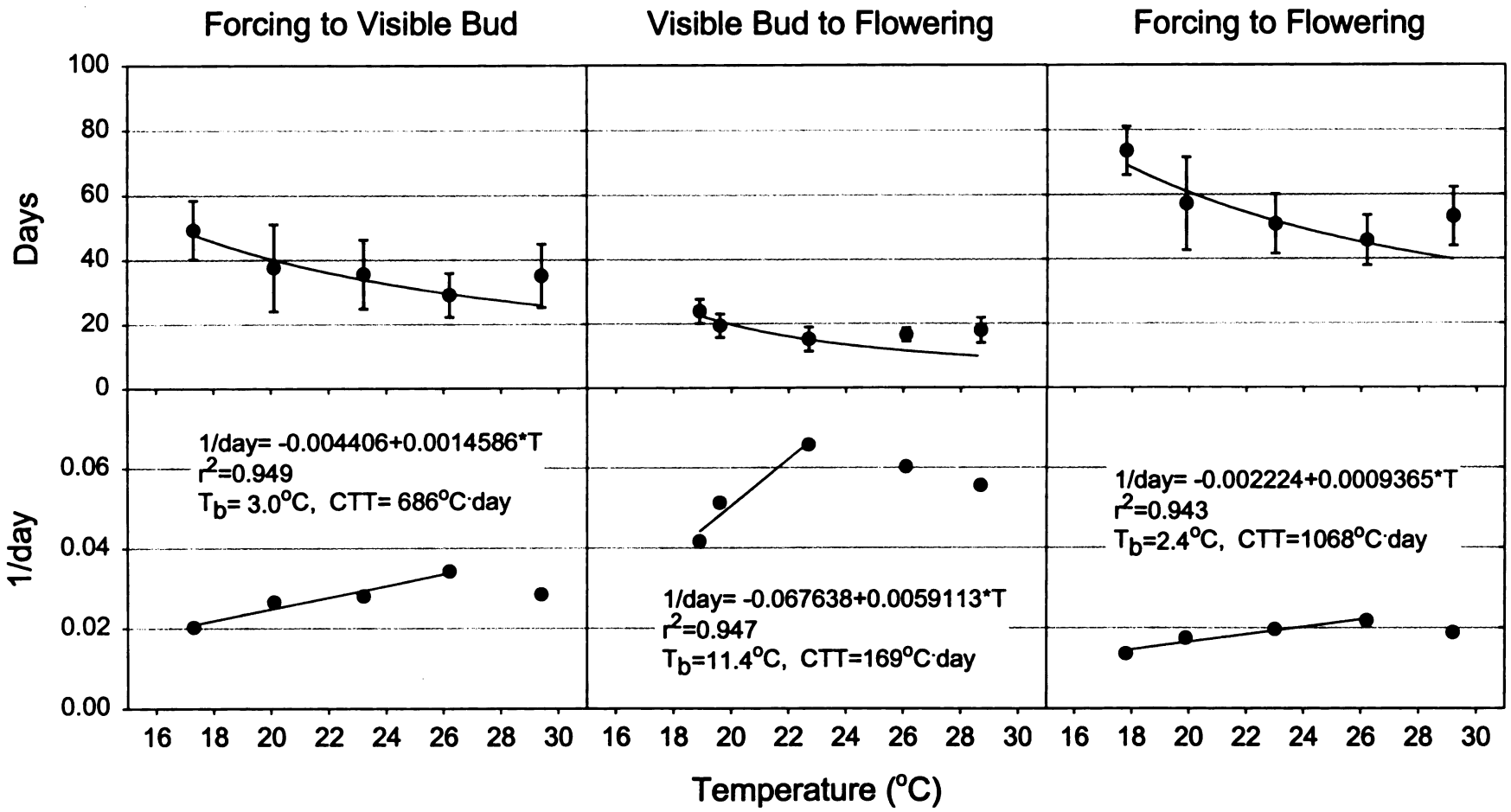

Figure 65. Influence of forcing temperature on time and rate toward flowering for *Hemerocallis* 'Stella de Oro' in year 2. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

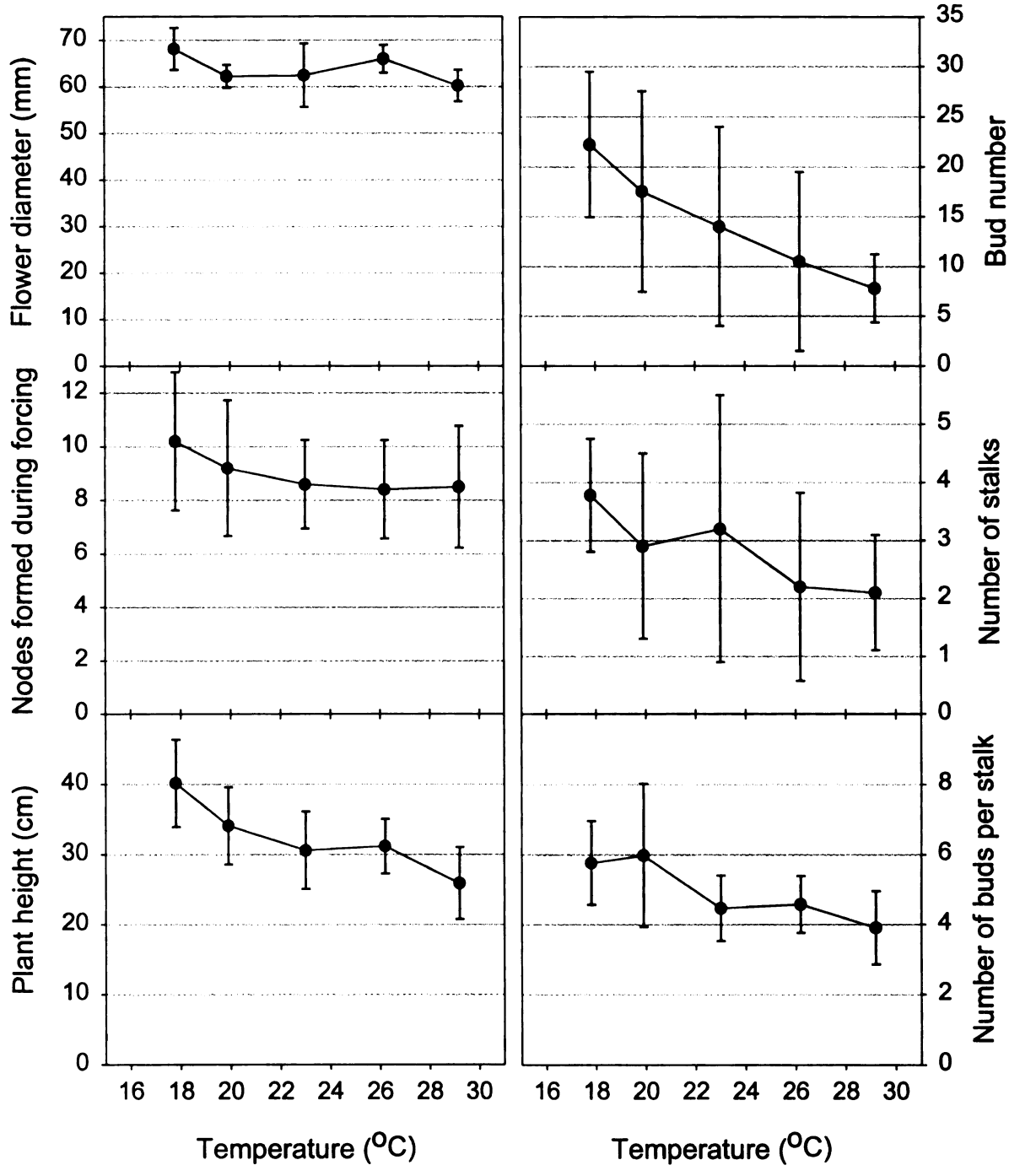

Figure 66. Influence of forcing temperature on plant height, number of nodes formed during forcing, diameter of open flowers, number of flowers, number of stalks per plant, and number of flowers per stalk for *Hemerocallis* 'Stella de Oro' in year 2. Error bars show standard deviation.

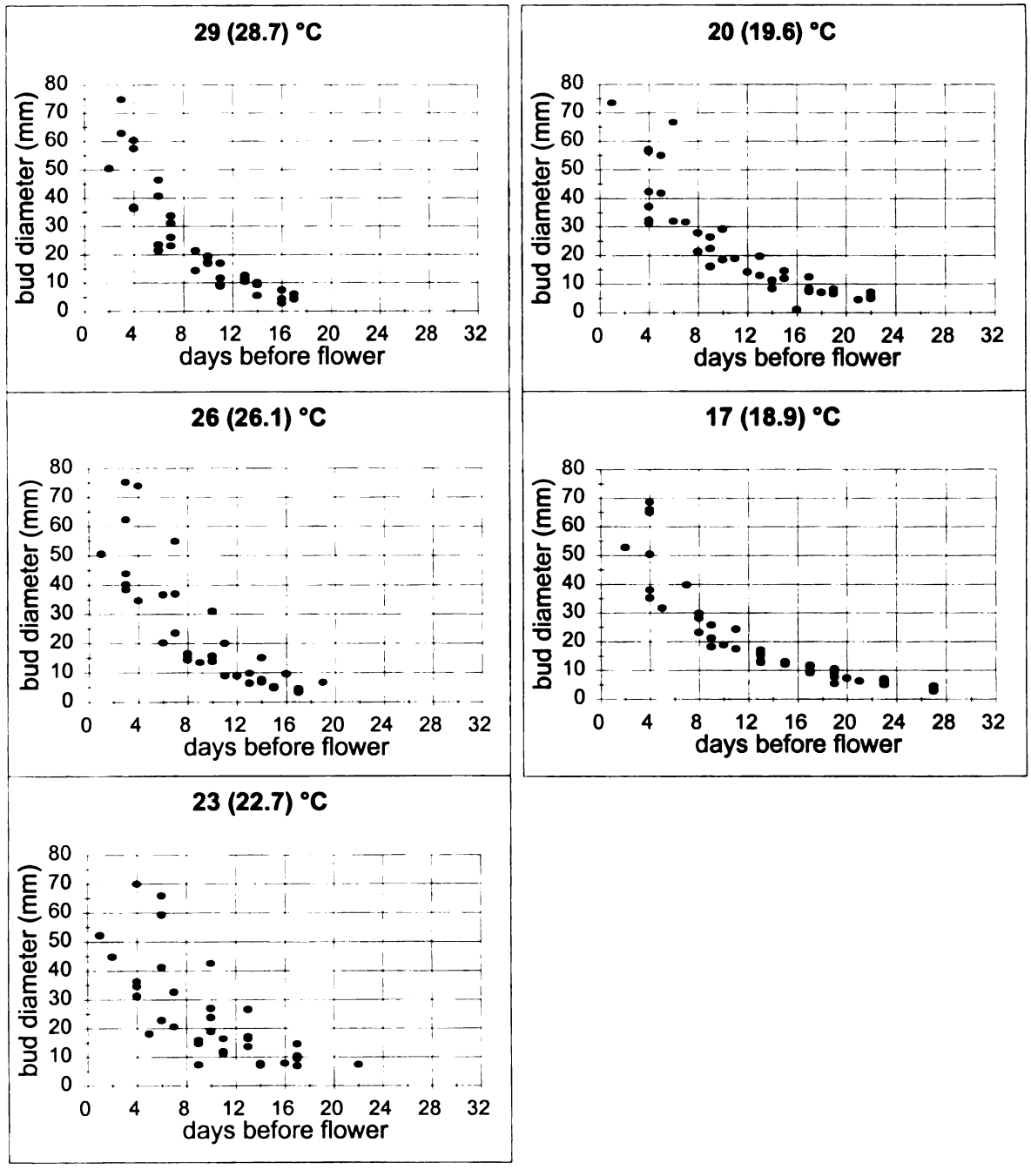

Figure 67. Relationship between bud diameter and number of days before flower for *Hemerocallis* 'Stella de Oro' in year 2. Actual temperatures for the indicated treatments are from average date of visible bud to average date of flower.

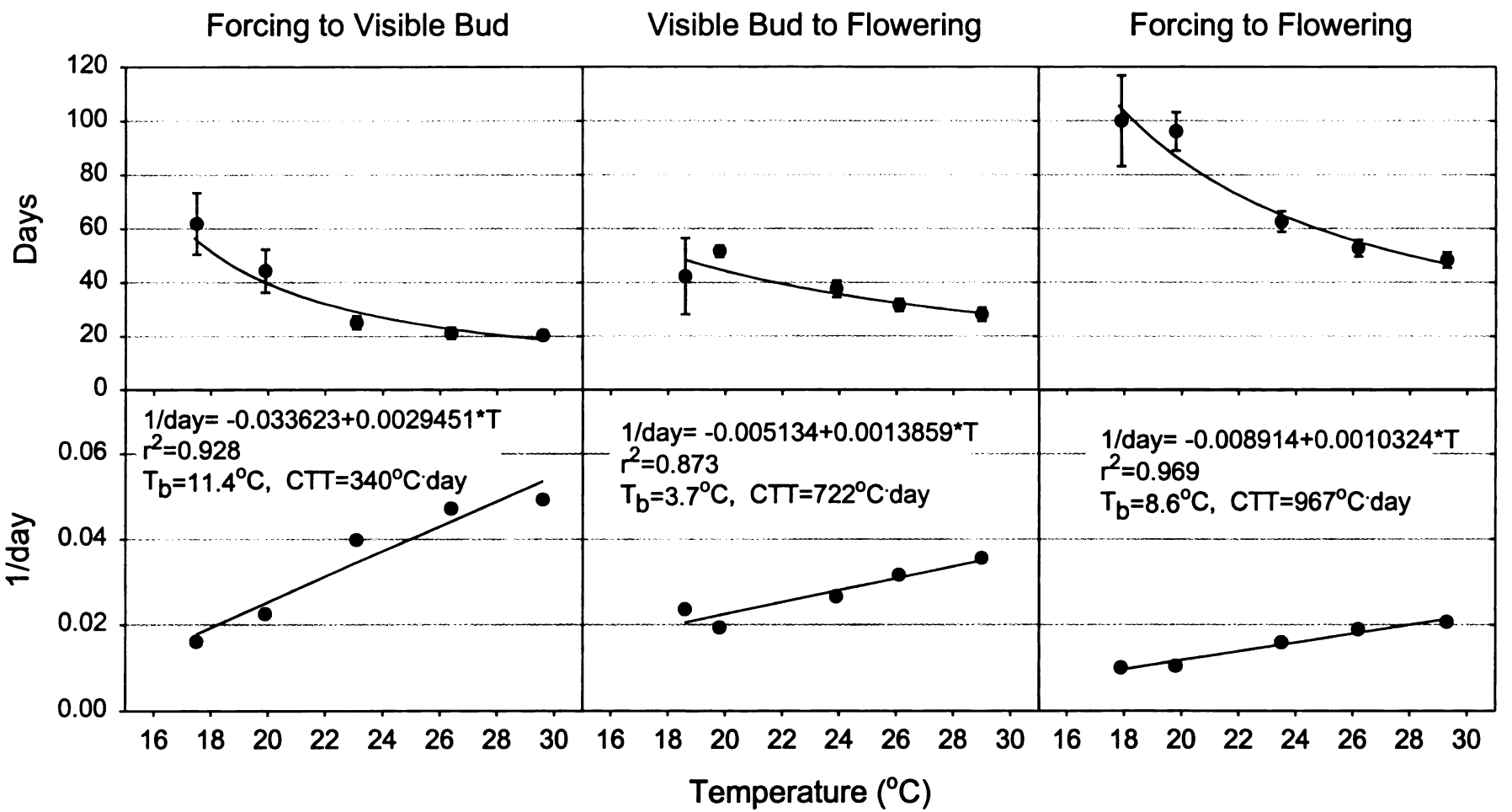

Figure 68. Influence of forcing temperature on time and rate toward flowering for *Hibiscus* 'Disco Belle Mix' in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

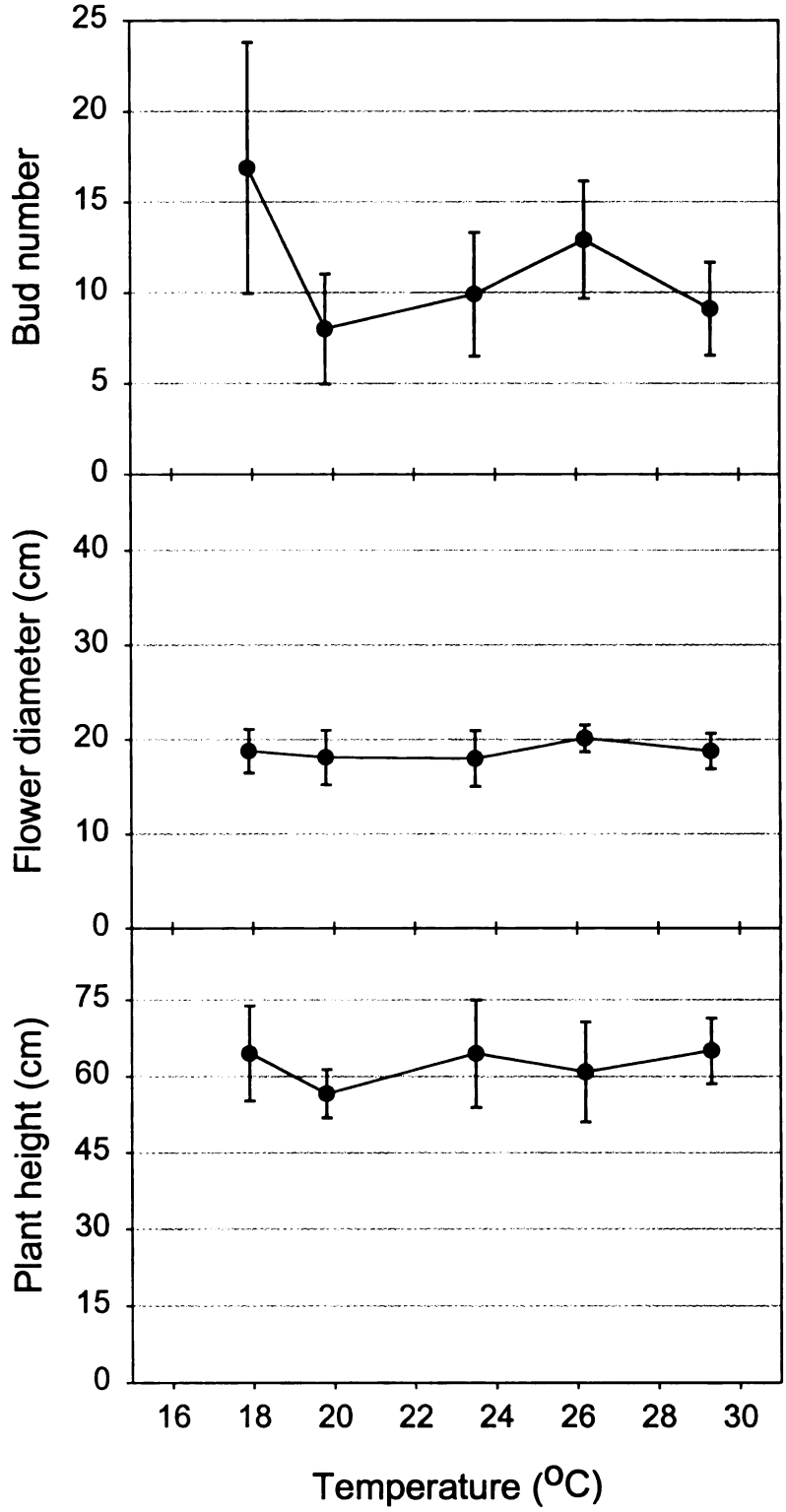

Figure 69. Influence of forcing temperature on number of flower buds, flower diameter, and plant height measured at first flower for *Hibiscus* 'Disco Belle Mix' in year 1. Error bars show standard deviation.

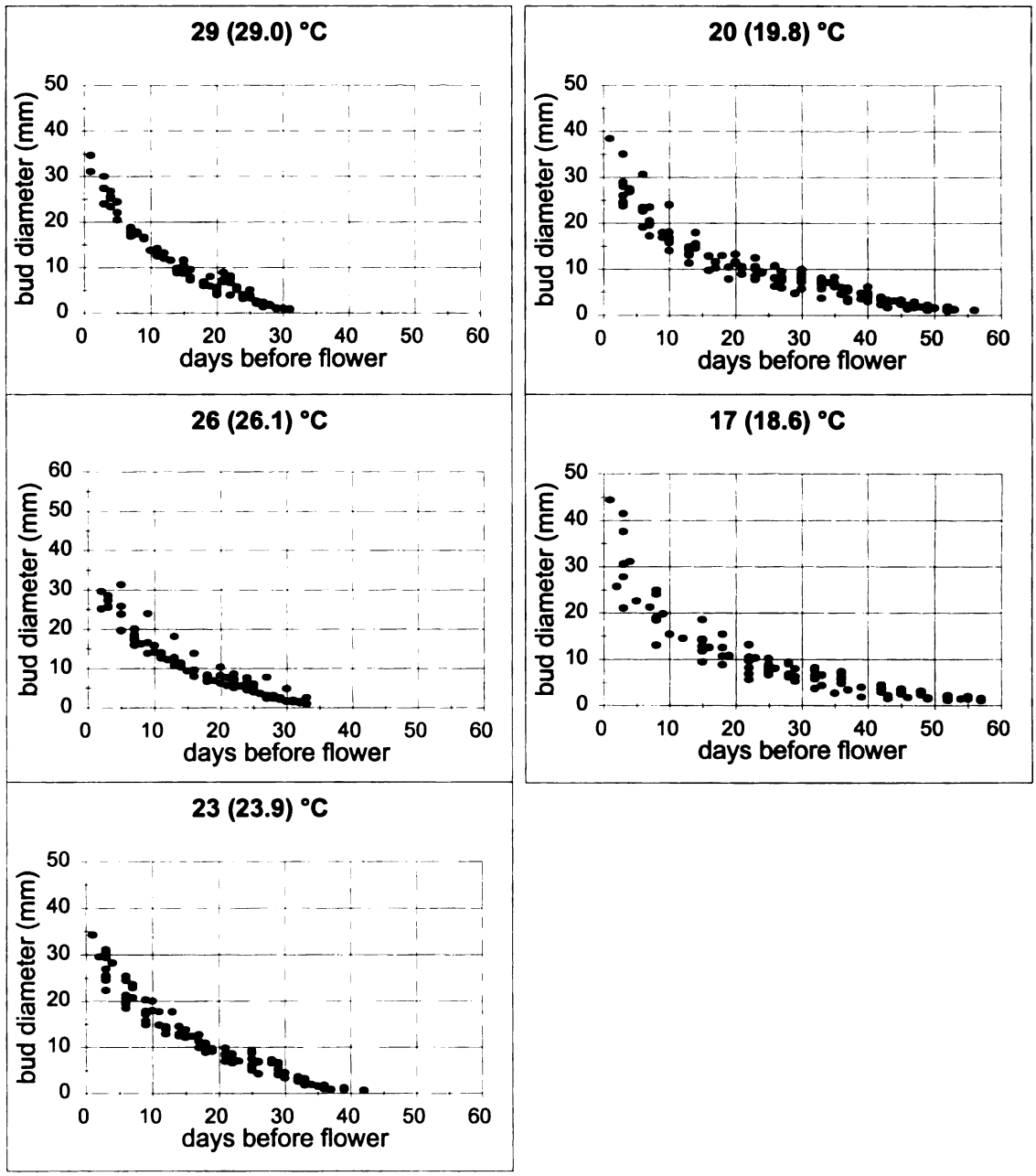

Figure 70. Relationship between bud diameter and number of days before flower for *Hibiscus* 'Disco Belle Mix' in year 1. Actual temperatures for the indicated treatments are from average date of visible bud to average date of flower.

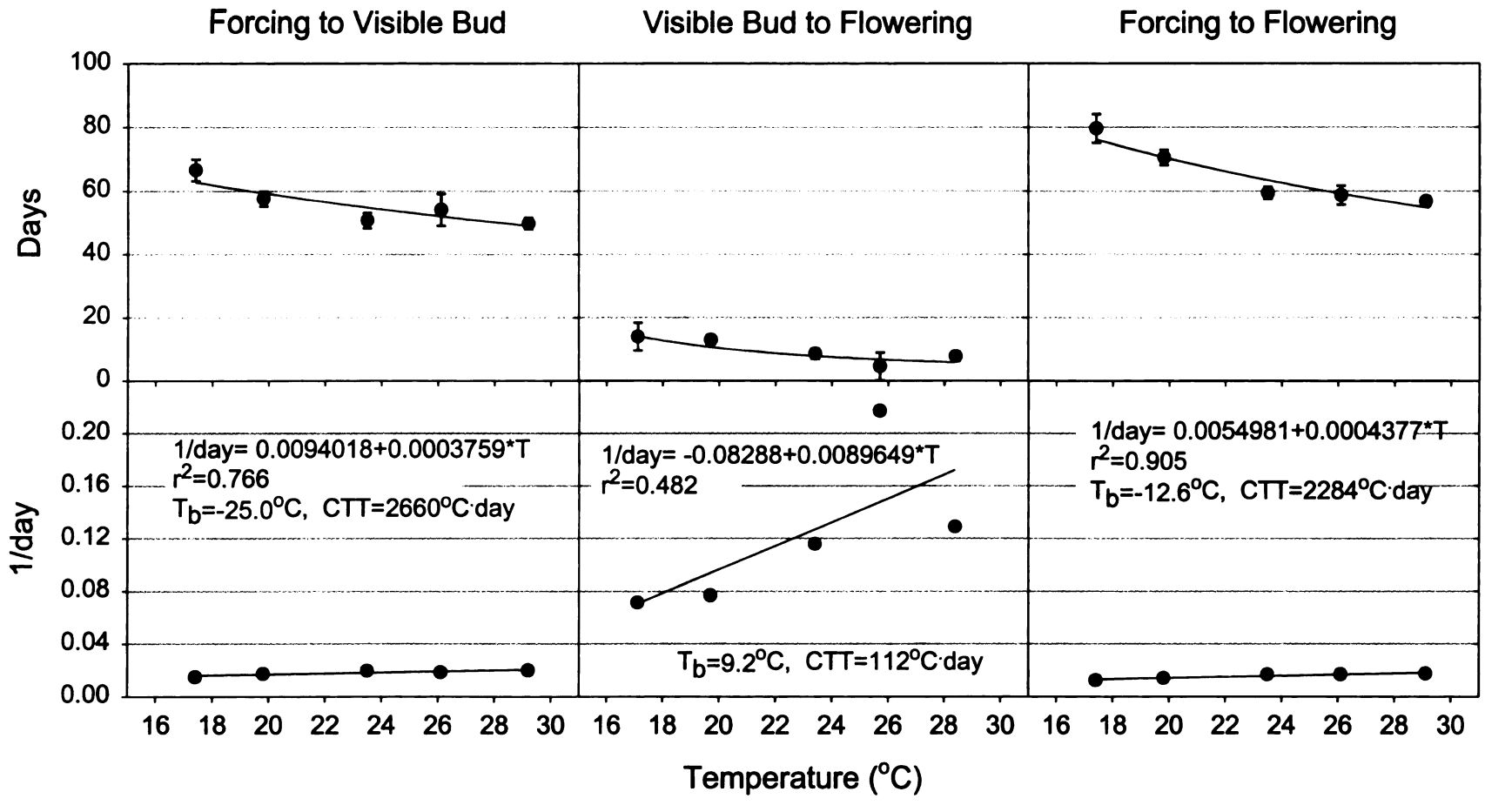

Figure 71. Influence of forcing temperature on time and rate toward flowering for *Phlox paniculata* 'Eva Cullum' in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

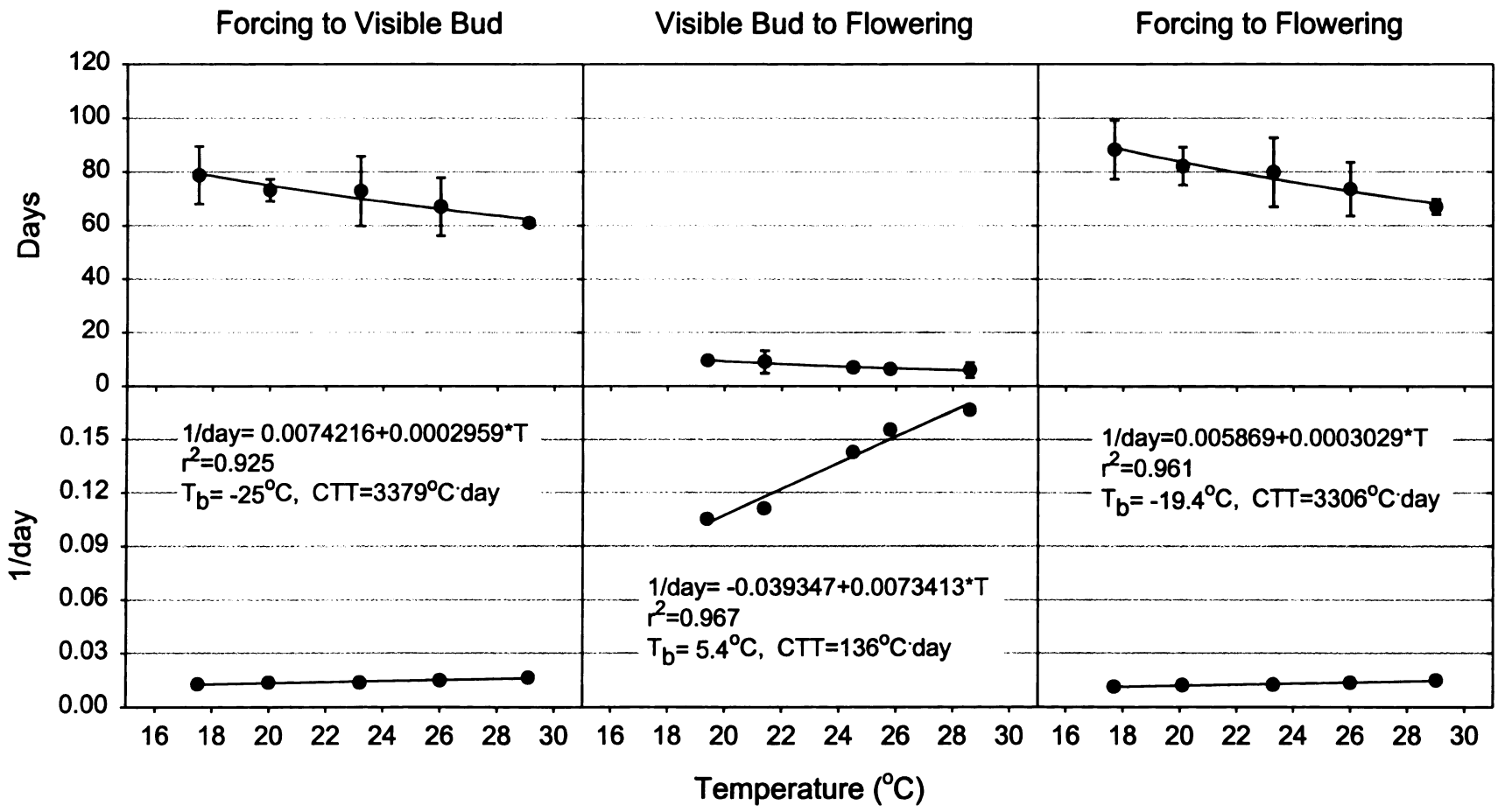

Figure 72. Influence of forcing temperature on time and rate toward flowering for *Phlox paniculata* 'Eva Cullum' in year 2. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

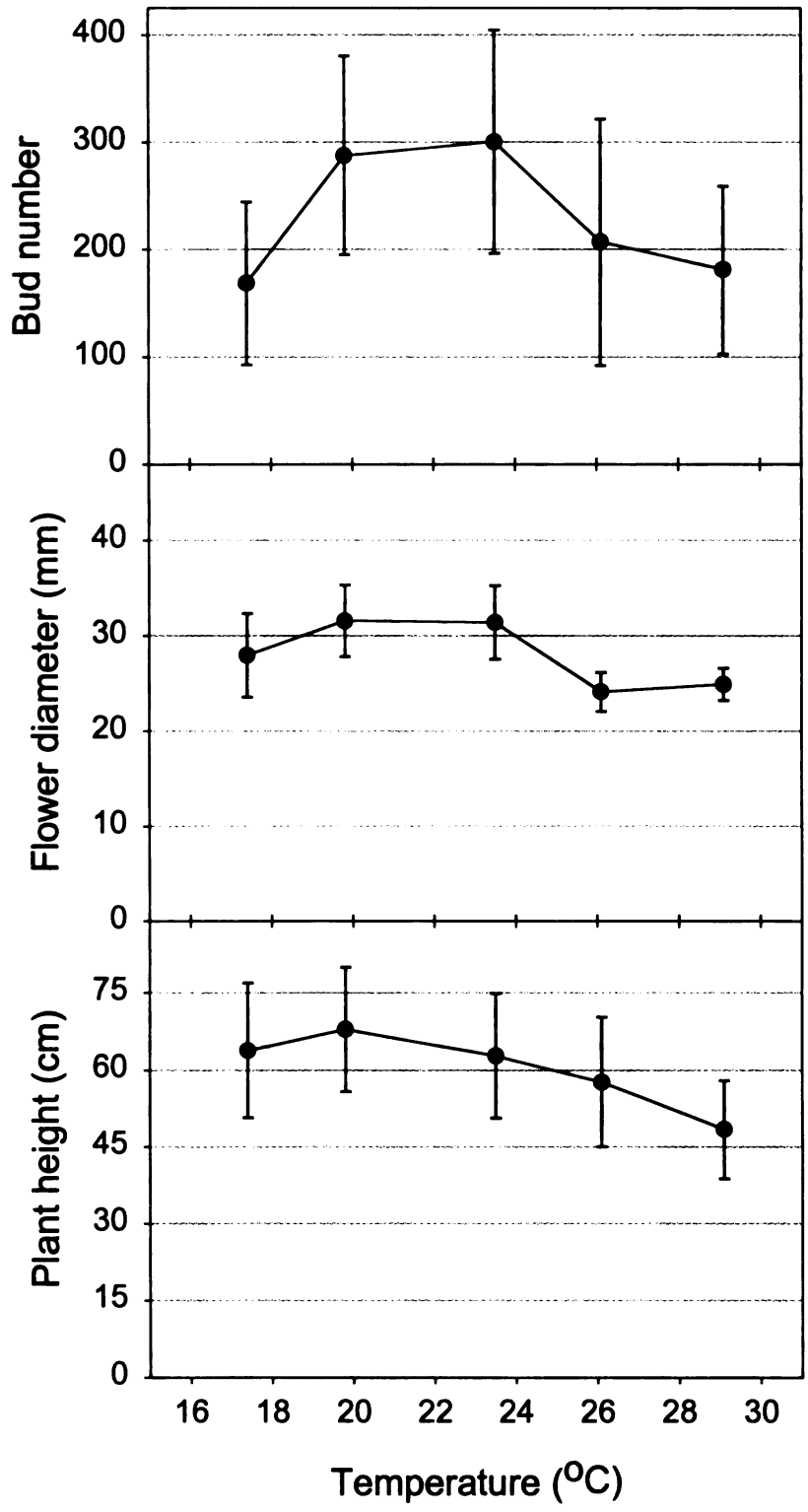

Figure 73. Influence of forcing temperature on number of flower buds, flower diameter, and plant height measured at first flower for *Phlox paniculata* 'Eva Cullum' in year 1. Error bars show standard deviation.

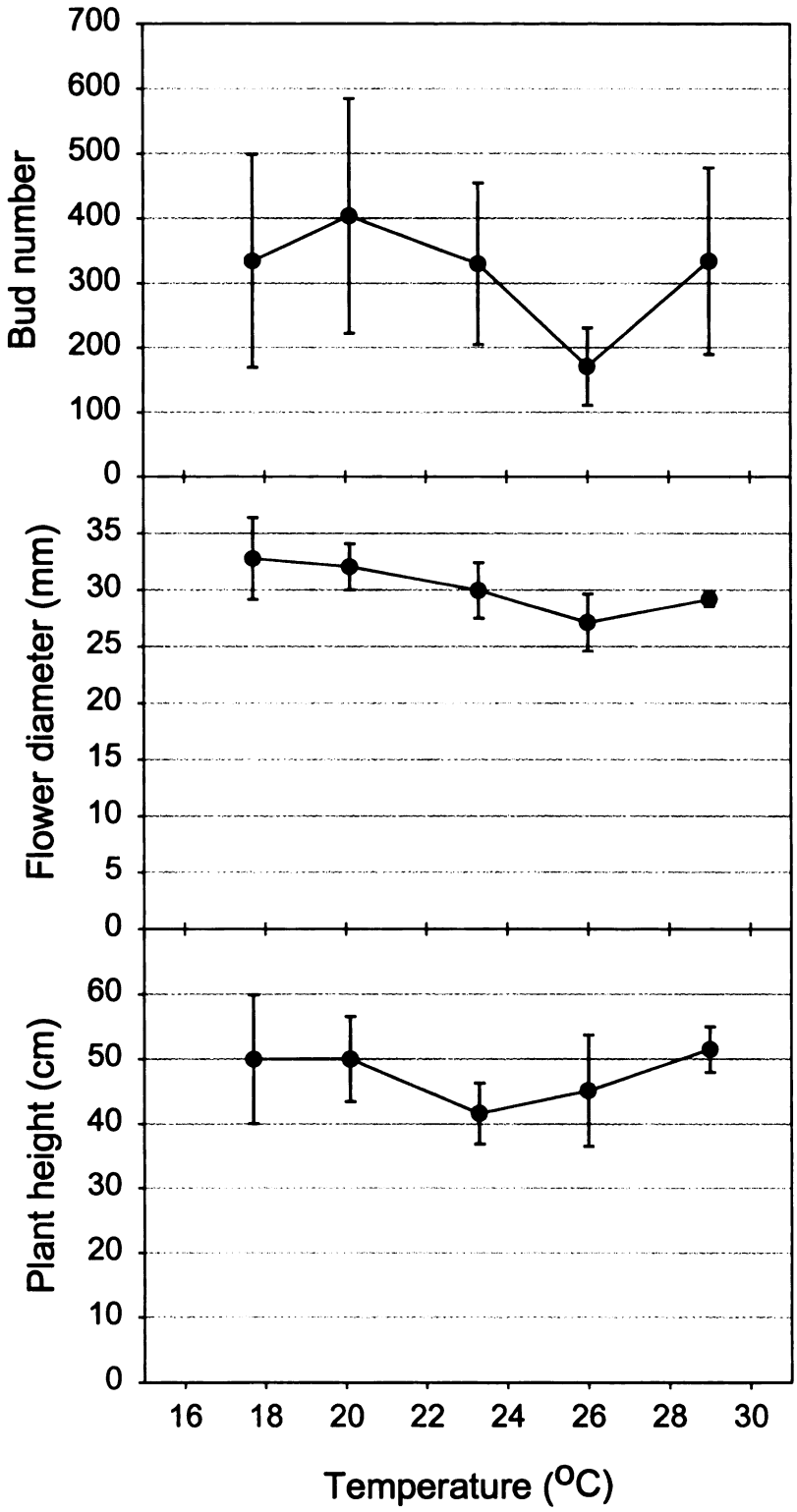

Figure 74. Influence of forcing temperature on number of flower buds, flower diameter, and plant height measured at first flower for *Phlox paniculata* 'Eva Cullum' in year 2. Error bars show standard deviation.

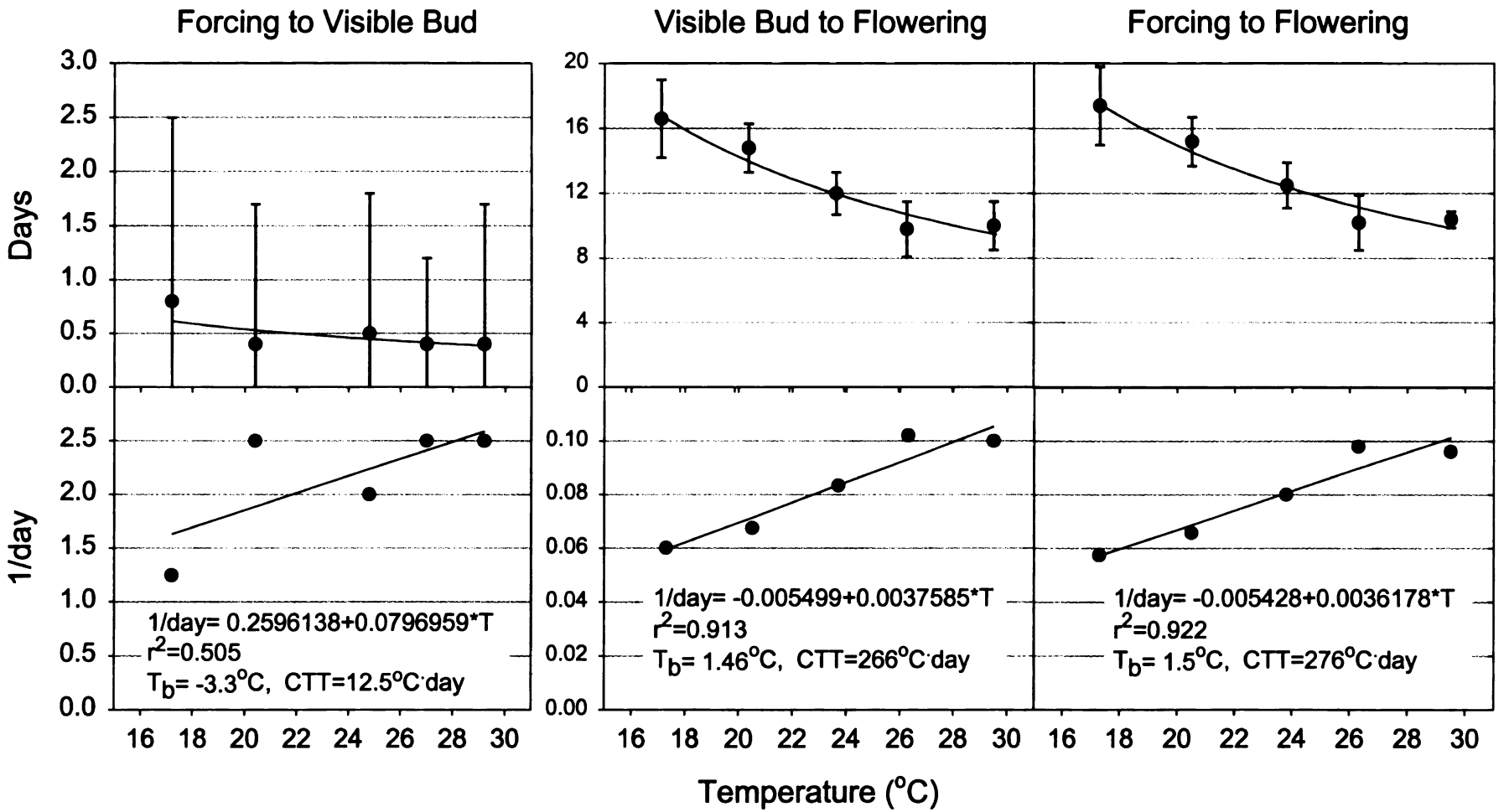

Figure 75. Influence of forcing temperature on time and rate toward flowering for *Phlox subulata* 'Emerald Blue' in year 2. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

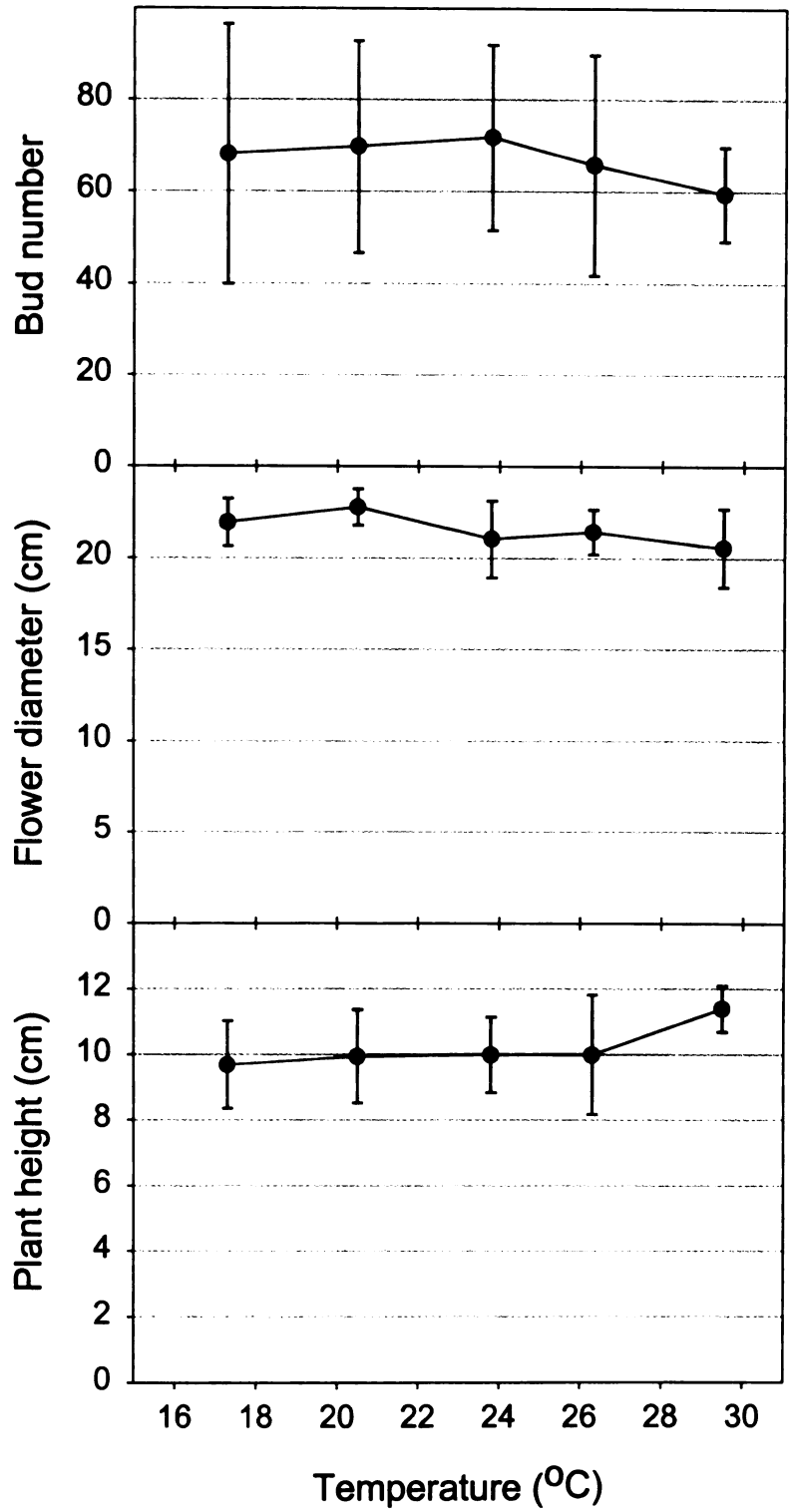

Figure 76. Influence of forcing temperature on number of flower buds, flower diameter, and plant height measured at first flower for *Phlox subulata* 'Emerald Blue' in year 2. Error bars show standard deviation.

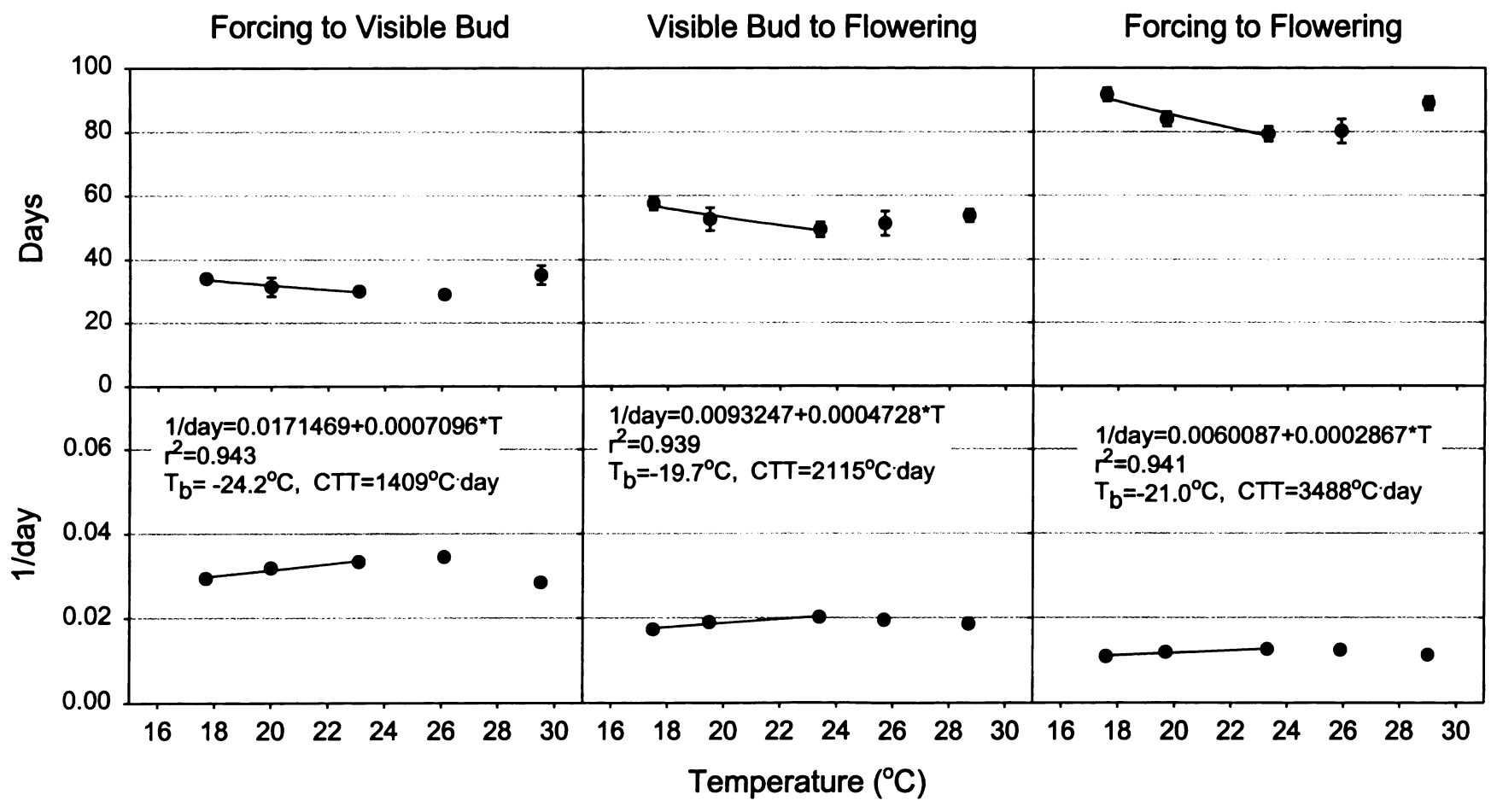

Figure 77. Influence of forcing temperature on time and rate toward flowering for *Sedum* 'Autumn Joy' in year 1. Lines represent predicted values from the regression equations. All error bars represent standard deviation. Base temperature (T_b) and cumulative thermal time (CTT) necessary to complete the indicated developmental stage were calculated from the regression.

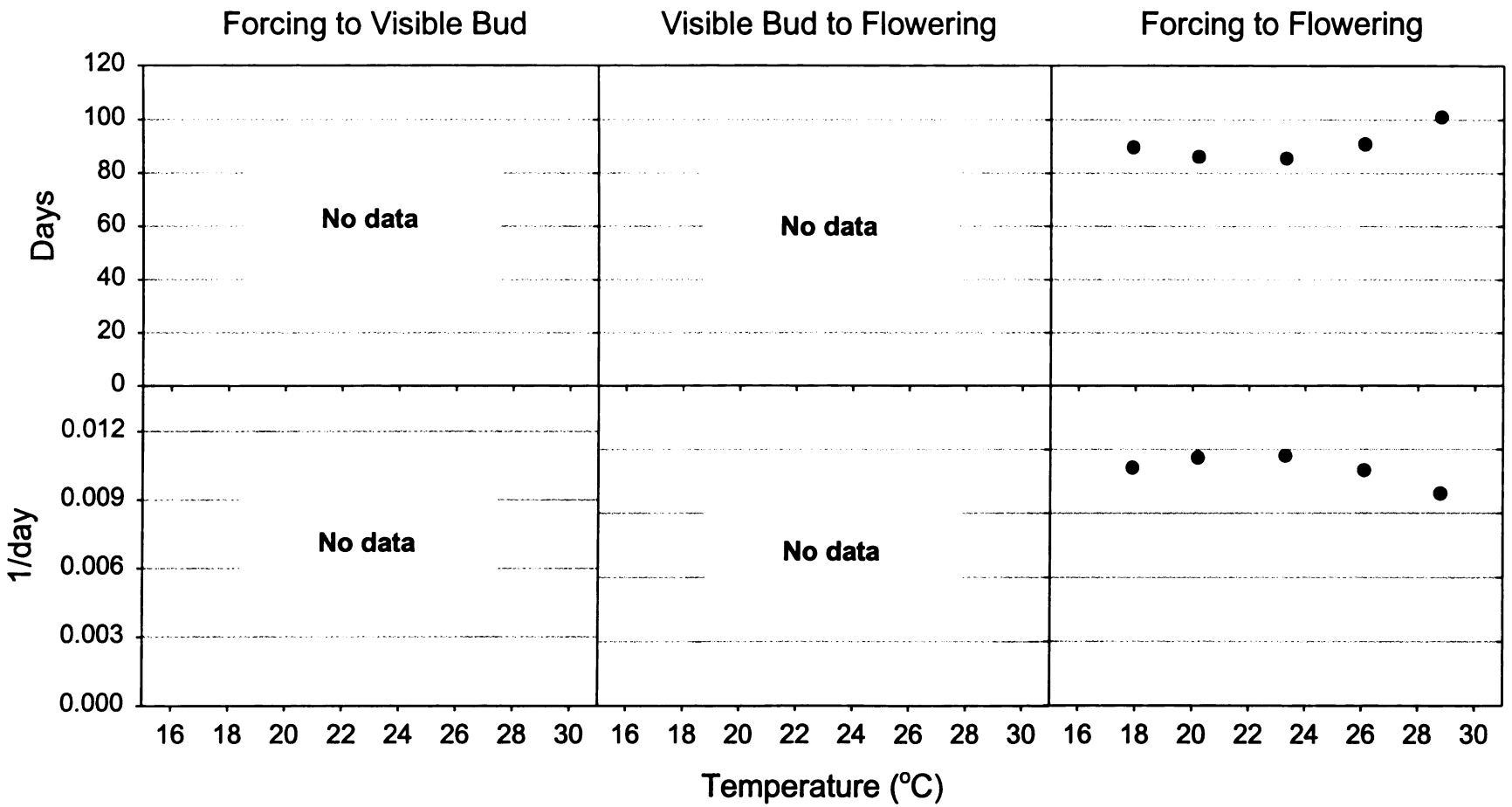

Figure 78. Influence of forcing temperature on time and rate toward flowering for *Sedum* 'Autumn Joy' in year 2. All error bars represent standard deviation (too small to see). Base temperature (T_b) and cumulative thermal time (CTT) were not calculated in this instance.

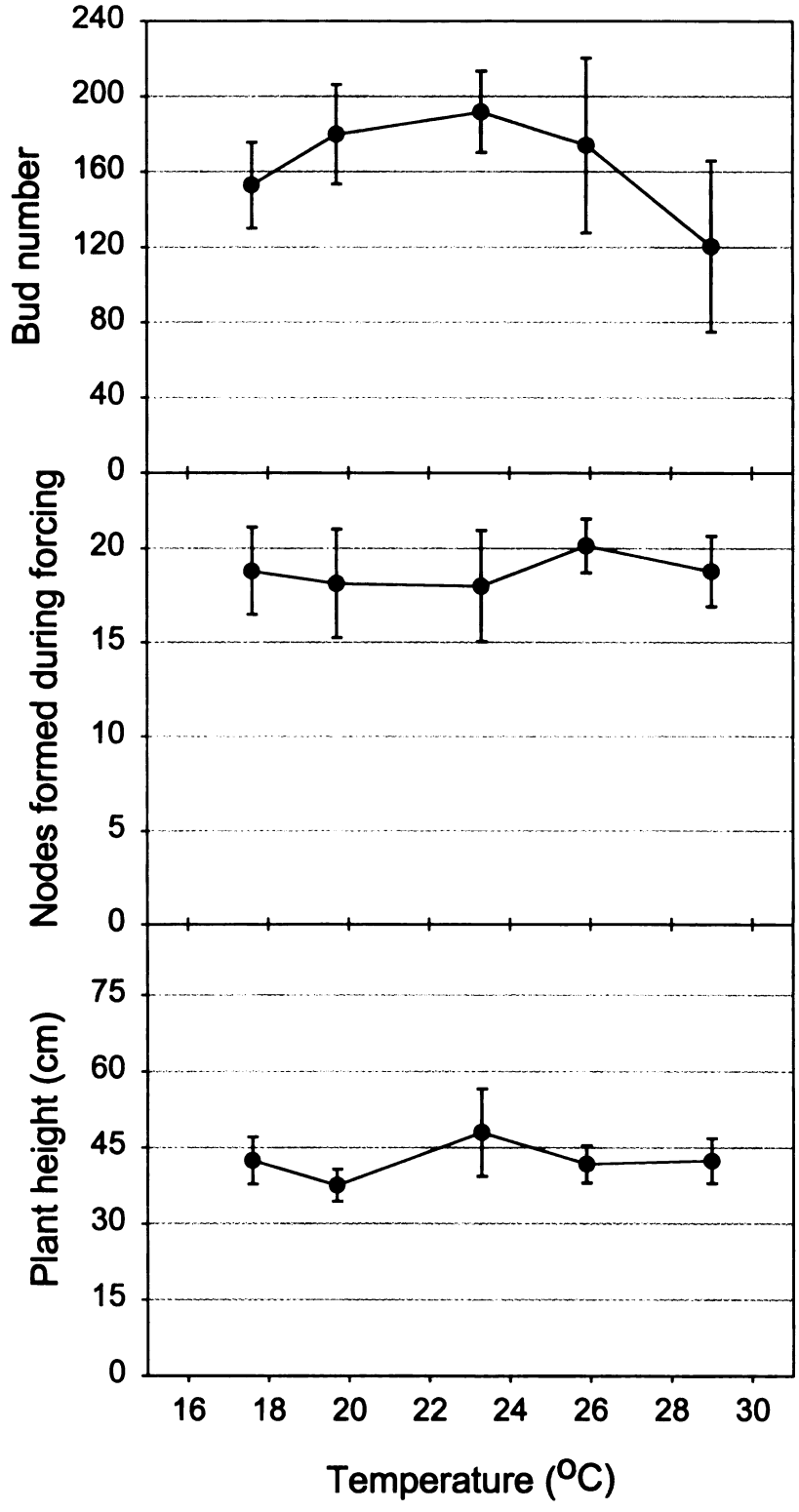

Figure 79. Influence of forcing temperature on number of flower buds, number of nodes formed during forcing, and plant height measured at first flower for *Sedum* 'Autumn Joy' in year 1. Error bars show standard deviation.

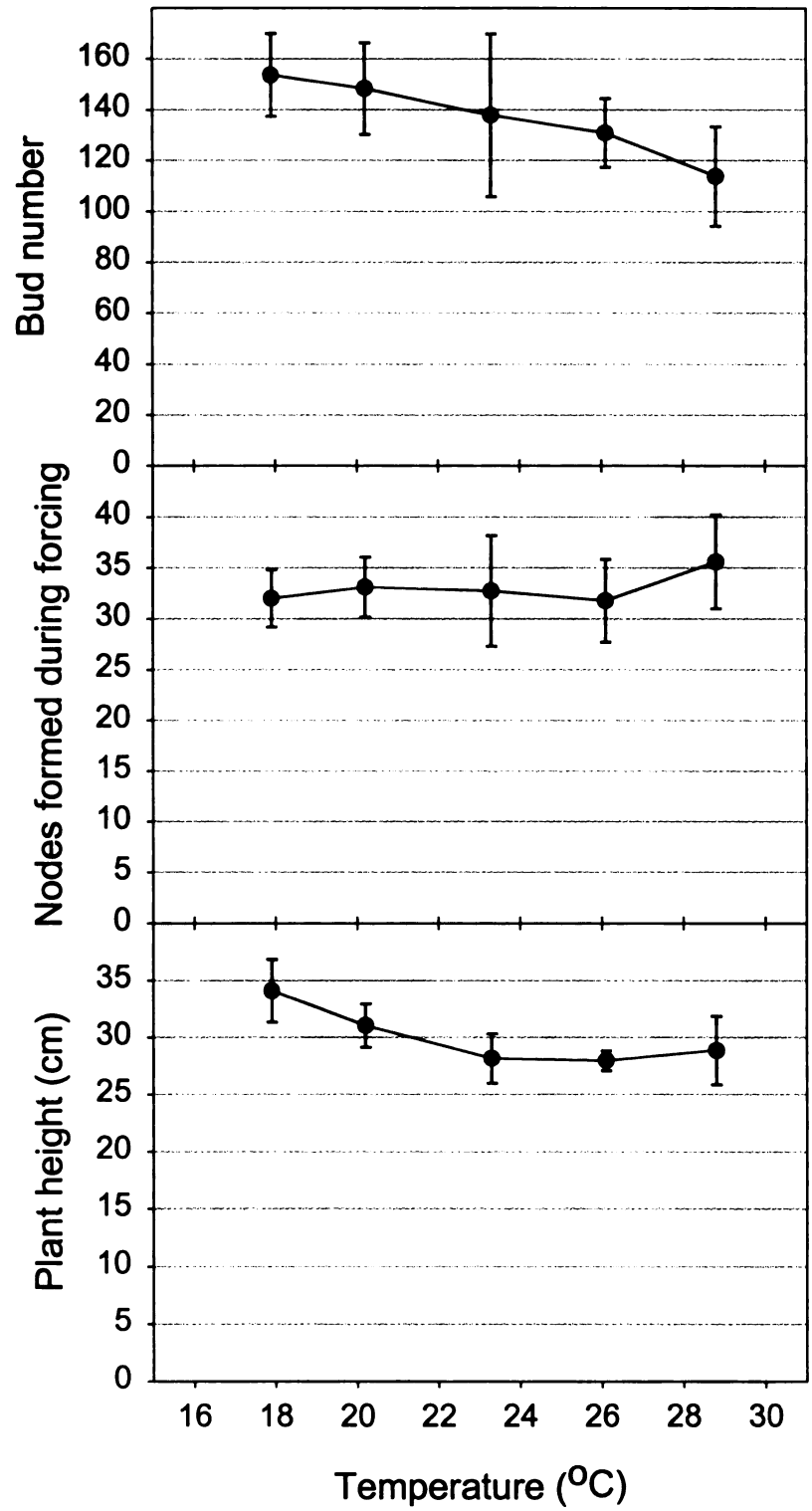

Figure 80. Influence of forcing temperature on number of flower buds, number of nodes formed during forcing, and plant height measured at first flower for *Sedum* 'Autumn Joy' in year 2. Error bars show standard deviation.