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MANIPULATING LIGHT AND TEMPERATURE FOR ENERGY-EFFICIENT GREENHOUSE PRODUCTION OF ORNAMENTAL CROPS

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MATTHEW GEORGE BLANCHARD

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Erik Runkle
Major Professor's Signature

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ABSTRACT

MANIPULATING LIGHT AND TEMPERATURE FOR ENERGY-EFFICIENT GREENHOUSE PRODUCTION OF ORNAMENTAL CROPS

By

Matthew George Blanchard

The cost of heating fuel for greenhouse crop production is a significant expense for growers in temperate climates. With the recent volatility in energy prices, some ornamental plant growers have adjusted their production temperatures without knowledge of its impact on crop timing or plant quality. The objectives of this research were to quantify and model the influence of mean daily temperature (MDT) and photosynthetic daily light integral (DLI) on flowering and plant quality of approximately 30 annual bedding plants commonly grown in controlled environments. During one experiment, 18 species of bedding plants were grown in environmental growth chambers at constant air temperature set points of 5, 7.5, 10, 15, 25, or 30 °C and under a photosynthetically active radiation intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ using a 16-h photoperiod. Nonlinear mathematical equations were developed for each species to predict the effect of constant temperatures on flowering rate (reciprocal of days to flower) and to estimate the base temperature (T_{min}) at which flowering rates were zero. The estimated T_{min} ranged from 1.1 °C in *Tagetes patula* L. to 9.9 °C in *Angelonia angustifolia* Benth. In separate experiments, the same species were grown in glass-glazed greenhouses at constant air temperature set points of 14, 17, 20, 23, or 26 °C and under a mean DLI of 3 to 19 $mol \cdot m^{-2} \cdot d^{-1}$ using a 16-h photoperiod. Flower development rates were predicted using a model that included a linear MDT function with the T_{min} multiplied by an exponential DLI saturation function. Within the temperature range studied, flower development rate increased as MDT

increased, and in some species, development rate began to decrease at higher MDTs. For example, under a mean DLI of 12 $mol \cdot m^{-2} \cdot d^{-1}$, as MDT increased from 14 to 23 °C, time to flower of *Petunia ×hybrida* Vilm.-Andr. 'Easy Wave Coral Reef' and 'Wave Purple' decreased from 51 to 22 d and 62 to 30 d, respectively. The estimated saturation DLI for flower development rate in most species studied ranged from 8 to 15 $mol \cdot m^{-2} \cdot d^{-1}$.

An additional study was performed with three species to validate models at day/night (16 h photoperiod) temperature set points of 20/14, 18/18, 16/22 (mean of 18 °C), 24/18, 22/22, or 20/26 °C (mean of 22 °C). Flowering times were similar among treatments with the same MDT but all species grown at 20/14 °C were 10 to 41% taller than those grown at 16/22 °C. Using computer software that estimates energy consumption for greenhouse heating (Virtual Grower version 2.51), energy inputs to produce these species for spring market dates were estimated to be 3 to 42% lower at a +6 °C day/night temperature difference compared with a constant temperature.

In a final study, *Impatiens hawkeri* Bull. shoot-tip temperature was quantified under several retractable greenhouse shade/energy screens during winter. An energy balance model was developed that predicted shoot-tip temperature using cover (glazing or screen) emissivity and five environmental parameters including dry-bulb, wet-bulb, cover temperature, transmitted shortwave radiation (300 to 3,000 nm), and greenhouse air velocity. At night and under an extended screen, the effective cover and shoot-tip temperature were 0.8 to 6.9 °C and 0.5 to 2.3 °C higher, respectively, than without a screen. Thus, screens extended overhead during cold nights can increase plant temperature and accelerate development.

DEDICATION

I dedicate this dissertation to my loving grandparents, Eleanor and Harold George who helped plant my first garden and started me down the horticulture path.

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PREFACE

In the U.S., annual bedding and garden plant production is the largest segment of the floriculture industry with a USDA-reported wholesale value of $1.3 billion in 2008. The majority of these crops are produced in heated greenhouses from January through May so that flowering plants are available to consumers for purchasing in the spring. During this time of year in temperate climates, high energy inputs can be required to maintain a desirable greenhouse temperature, making fuel for heating costs one of the largest floriculture production expenses (after labor costs). Rising and volatile energy prices and shrinking profit margins have motivated many ornamental plant growers to improve energy conservation and to minimize energy inputs for crop production in controlled environments.

Energy-efficient and predictable commercial production of greenhouse crops requires information on how species respond to the environment so that they can be accurately scheduled for predetermined market dates. Plant growth and development in response to the environment can be described quantitatively using mathematical equations or models. Models that describe a biological process can be used to either facilitate the understanding of a system or to predict a future condition. In controlled environment experiments, it is often a challenge to deliver all possible levels of an environmental factor. Therefore, models can be used to predict a response under conditions that were not tested, but are within the typical range(s) of the parameter(s) studied.

This research project quantified and modeled the influence of mean daily

temperature (MDT) and mean photosynthetic daily light integral (DLI) on flowering and plant quality of approximately 30 annual bedding plants grown in controlled greenhouse environments. Nonlinear mathematical equations were developed for each species to predict the effect of MDT on flowering rate (reciprocal of days to flower), the estimated base temperature (T_{min}; the temperature at which flowering development rate is zero), and the estimated saturation DLI for highest flower development rate DLI_{sat}, when maximum development rate was 99%. During some experiments, models were validated with independent data and the predicted responses were compared with observed data.

Flower development responses to temperature indicated that there is considerable variability in thermal tolerance among genera. For example, the estimated T_{min} ranged from 1.1 °C in French marigold (*Tagetes patula* L.) to 9.9 °C in angelonia (*Angelonia angustifolia* Benth.). Under a DLI of 10 $mol \cdot m^{-2} \cdot d^{-1}$, some species such as cosmos (*Cosmos sulphureus* L.) and dahlia (*Dahlia ×hybrida* Cav.) had a narrow temperature range (14 to 17 °C) between T_{min} and the temperature at which flower development rate was greatest (T_{opt}). Other species such as French marigold and black-eyed Susan (*Rudbeckia hirta* L.), had a wide temperature range between T_{min} and T_{opt}, which was estimated to exceed 25 °C. The different temperature responses among species could be attributed to their indigenous habitat or criteria used for breeding selection. For example, black-eyed Susan has a native distribution throughout temperate and semi-tropical regions of North America. Black-eyed Susan had a T_{min} for flower development of 4.6 °C and is apparently adapted to flower during the summer in habitats with variable temperature conditions. In contrast, cosmos is native to semi-tropical regions of North, Central, and South America, Africa, and Asia. Therefore, is not surprising that cosmos

had a higher T_{min} for flower development of 7.2 °C.

A correlation was found between T_{min} and the relative delay in flowering as temperature decreased from 20 to 15 °C: species with a higher T_{min} had a greater delay than those with a lower T_{min}. Greenhouse growers could use this information to group species with similar environmental responses. Crops with only a slight flowering delay when greenhouse temperature was lowered could be grouped together and grown at a cool temperature set point without a considerable increase in production time (e.g., more than 1 week).

The mathematical models presented in this dissertation also describe the influence of DLI on flower development rate, which was modeled as a multiplier of the temperature response. Flowering rate increased exponentially as DLI increased and approached saturation (DLI_{sat}) between 8 to 15 $mol \cdot m^{-2} \cdot d^{-1}$ for most species tested. Increasing the DLI above DLI_{sat} did not accelerate flower development rate. This information reinforces that supplemental lighting can have the largest effect on reducing crop time when the ambient DLI is low. In many species, the DLI for the greatest crop quality (e.g., maximum flower bud or inflorescence number) was higher than DLI_{sat}. For example, zinnia (*Zinnia elegans* Jacq.) had a DLI_{sat} of 12.5 $mol \cdot m^{-2} \cdot d^{-1}$ for flowering rate, but inflorescence number continued to increase under the DLI range studied (3 to 19 $mol \cdot m^{-2} \cdot d^{-1}$). Commercial growers that are able to obtain a higher price for a higher quality crop may consider using supplemental light to increase the DLI above DLI_{sat}.

This research also compared different hybrids within a genus to determine if models developed for one cultivar could be used to predict flowering responses in another cultivar of the same species. Although hybrids within a species had similar

growth responses to temperature and DLI, the models generated for one cultivar did not accurately predict flower development rate, flower number, or plant height for the other cultivars. The different environmental responses among cultivars could be caused by genetic differences and/or by different breeding selection criteria such as growth form, production time, and heat tolerance. Although it was necessary to develop unique models for each crop, cultivars of the same species generally had a similar T_{min} and DLI_{sat} for flower development rates. For example, petunia (*Petunia ×hybrida* Vilm.-Andr.) 'Easy Wave Coral Reef' and 'Wave Purple' had an estimated T_{min} and DLI_{sat} within 1.8 °C and 0.3 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. However, these cultivars had different cumulative degree-day (°C·d) requirements to reach flowering. Therefore, in future research, the main cultivar-specific parameter for flower development rate could focus on estimating the thermal time for flowering. This could be determined by growing plants at a single MDT, which would allow for rapid adaptation of these models to new cultivars. Further research is warranted to test this approach.

The developed mathematical models were based on crops grown at constant temperature set points. However, greenhouse growers often utilize different day and night temperature set points during crop production. A study was performed with three species to compare growth and flowering times at constant and a plus 6 °C differential day/night temperature set points. This research quantified similar flowering times at different day/night treatments with the same MDT and indicated that these crop models could also be used to predict flowering at fluctuating temperature set points. This response reinforces the paradigm that flowering rate is a function of the MDT and, within limits, the effects of day and night temperature on progress towards flowering are equal.

One strategy that is used by some greenhouses to save energy for heating is to lower temperature set points during periods when the greenhouse heat loss is high (typically when the temperature differential between inside and outside is high) and raise set points when the heat loss is low. This environmental control strategy typically delivers a higher day than night temperature, a higher temperature on sunny days and lower on cloudy day, but maintains a target mean temperature during a pre-determined period (e.g., 5 days). Additional research could investigate delivering a low MDT after transplant for a specific duration (e.g., 2 weeks) and then growing at a higher MDT until the plants are in flower. The opposite temperature strategy of beginning production at a high MDT and ending at a low MDT could also be studied.

Others methods to reduce energy costs for greenhouse heating include energy conservation methods, such as the installation of retractable thermal screens. Thermal screens can be extended over a greenhouse crop from sunset to sunrise and reduce the heat loss to the outside environment. This dissertation presents research information on the influence of retractable greenhouse shade/energy screens on plant shoot-tip temperature of New Guinea impatiens (*Impatiens hawkeri* Bull.). At night and under an extended screen, the effective cover (glazing or screen) and shoot-tip temperature were 0.8 to 6.9 °C and 0.5 to 2.3 °C higher, respectively, than without a screen. An energy balance model was developed that can be used to predict shoot-tip temperature under different screen materials and environmental conditions. The results from this experiment indicated that a retractable greenhouse screen has the potential to decrease energy costs for heating and also to increase plant temperature and accelerate development.

To facilitate the application of this research information by the greenhouse industry, these crop development models will be integrated into a free computer software program, Virtual Grower, created by Jonathan Frantz and colleagues of the USDA-ARS Greenhouse Production Group in Toledo, Ohio. The outcomes of this interactive software will include crop timing and the predicted energy consumption and cost based on greenhouse location and user inputs. This tool can be used to identify the target crop production temperature that results in the least amount of energy consumed on a per-crop basis.

Collectively, the scientific information presented in this dissertation has added to the understanding of how temperature and DLI influence plant growth and development of many popular bedding plants. This new information can be used by the greenhouse industry and educators to improve the predictability of flowering time of these ornamental crops and to assist growers in determining energy-efficient production practices.

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QUANTIFYING THE THERMAL FLOWERING RATES OF EIGHTEEN SPECIES OF ANNUAL BEDDING PLANTS

Quantifying the Thermal Flowering Rates of Eighteen Species of Annual Bedding Plants

Matthew G. Blanchard[1] and Erik S. Runkle[2]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

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[1]Ph.D. candidate.

[2]Corressponding author and to whom reprint requests should be addressed. Email address: runkleer@msu.edu.

Abstract

The effect mean daily air temperature (MDT) on flowering rate (the reciprocal of days to flower) was quantified for 18 species of annual bedding plants. Plants were grown in environmental growth chambers at constant air temperature set points of 5, 7.5, 10, 15, 25, or 30 °C and under 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of light with a 16-h photoperiod. Nonlinear mathematical equations were developed to predict the effect of MDT on flowering rate and to estimate the base, optimum, and maximum temperatures (T_{min}, T_{opt}, and T_{max}), which are the temperatures at which flowering rates are zero (low temperature), maximal, and zero once again (high temperature), respectively. The estimated T_{min} varied among species and ranged from 1.1 °C in French marigold (*Tagetes patula* L.) to 9.9 °C in angelonia (*Angelonia angustifolia* Benth.). T_{opt} and T_{max} could only be estimated for 8 to 10 species with the temperature range tested. T_{opt} ranged from 19.1 °C in dahlia (*Dahlia ×hybrida* Cav.) to 28.0 °C in blue salvia (*Salvia farinacea* Benth.), while T_{max} ranged from 30.3 °C in snapdragon (*Antirrhinum majus* L.) to 31.7 °C in moss rose (*Portulaca grandiflora* Hook.). Angelonia, browallia (*Browallia speciosa* Hook.), cosmos (*Cosmos sulphureus* Cav.), dahlia, and snapdragon grown at 25 or 30 °C developed a mean of 2 to 7 more nodes before flowering compared with plants grown at ≤15 °C. The results indicate that in many species, flowering rate in response to MDT is asymmetrical around T_{opt} and the temperature range between T_{min} and T_{opt} is wider than that between T_{opt} and T_{max}. This information could be used to improve the predictability of flowering time of these ornamental crops and to assist growers in determining energy-efficient production temperatures.

Introduction

Scheduling greenhouse crops for specific market dates requires information on how the environment influences plant growth and development (Heins et al., 2000). Empirical models have been developed for several economically important floriculture crops such as chrysanthemum [*Chrysanthemum ×grandiflorum* (Ramat.) Kitam.; Larsen and Persson, 1999], Easter lily (*Lilium longiflorum* Thunb.; Erwin and Heins, 1990), poinsettia (*Euphorbia pulcherrima* Willd. ex Klotz; Lui and Heins, 2002), petunia (*Petunia ×hybrida* Vilm.-Andr.; Adams et al., 1998), and potted rose (*Rosa* L.; Steininger et al., 2002) that predict crop time or quality under various environmental conditions.

Plant developmental responses to temperature, such as flowering or leaf unfolding time, are primarily influenced by the mean daily temperature (MDT) (Roberts and Summerfield, 1987). The time required for the completion of a developmental stage can be converted to a rate by calculating the reciprocal of time (e.g., 1/d). The rate of plant development in response to MDT increases between the base and optimum temperature. The base temperature (T_{min}) is the species-specific temperature at or below which the rate of progress towards a developmental stage is zero. T_{min} has been estimated for different developmental stages in several floriculture crops. For example, T_{min} for leaf unfolding and flower bud development rates (the reciprocals of days to unfold one leaf or days to flower) in Easter lily were calculated to be 1.1 °C and 3.5 °C, respectively (Erwin and Heins, 1990; Karlsson et al., 1988). T_{min} for the flowering rate from visible flower bud to open flower in campanula (*Campanula carpatica* Jacq.) was calculated to be −1.8

°C, while potted rose had an estimated T_{min} of 8.1 to 9.5 °C from budbreak to open flower (Niu et al., 2001; Steininger et al., 2002).

As MDT increases above T_{min}, development rate increases until a maximum rate at the species-specific optimum temperature (T_{opt}). For example, T_{opt} for the flowering rate of pansy (*Viola ×wittrockiana* Gams.) and geranium (*Pelargonium ×hortorum* Bailey) was calculated to be 21.7 °C and 28.3 °C, respectively (Adams et al., 1997; Armitage et al., 1981). When MDT >T_{opt}, development rate decreases as MDT increases and the rate becomes zero at the maximum temperature (T_{max}). Estimation of T_{min}, T_{opt}, and T_{max} requires quantification of a developmental event at a wide range of MDTs and therefore, these values have been estimated on a small number of floriculture crops including chrysanthemum (Larsen and Persson, 1999), dahlia (*Dahlia pinnata* Cav.; Brøndum and Heins, 1993), cineraria (*Pericallis ×hybrida* R. Nordenstam; Yeh et al., 1999), and African violet (*Saintpaulia ionantha* Wendl.; Faust and Heins, 1993). For example, a model developed for African violet predicted T_{min}, T_{opt}, and T_{max} for leaf unfolding rate to be 8.0 °C, 23.0 to 25.5 °C, and 30.8 °C, respectively (Faust and Heins, 1993).

Relationships between MDT and plant development rates have been modeled using linear, quadratic, cubic, and exponential functions (Landsberg, 1977; Larson, 1990). For example, a linear model predicted that flowering rate in tickseed (*Coreopsis grandiflora* Hogg ex Sweet. 'Sunray') increased from 0.013 to 0.028 as MDT increased from 15 to 25 °C (Yuan et al., 1998). In Rieger begonia (*Begonia ×hiemalis* Fotsch), a polynomial model predicted that as MDT increased from 13 to 21 °C, leaf unfolding rate increased from 0.072 to 0.116 (Karlsson, 1992).

The response of a development rate to MDT has been described as either a symmetrical (Pearson et al., 1993; Volk and Bugbee, 1991) or asymmetrical (Brøndum and Heins, 1993; Faust and Heins, 1993, 1994) peak-shape around T_{opt}. For example, a model generated for chrysanthemum predicted that flowering rate had a symmetrical response to MDT; development rate increased linearly as MDT increased from T_{min} to T_{opt}, and then decreased at the same, but opposite slope from T_{opt} to T_{max} (Pearson et al., 1993). In contrast, Brøndum and Heins (1993) supposed that most biological responses to temperature were asymmetrical and developed a model to predict flowering rate in dahlia that increased from T_{min} to T_{opt} and then decreased from T_{opt} to T_{max} with a greater slope. Scientific studies to determine flowering rates at MDTs above T_{opt} have been performed on few crops, and it is unknown if other species display a similar asymmetrical temperature response around T_{opt} (Summerfield and Roberts, 1991).

A useful outcome in the generation of crop models is the estimation of T_{min} and T_{opt} for flowering rate; thermal time is only accumulated at temperatures $>T_{min}$ and $\leq T_{opt}$ (Roberts and Summerfield, 1987; Wang, 1960). Therefore, determination of T_{min} and T_{opt} are important for accurate thermal time predictions (Arnold, 1959; Wang, 1960; Yeh et al., 1999). For example, calculation of thermal time in maize (*Zea mays* L.) grown at 18.3 °C with a T_{min} that was ±5.6 °C different from the estimate of 7.2 °C caused an error of ±900 degree days (°C·d; Arnold, 1959). The estimated T_{min} is also important when quantifying the photothermal ratio (PTR) to predict plant growth and quality. PTR is the ratio of radiant energy to thermal energy and is calculated as the product of daily light integral (DLI, $mol \cdot m^{-2} \cdot d^{-1}$) and °C·d above T_{min} (Liu and Heins, 2002).

T_{min} for flowering rate has been estimated for several flowering potted plants and temperate herbaceous perennials, but estimates for ornamental annual species is lacking. Notable exceptions include vinca (*Catharanthus roseus* L.), celosia (*Celosia argentea* L. var. *plumosa* Voss), impatiens (*Impatiens walleriana* Hook.f.), geranium, petunia, red salvia (*Salvia splendens* F. Sello ex Roem & Schult.), French marigold (*Tagetes patula* L.), and pansy (Adams et al., 1996, 1998; Armitage, 1981; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Pietsch et al., 1995; Pramuk and Runkle, 2005). The estimation of T_{min} for additional annual species could be useful in the development of crop models that predict flowering rates under different environment conditions. In addition, estimates of T_{min} could be used to determine which annual species tolerate low production temperatures and identify energy-efficient growing strategies.

The objective of this study was to quantify the influence of MDT on flowering time during the finish stage of 18 species of annual bedding plants, and from that data, to develop mathematical models that estimate T_{min} and T_{opt} for flowering rates.

Materials and Methods

Seeds of African marigold (*Tagetes erecta* L. 'Antigua Primrose'), angelonia (*Angelonia angustifolia* Benth. 'Serena Purple'), black-eyed Susan (*Rudbeckia hirta* L. 'Toto Rustic'), blue salvia (*Salvia farinacea* Benth. 'Victoria Blue'), browallia (*Browallia speciosa* Hook. 'Bells Marine'), cosmos (*Cosmos sulphureus* Cav. 'Cosmic Orange'), dahlia (*Dahlia ×hybrida* 'Figaro Mix'), dianthus (*Dianthus chinensis* L. 'Super Parfait Raspberry'), French marigold 'Janie Flame', gazania [*Gazania rigens* (L.) Gaertn. 'Daybreak Bronze'], moss rose (*Portulaca grandiflora* Hook. 'Margarita Apricot'),

pentas [*Pentas lanceolata* (Forssk.) Deflers 'Graffiti Lavender'], petunia 'Dreams Neon Rose' and 'Wave Purple', snapdragon (*Antirrhinum majus* L. 'Montego Orange Bicolor'), verbena (*Verbena* ×*hybrida* Groenl. & Ruempl. 'Quartz Waterfall Mix'), viola (*Viola cornuta* L. 'Sorbet Plum Velvet'), and zinnia (*Zinnia elegans* Jacq. 'Dreamland Coral') were sown in plug trays [288-cell size (6-ml volume)] by a commercial greenhouse (C. Raker & Sons, Litchfield, MI). After germination, plugs were received at Michigan State University (MSU) and were grown in a controlled environmental growth chamber (TC-2; Environmental Growth Chambers, Chagrin Falls, OH) at a temperature set point of 20 °C. A 16-h photoperiod was provided by 215-W cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and 60-W incandescent lamps (INC; Philips), at a CWF:INC (by W) of 3.6, and at an intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. All plugs were thinned to one seedling per cell. During the plug stage, plants were irrigated as necessary with well water acidified with H_2SO_4 to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$ and containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively. The water was supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, Mn, and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

When seedlings were ready for transplant [16 to 44 d after seed sow, depending on species (Table 1.1)], plugs were transplanted into 10-cm round plastic containers (480-ml volume) filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). The mean node number at transplant for each species is presented in Table 1.1. Eight plants of each species were randomly assigned to treatments and grown in controlled environmental growth chambers (TC-2;

Environmental Growth Chambers) at constant air temperature set points of 5, 7.5, 10, 15, 25, or 30 °C and under the light parameters previously described. Before plants were transferred to 5, 7.5, or 10 °C, they were grown for 1 week at 15 °C followed by 1 week at 10 °C to acclimate plants to the low temperatures.

The experiment was performed twice with each species and the time from seed sow to transplant was the same or ±7 d between replications (Table 1.1). Species in which a treatment elicited ≥50% plant death or plants required ≥170 d to flower in the first replication were not grown at those temperatures during the second replication. Plants were top irrigated as necessary with well water that was acidified as described previously. The water was supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$) 125 N, 11 P, 126 K, 13 Ca, 1 Fe, 0.5 Cu, Mn, and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc.).

Environmental Monitoring

Air temperature was independently measured in each chamber by an aspirated, shielded thermocouple (0.13-mm type E; Omega Engineering, Stamford, CT) positioned at bench height. At two temperature treatments, the *PPF* was measured by a quantum sensor (LI-190SA; LI-COR, Inc., Lincoln, NE) positioned 16 cm above the height of the containers. The height was determined to be representative of the canopy height for the species grown. For treatments that did not contain a quantum sensor, the *PPF* was measured weekly at 25 cm above the bench with a line quantum sensor (Apogee Instruments, Inc., Logan, UT). Bulbs were replaced or the height of the lamp loft was adjusted to maintain a *PPF* of 180 $mol \cdot m^{-2} \cdot d^{-1}$. In each temperature treatment, a

thermocouple (0.13-mm type E; Omega Engineering) was inserted 0.5 cm below the shoot tip of five different plants and the actual plant temperature was recorded. Thermocouples were repositioned weekly as plants developed.

Environmental measurements were collected every 10 s and 10-min means were recorded by data loggers (CR10X; Campbell Scientific, Logan, UT). Mean daily plant temperature for both replications at 5, 7.5, 10, 15, 20, 25, and 30 °C was +1.9, +1.2, +0.9, +1.5, +0.3, +0.3, and −0.2 °C relative to mean daily air temperature, respectively. In each treatment, water vapor was injected into the air if the vapor-pressure deficit (VPD) was >0.8 kPa. The actual mean VPD at 5, 7.5, 10, 15, 20, 25, and 30 °C for both replications was 0.5, 0.4, 0.4, 0.9, 0.7, 0.8, and 1.7 kPa, respectively.

Data Collection and Analysis

The date of first open flower was recorded and time to flower was calculated for each plant. Plants were considered in flower according to individual flowering characteristics for each species (Table 1.1). When each plant flowered, the number of nodes on the primary shoot below the first open flower was recorded. Data were analyzed using the calculated MDT for each plant from transplant to the date of flowering. Flowering time data were converted to flowering rates.

A nonlinear model was used to describe the relationship between the flowering rate and MDT for each species (Landsberg, 1977; Reed et al., 1976):

$$1/d \text{ to flower} = A \times (MDT - T_{min}) \times (T_{max} - MDT)^{B} \quad [1]$$

where $A = R_{max} / ((T_{opt} - T_{min}) \times (T_{max} - T_{opt})^{B})$ [2]

and $B = (T_{max} - T_{opt}) / (T_{opt} - T_{min})$ [3]

where MDT = mean daily air temperature (°C), T_{min} and T_{max} are the minimum and maximum temperatures, respectively. When MDT is $\leq T_{min}$ or $\geq T_{max}$, development rate is zero. T_{opt} is the temperature where the maximum development rate occurs (R_{max}) and the "B" value defines the skew of the function. This asymmetrical model was chosen because it describes a biological response to temperature, such as net photosynthesis (Neilson et al., 1972; Reed, 1976). With this function, a temperature-dependent promotion of development occurs when $T_{min} < MDT \leq T_{opt}$ and a temperature-dependent inhibition of development occurs when $T_{opt} < MDT < T_{max}$ (Larsen, 1990). This function has also been used to model the influence of temperature on flowering rate in dahlia (Brøndum and Heins, 1993) and leaf unfolding and leaf expansion rate in African violet (Faust and Heins, 1993, 1994). In angelonia, dianthus, gazania, pentas, and viola, T_{max} could not be estimated from the observed data and was fixed at 35.0 °C so that the nonlinear model could be solved.

In African marigold, black-eyed Susan, French marigold, petunia, and zinnia, T_{opt} and T_{max} could not be estimated from the observed data using Eq. [1] because there was not enough data points for the nonlinear model to converge. Therefore, an exponential function was used to describe the relationship between flowering rate and MDT (Larsen, 1990):

$$1/d \text{ to flower} = R_{max} \times (1 - \exp(-C \times (MDT - T_{min})) \quad [4]$$

where T_{min} is the temperature at or below which the development rate is zero and R_{max} is the maximum development rate. This function has been used to model leaf unfolding and flowering rates in chrysanthemum (Hidén and Larsen, 1994; Larsen and Hidén, 1995; Larsen and Persson, 1999) and cineraria (Larsen, 1988, 1989).

Parameter estimates (T_{min}, T_{opt}, T_{max}, R_{max}, and C) for the nonlinear functions (Eqs. [1] and [4]) were estimated with the nonlinear regression procedure (NLIN) of SAS (version 9.1; SAS Institute, Cary, NC). Initial parameter estimates were obtained from graphs of the observed data. Models were generated using 70 to 109 observations for each species. After the nonlinear models were generated, R^2 values were determined by performing linear regression analysis on the predicted versus observed data as recommended by Maceina and Pereira (2007). Data for the number of nodes at flower were pooled between replications and were analyzed using SAS mixed-model procedure (PROC MIXED), and pairwise comparisons between treatments were performed using Tukey's honestly significant difference test at $P \leq 0.05$.

Results

At least 50% of plants died when African marigold, black-eyed Susan, and dahlia were grown at 5 °C; blue salvia, browallia, cosmos, pentas, and zinnia were grown at ≤7.5 °C; and angelonia and rose moss were grown at ≤10 °C. At 30 °C, plants of browallia, dahlia, and verbena had ≥50% death. Petunia 'Wave Purple' and verbena grown at 5 °C continued to develop new leaves, but had a low flowering rate and plants

were removed from the treatment after 258 d. Cosmos grown at 30 °C had 13% death and, although the remaining plants unfolded new leaves, only 38% of plants had a visible inflorescence after 65 d.

The coefficients of determination (R^2) for the nonlinear flowering rate models ranged from 0.74 to 0.94 in the 18 species studied (Table 1.2). In some species, variability in flowering time was high when plants were grown at an MDT near T_{min} or $>T_{opt}$. For example, in black-eyed Susan (T_{min} = 4.0 °C), flowering rate in plants grown at 5 or 7.5 °C ranged from 0.0043 to 0.011, while flowering rate at 25 °C varied by only 0.0085. In all species, the rate of flowering increased as MDT increased until T_{opt} (Fig. 1.1 and 1.2). For example, flowering rate in dianthus increased from 0.0048 at 6.0 °C to 0.033 at 26.0 °C.

The estimated T_{min} where flowering rate is zero varied among species and ranged from 1.1 °C in French marigold to 9.9 °C in angelonia (Table 1.2). Species that had a $T_{min} \leq 5.0$ °C were African marigold, black-eyed Susan, dianthus, French marigold, gazania, petunia 'Dreams Neon Rose', snapdragon, and viola. Those in which $T_{min} > 5.0$ °C were angelonia, blue salvia, browallia, cosmos, dahlia, moss rose, petunia 'Wave Purple', verbena, and zinnia.

Among the species in which T_{opt} could be estimated, it ranged from 19.1 °C in dahlia to 28.0 °C in blue salvia (Table 1.2). For the species in which the T_{opt} could be estimated, dahlia had the lowest R_{max} at 0.0204, while viola had the highest R_{max} at 0.0831. At the MDT range used in this study, sufficient data existed to model the response of flowering rate to MDT at $>T_{opt}$ for only seven species. The estimated T_{max} for blue salvia, browallia, cosmos, dahlia, moss rose, snapdragon, and verbena ranged

from 30.3 to 31.7 °C. In these species, the rate of flowering decreased rapidly from T_{opt} to T_{max}.

As temperature decreased, node number at first flowering in African marigold, angelonia, blue salvia, browallia, cosmos, dahlia, dianthus, moss rose, petunia 'Wave purple', snapdragon, verbena, and zinnia decreased linearly, quadratically, or both (Table 1.3). Plants of angelonia, browallia, cosmos, dahlia, and snapdragon grown at 25 or 30 °C developed a mean of 2 to 7 more nodes before flowering compared with plants grown at ≤15 °C. There were no significant differences in node number among treatments for black-eyed Susan, French marigold, gazania, petunia 'Dreams Neon Rose', and viola.

Discussion

The nonlinear models used to predict T_{min}, T_{opt}, and T_{max} were selected because they described a biological response to MDT and had relatively high coefficients of determination. Previous studies have used a linear model to describe the relationship between MDT and development rate (Karlsson, 1988; Niu et al., 2001; Pietsch, 1995). Exponential models were used in this study because plots of the observed data for each species indicated that at higher temperatures, flower development rate approached saturation, and in some species became maximal. In addition, many previous studies that used linear models were not performed at high temperatures to quantify development rate near T_{opt}, and therefore a linear function was appropriate.

Our flowering rate models were generated with data from plants grown at a relatively wide temperature range, from 5 to 30 °C. Although these crops are rarely grown at <10 °C during commercial greenhouse production, the low temperatures used in

our experiments were included to improve the predictions of T_{min}. Our estimates for T_{min} are comparable with previous published flowering models on the same species. For example, we estimated that dahlia had a T_{min} of 5.6 °C, which is only 0.4 °C higher than the T_{min} reported by Brøndum and Heins (1993) for development rate from visible flower bud to open flower. Mattson and Erwin (2003) predicted that petunia 'Dreams Rose' and 'Wave Purple' had a T_{min} 2.4 and 0.4 °C lower, respectively, than our estimates.

Among the 18 species investigated, the estimated T_{min} for flowering ranged from 1.1 to 9.9 °C, which indicates the variability in thermal tolerance among genera. T_{min} can be used to categorize species according to their temperature response; crops can be considered tolerant of or sensitive to low temperature. For example, species such as French marigold and snapdragon had a T_{min} <5.0 °C and could be described as low temperature-tolerant. A T_{min} <5.0 °C for flowering rate has also been calculated for other ornamental crops such as blanket flower [(*Gaillardia* ×*grandiflora* Van Houtte), 3.3 °C; Yuan et al., 1998], Shasta daisy ([*Leucanthemum* ×*superbum* Bergman ex J. Ingram), −3.4 °C; Yuan et al., 1998], cineraria (1.7 °C; Yeh et al., 1999), and black-eyed Susan [(*Rudbeckia fulgida* Ait.), −1.3; Yuan et al., 1998].

We can categorize low temperature-sensitive crops as those that had a T_{min} >5.0 °C, which includes angelonia and blue salvia. If these crops are grown at <5.0 °C for an extended period of time, plant development ceases and chilling injury or death could occur. Examples of additional ornamental crops that had a reported T_{min} >5.0 °C for flowering rate include tickseed (6.8 °C; Yuan et al., 1998), rose mallow [(*Hibiscus moscheutos* L.), 12.2 °C; Wang et al., 1998], geranium (8.7; Armitage et al., 1981), red

salvia (7.0 °C; Moccaldi and Runkle, 2007), and potted rose (8.1 to 9.5 °C; Steininger et al., 2002).

The estimated T_{min}, T_{opt}, and T_{max} indicate the variation among species in the temperature range between where flowering rate is zero and maximum. Species that had a calculated difference between T_{min} and T_{opt} of 14 to 17 °C include angelonia, cosmos, dahlia, and moss rose; 18 to 20 °C include blue salvia, browallia, pentas, and verbena; and 22 to 24 °C include dianthus, gazania, snapdragon, and viola. In African marigold, black-eyed Susan, French marigold, petunia 'Dreams Neon Rose', and petunia 'Wave Purple', T_{opt} could not be estimated, and therefore, the temperature range between T_{min} and T_{opt} is >25 °C. The different temperature ranges among species could be related to their indigenous habitat (Jones, 1992) or criteria used for breeding selection. The identification of crops that develop at a wide temperature range could be used by breeders to improve low and high temperature tolerance (Summerfield et al., 1991).

Among the species in which T_{max} could be estimated, the calculated difference between T_{opt} and T_{max} was 3 to 5 °C in blue salvia, browallia, and snapdragon; 7 to 8 °C in cosmos, moss rose, and verbena; and 11 °C in dahlia. These results indicate that in these species, flowering rate in response to MDT is asymmetrical around T_{opt} and the temperature range between T_{min} and T_{opt} is considerably wider than the range between T_{opt} and T_{max}. Flowering rate models for other ornamental crops have described a similar asymmetrical response to temperature. For example, a model developed for 30 chrysanthemum cultivars predicted T_{opt} to be 14.2 °C >T_{min} and 9.2 °C <T_{max} (Larsen and Persson, 1999). In cineraria, T_{opt} was estimated to be 20.6 °C >T_{min} and 14.8 °C

$<T_{max}$ (Yeh et al., 1999), while dahlia had a T_{opt} 19 °C $>T_{min}$ and 8.9 °C $<T_{max}$ (Brøndum and Heins, 1993).

Our T_{min} estimations are for plants grown under a mean DLI of 10.4 $mol \cdot m^{-2} \cdot d^{-1}$, but in some species, DLI could influence T_{min}. For example, T_{min} in celosia and impatiens decreased from 11.7 to 10.2 °C and 7.5 to 4.3 °C, respectively, as DLI increased from 5 to 15 $mol \cdot m^{-2} \cdot d^{-1}$ (Pramuk and Runkle, 2005). Similarly in vinca, the mean T_{min} decreased from 10.2 to 7.2 °C as DLI increased from 18 to 30 $mol \cdot m^{-2} \cdot d^{-1}$ (Pietsch et al., 1995). In other species such as French marigold and red salvia, DLI had little or no affect on T_{min} (Moccaldi and Runkle, 2007). The T_{min} for some species could decrease as DLI increases because a higher DLI could increase plant temperature. Faust and Heins (1997) reported that vinca shoot-tip temperature increased by 1.7 °C as irradiance from high-pressure sodium lamps increased from 0 to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

As MDT decreased from T_{opt} to T_{min}, flowering rate decreased; however this response to temperature varied among species. For example, our models predicted that as temperature decreased from 20 to 15 °C, time to flower increased by 4 to 8 d in French marigold, dahlia, petunia 'Dreams Neon Rose', snapdragon, and viola; 11 to 18 d in African marigold, cosmos, dianthus, gazania, moss rose, petunia 'Wave Purple', verbena, and zinnia; and 20 to 38 d in angelonia, black-eyed Susan, blue salvia, browallia, and pentas. The relative delay in flowering as temperature decreased from 20 to 15 °C was significantly correlated ($P \leq 0.001$) with T_{min}, and species with a high T_{min} had a greater delay than those with a low T_{min}. For example, viola had an estimated T_{min} of 4.1 °C and a 4-d increase in time to flower at 15 °C versus 20 °C, while pentas had a T_{min} of 9.3

°C and 32-d increase in flowering time at 15 °C versus 20 °C. This information indicates that during greenhouse production, changing temperature set points can influence the scheduling of crops differently. If MDT is lowered from 20 to 15 °C, the time required to produce a crop would increase the most in species with a high T_{min}.

The decreased flowering rate at an MDT $>T_{opt}$ can be referred to as heat delay (Wang et al., 2008). High temperature can delay flowering by inhibiting flower induction, initiation, and/or development (Warner and Erwin, 2006). In some species that exhibited heat delay at an MDT $>T_{opt}$, plants developed more nodes before flowering compared to plants grown at an MDT $<T_{opt}$. For example, snapdragon had an estimated T_{opt} of 25.7 °C and developed a mean of 2.8 more nodes before flowering at 30 °C versus 25 °C. Warner and Erwin (2005) also reported that the number nodes below the first open flower increased in calendula (*Calendula officinalis* L.), impatiens, and wishbone flower (*Torenia fournieri* Linden ex. E. Fourn) as temperature increased from 20 to 32 °C. The higher node number before flowering indicates that in these species, high temperatures delayed flowering developmentally.

Under the environmental conditions provided in this study, a high percentage of browallia, dahlia, and verbena died when grown at a constant 30 °C. Semeniuk (1975) reported that as MDT increased from 20 to 31 °C, flowering rate in browallia decreased and plants grown at the highest MDT were stunted with abnormal flowers and failed to develop seeds. African violet grown at a 30 °C day temperature had chlorotic leaves and no inflorescence development, while geranium grown at 32 °C developed chlorotic leaves and died (Armitage et al., 1981; Faust and Heins, 1994). Plant stress at high temperature results from a decline in normal protein synthesis, which is substituted by the synthesis of

heat shock and stress proteins (Moseley, 1997). In addition to biochemical changes, exposure to high temperature can decrease cell membrane thermostability and result in electrolyte leakage (Wang et al., 2008).

The temperature that had the highest rate of flowering may not be similar to the T_{opt} for other physiological or developmental processes. For example, the estimated T_{opt} for flowering rate is ≥27.2 °C in angelonia, French marigold, petunia 'Dreams Neon Rose', and petunia 'Wave Purple', but T_{opt} for net photosynthesis is 19.8 to 20.8, 15.5 °C, 14.1 °C, and 20.0 °C, respectively (Miller et al., 2001; Niu et al., 2006; van Iersel, 2003). In Easter lily, flowering rate had a T_{opt} of 26.0 °C, but maximum leaf unfolding rate occurred at >30 °C (Erwin and Heins, 1990; Karlsson et al., 1988). The T_{opt} for flowering rate also may not correlate with the temperature that elicits the highest plant quality. Pietsch et al. (1995) calculated that T_{opt} for flowering rate in vinca was ≈35 °C, but flower diameter was 12 to 30% greater at 25 °C versus 30 °C. Similarly, in impatiens grown at 14 to 26 °C and under 15 $mol \cdot m^{-2} \cdot d^{-1}$, flowering rate was highest at 26 °C, but as MDT decreased, flower number, flower diameter, and dry weight at flowering increased by 141%, 25% and 52%, respectively (Pramuk and Runkle, 2005). These results collectively indicate that there can be a trade-off between fast cropping time and plant quality. A growing temperature that elicits the shortest time to flower may result in a crop that is poor quality and unmarketable.

These experiments were performed at constant temperature set points to allow modeling of the data without possible interactions between day and night temperatures. These models may not be valid under conditions when the day or night temperature is $<T_{min}$ or $>T_{max}$. For example, flower initiation and development in poinsettia was

delayed when night temperature was 27 to 30 °C regardless of MDT (Berghage, 1989). Fluctuating day/night temperature studies with other crops such as dahlia (Brøndum and Heins, 1993), pansy (Niu et al., 2000), and vinca (Pietsch et al., 1995) indicated that if the day and night temperatures were between T_{min} and T_{max} then flowering time is controlled by MDT. For example, Brøndum and Heins (1993) created 25 factorial day/night treatments by moving plants among temperatures of 10, 15, 20, 25, and 30 °C and quantified that dahlia development rate was related to MDT. These results collectively suggest that our calculated T_{min} values would be similar for plants grown at constant and fluctuating temperature regimens.

Table 1.1. Time from seed sow to transplant (TP), mean node number at TP, and characteristics used to determine flowering date for 18 species of bedding plants in two experimental replicates.

Species	Time from seed sow to TP (d)	Mean node no. at TP	Flowering characteristic
African marigold 'Antigua Primrose'	19 or 23	6.0	1 inflorescence with ≥50% of petals reflexed
Angelonia 'Serena Purple'	40	5.8	3 flowers open on an inflorescence
Black-eyed Susan 'Toto Rustic'	31	5.5	1 inflorescence with 1 whorl of petals reflexed
Blue salvia 'Victoria Blue'	34	4.0	3 flowers open on an inflorescence
Browallia 'Bells Marine'	40	5.9	1 flower open
Cosmos 'Cosmic Orange'	23	2.6	1 inflorescence with 1 whorl of petals reflexed
Dahlia 'Figaro Mix'	26	3.2	1 inflorescence with 1 whorl of petals reflexed
Dianthus 'Super Parfait Raspberry'	38	5.3	1 inflorescence with 1 whorl of petals reflexed
French marigold 'Janie Flame'	19 or 23	6.4	1 inflorescence with ≥50% of petals reflexed
Gazania 'Daybreak Bronze'	31	4.7	1 inflorescence with petals reflexed
Moss rose 'Margarita Apricot'	44	18.8	1 flower open
Pentas 'Graffiti Lavender'	40	3.9	8 flowers open on an inflorescence
Petunia 'Dreams Neon Rose'	31	10.0	1 flower open
Petunia 'Wave Purple'	33	7.7	1 flower open
Snapdragon 'Montego Orange Bicolor'	41	3.1	2 flowers open on an inflorescence
Verbena 'Quartz Waterfall Mix'	32	4.2	8 flowers open on an inflorescence
Viola 'Sorbet Plum Velvet'	38	6.5	1 flower open
Zinnia 'Dreamland Coral'	16 or 23	2.2	1 inflorescence with 1 whorl of petals reflexed

Table 1.2. Parameter estimates for nonlinear models (Eqs. [1] and [4]) relating flowering rate to mean daily air temperature in 18 bedding plant species. Parameter estimates were used to generate Figs. 1.1 and 1.2. Base (T_{min}) and maximum temperatures (T_{max}), are the temperatures at which flowering rates are zero (low and high temperature, respectively), and the optimum temperature (T_{opt}) is the temperature where the maximum development rate occurs (R_{max}). *C* defines the skew of the function. T_{min}, T_{opt}, and T_{max} are in °C. CI = confidence interval.

Eq.	Parameter	Estimate	Asymptotic 95% CI (±)	No.[z]	r^{2y}
		African marigold 'Antigua Primrose'			
[4]	T_{min}	4.4	0.7	86	0.90
	R_{max}	0.0396	0.0080		
	C	0.0560	0.0207		
		Angelonia 'Serena Purple'[x]			
[1]	T_{min}	9.9	0.4	80	0.94
	T_{opt}	27.2	0.9		
	R_{max}	0.0354	0.0013		
		Black-eyed Susan 'Toto Rustic'			
[4]	T_{min}	4.6	1.2	86	0.92
	R_{max}	0.0774	0.0564		
	C	0.0194	0.0182		
		Blue salvia 'Victoria Blue'			
[1]	T_{min}	9.4	1.0	70	0.89
	T_{opt}	28.0	0.9		
	T_{max}	31.0	0.6		
	R_{max}	0.0294	0.0019		
		Browallia 'Bells Marine'			
[1]	T_{min}	8.9	0.6	88	0.91
	T_{opt}	26.7	0.5		
	T_{max}	30.4	0		
	R_{max}	0.0296	0.0014		
		Cosmos 'Cosmic Orange'			
[1]	T_{min}	7.2	0.7	83	0.88
	T_{opt}	23.7	0.8		
	T_{max}	30.3	30.3		
	R_{max}	0.0354	0.0015		
		Dahlia 'Figaro Mix'			
[1]	T_{min}	5.6	0.5	97	0.89
	T_{opt}	19.1	0.6		
	T_{max}	30.4	0		
	R_{max}	0.0204	0.0008		

Table 1.2 (cont'd).

Eq.	Parameter	Estimate	Asymptotic 95% CI (±)	No.[z]	r^{2y}
		Dianthus 'Super Parfait Raspberry'[x]			
[1]	T_{min}	3.9	0.9	103	0.90
	T_{opt}	26.9	1.2		
	R_{max}	0.0333	0.0014		
		French marigold 'Janie Flame'			
[4]	T_{min}	1.1	1.6	104	0.94
	R_{max}	0.104	0.0403		
	C	0.0282	0.0171		
		Gazania 'Daybreak Bronze'			
[1]	T_{min}	4.8	0.8	109	0.90
	T_{opt}	27.6	1.0		
	T_{max}	35.0	–		
	R_{max}	0.0303	0.0011		
		Moss rose 'Margarita Apricot'			
[1]	T_{min}	8.9	0.7	85	0.83
	T_{opt}	23.9	0.9		
	T_{max}	31.7	1.2		
	R_{max}	0.0316	0.0017		
		Pentas 'Graffiti Lavender'[x]			
[1]	T_{min}	9.3	0.5	83	0.94
	T_{opt}	27.8	0.9		
	R_{max}	0.0274	0.0011		
		Petunia 'Dreams Neon Rose'			
[4]	T_{min}	2.8	2.0	100	0.89
	R_{max}	0.3357	0.6607		
	C	0.00952	0.02162		
		Petunia 'Wave Purple'			
[4]	T_{min}	5.5	1.2	77	0.95
	R_{max}	0.0965	0.0437		
	C	0.0268	0.0174		
		Snapdragon 'Montego Orange Bicolor'			
[1]	T_{min}	2.0	1.6	101	0.74
	T_{opt}	25.7	0.9		
	T_{max}	30.3	0		
	R_{max}	0.0428	0.0023		
		Verbena 'Quartz Waterfall Mix'			
[1]	T_{min}	5.1	1.1	92	0.75
	T_{opt}	24.2	0.9		
	T_{max}	31.0	0		
	R_{max}	0.0227	0.0013		

Table 1.2 (cont'd).

Eq.	Parameter	Estimate	Asymptotic 95% CI (±)	No.[z]	r^{2y}
	C	0.0576	0.0174		
		Viola 'Sorbet Plum Velvet'[x]			
[1]	T_{min}	4.1	1.2	109	0.79
	T_{opt}	26.4	1.3		
	R_{max}	0.0831	0.0034		
		Zinnia 'Dreamland Coral'			
[4]	T_{min}	7.8	0.5	96	0.94
	R_{max}	0.0541	0.0094		

[z]Number of observations in data set.

[y]Generated by performing linear regression analysis on the predicted versus observed data.

[x]T_{max} could not be estimated from observed data and was fixed at 35.0 °C so the nonlinear model could be solved.

Table 1.3. The effect of temperature on the number of nodes on the primary flowering shoot at first open flower in 18 species of bedding plants. Plants were grown in controlled environmental growth chambers under a 16-h photoperiod and a daily light integral of 10.4 $mol \cdot m^{-2} \cdot d^{-1}$. Data were pooled between replications. L = linear; Q = quadratic.

	Temperature set point (°C)							
Species	5	7.5	10	15	20	25	30	Trend
African marigold 'Antigua Primrose'	10.8 c[z]	15.6 ab	15.2 b	17.0 ab	18.3 a	17.9 a	17.8 ab	L^{***} Q^{***}
Angelonia 'Serena Purple'	–[y]	–	9.5 b	11.3 b	11.2 b	12.8 b	16.9 a	$L^{***}Q^{*}$
Black-eyed Susan 'Toto Rustic'	12.5 a	14.6 a	15.5 a	15.4 a	14.3 a	12.8 b	13.5 a	$L^{NS}Q^{NS}$
Blue salvia 'Victoria Blue'	–	–	14.3 ab	15.6 a	10.4 c	10.6 c	11.9 bc	$L^{***}Q^{*}$
Browallia 'Bells Marine'	–	–	13.1 c	14.3 bc	15.2 ab	16.1 a	–	$L^{***}Q^{NS}$
Cosmos 'Cosmic Orange'	–	–	7.7 bc	7.4 bc	7.3 bc	8.7 b	14.5 a	L^{***} Q^{***}
Dahlia 'Figaro Mix'	–	9.0 b	8.8 b	8.9 b	12.4 a	13.2 a	–	$L^{***}Q^{*}$
Dianthus 'Super Parfait Raspberry'	12.0 a	11.4 b	11.8 b	12.3 ab	12.2 ab	12.3 ab	13.9 a	$L^{***}Q^{NS}$
French marigold 'Janie Flame'	8.1	7.4	7.6	7.6	7.6	7.8	9.0	NS
Gazania 'Daybreak Bronze'	13.6	13.9	13.9	12.7	12.8	12.7	13.2	NS
Moss rose 'Margarita Apricot'	–	–	–	26.3 b	28.7 ab	30.4 a	27.2 ab	$L^{NS}Q^{**}$
Pentas 'Graffiti Lavender'	–	–	5.6 b	7.0 a	6.9 a	6.5 a	6.4 ab	$L^{NS}Q^{***}$
Petunia 'Dreams Neon Rose'	12.8	12.4	13.5	13.7	13.8	13.8	14.3	NS
Petunia 'Wave Purple'	–	25.6 a	23.0 a	17.2 b	18.1 b	18.5 b	19.8 b	L^{***} Q^{***}
Snapdragon 'Montego Orange'	8.9 b	9.1 b	8.9 b	8.9 b	8.4 b	8.3 b	11.1 a	$L^{***}Q^{NS}$
Verbena 'Quartz Waterfall Mix'	–	12.4 a	10.3 bc	9.6 c	11.3 ab	11.7 ab	11.8 abc	$L^{NS}Q^{**}$
Viola 'Sorbet Plum Velvet'	8.8	8.7	8.3	7.8	8.5	8.4	7.9	NS
Zinnia 'Dreamland Coral'	–	–	6.0 b	6.6 ab	6.4 b	6.5 b	7.3 a	$L^{***}Q^{NS}$

[z]Means within rows followed by the same letter are not significantly different by Tukey's honestly significant difference test at $P \leq 0.05$.

[y]Treatment not included in analysis because ≥75% of plants died.

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

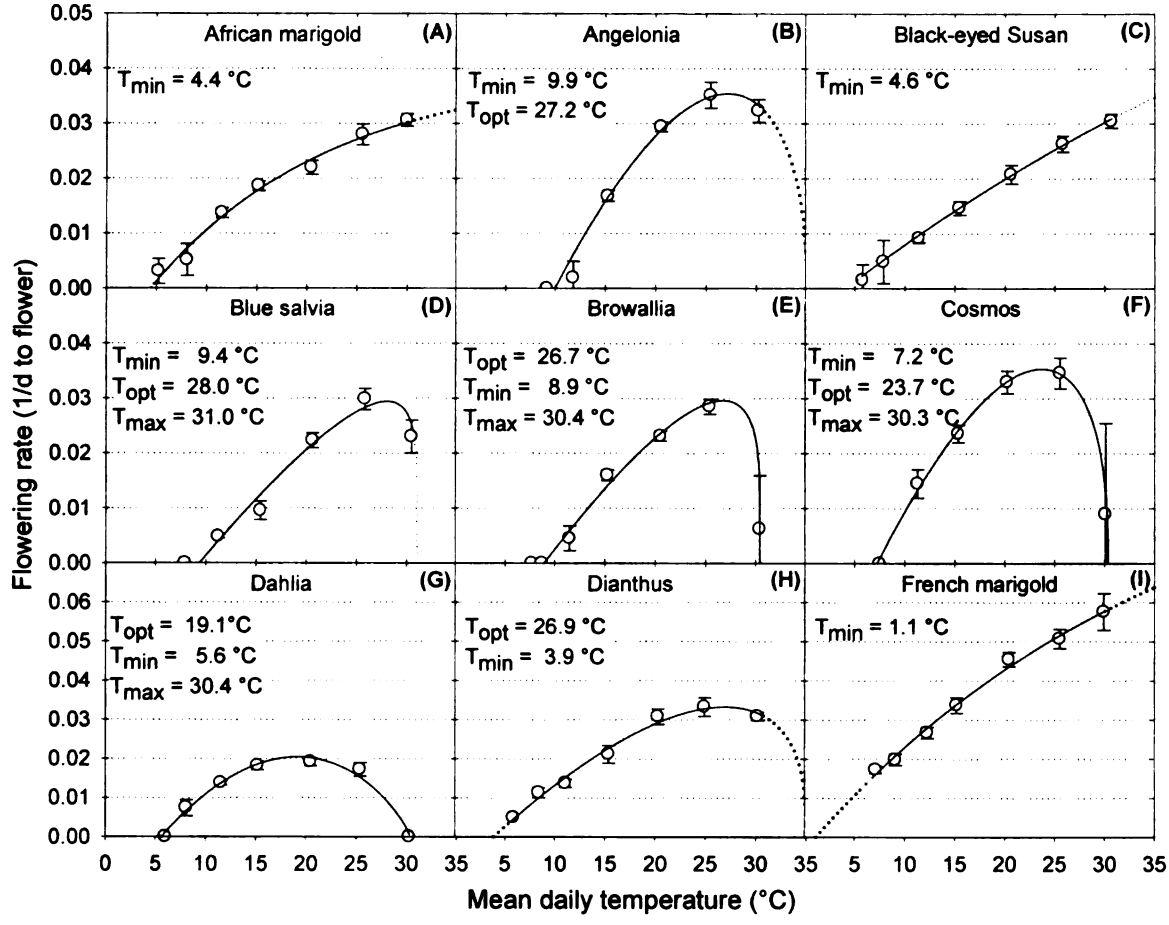

Fig. 1.1. Observed and predicted flowering rates in 9 species of bedding plants as a function of mean daily temperature based on Eq. [1] (panel B, D-H) and Eq. [4] (panel A, C, and I) and parameter estimates from Table 1.2. Circles represent the means of replication 1 and 2. Dashed lines represent predictions outside of the observed data range. Data points represent treatment means and error bars represent 95% confidence intervals. T_{max} in panels B and H could not be estimated from observed data and was fixed at 35.0 °C so Eq. [1] could be solved.

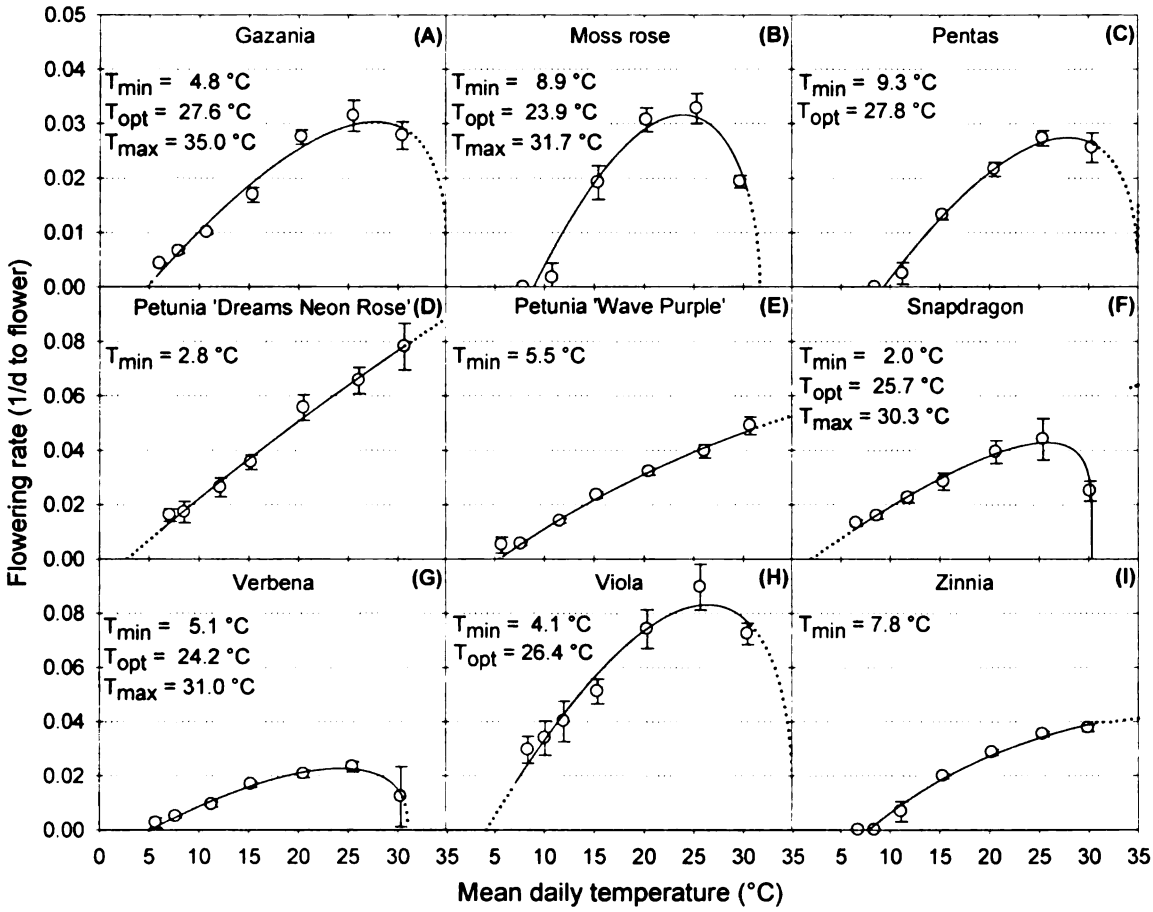

Fig. 1.2. Observed and predicted flowering rates in 9 species of bedding plants as a function of mean daily temperature based on Eq. [1] (panel A-C, F-H) and Eq. [4] (panel D, E, and I) and parameter estimates from Table 1.2. Circles represent the means of replication 1 and 2. Dashed lines represent predictions outside of the observed data range. Data points represent treatment means and error bars represent 95% confidence intervals. T_{max} in panel A, C, and H could not be estimated from observed data and was fixed at 35.0 °C so Eq. [1] could be solved.

Literature Cited

Adams, S.R., S. Pearson, and P. Hadley. 1996. Modeling growth and development of pansy cv. Universal Violet in response to photo-thermal environment: Application for decision support and scheduling. Acta Hort. 417:23–32.

Adams, S.R., S. Pearson, and P. Hadley. 1997. The effects of temperature, photoperiod and light integral on the time to flowering of pansy cv. Universal Violet (*Viola* ×*wittrockiana* Gams.). Ann. Bot. 80:107–112.

Adams, S.R., P. Hadley, and S. Pearson. 1998. The effects of temperature, photoperiod, and photosynthetic photon flux on the time to flowering of *Petunia* 'Express Blush Pink'. J. Amer. Soc. Hort. Sci. 123:577–580.

Armitage, A.M., W.H. Carlson, and J.A. Flore. 1981. The effect of temperature and quantum flux density on the morphology, physiology, and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 106:643–647.

Arnold, C. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Amer. Soc. Hort. Sci. 74:430–445.

Berghage, R.D. 1989. Modeling stem elongation in the poinsettia. Ph.D. Dissertation, Dept. of Horticulture, Michigan State Univ., East Lansing.

Berghage, R.D., R.D. Heins, and J.E. Erwin. 1990. Quantifying leaf unfolding in the poinsettia. Acta Hort. 272:243–247.

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.

Erwin, J.E. and R.D. Heins. 1990. Temperature effects on lily development rate and morphology from the visible bud stage until anthesis. J. Amer. Soc. Hort. Sci. 115:644–646.

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

Faust, J.E. and R.D. Heins. 1994. Modeling inflorescence development of the African violet (*Saintpaulia ionantha* Wendl.). J. Amer. Soc. Hort. Sci. 119:727–734.

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.

Heins, R.D., B. Liu, and E.S. Runkle. 2000. Regulation of crop growth and development based on environmental factors. Acta Hort. 514:13–22.

Hidén, C. and R.U. Larsen. 1994. Predicting flower development in greenhouse grown chrysanthemum. Scientia Hort. 58:123–138.

Jones, H.G. 1992. Plants and microclimate. 2nd ed. Cambridge Univ. Press, New York, NY.

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

Karlsson, M.G. 1992. Leaf unfolding rate in *Begonia ×hiemulis* [sic]. HortScience 27:109–110.

Landsberg, J.J. 1977. Some useful equations for biological studies. Expt. Agr. 13:273–286.

Larsen, R.U. 1988. A prediction model of the development rate of the pot plant *Senecio* × *hybridus* Hyl. a case study. Acta Hort. 230:381–388.

Larsen, R.U. 1989. A prediction model for floral development of *Senecio* × *hybridus* Hyl. 'Molls Stams'. Acta Hort. 248:247–254.

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

Larsen, R.U. and C. Hidén. 1995. Predicting leaf unfolding in flower induced shoots of greenhouse grown chrysanthemum. Scientia Hort. 63:225–239.

Larsen, R.U. and L. Persson. 1999. Modeling flower development in greenhouse chrysanthemum cultivars in relation to temperature and response group. Scientia Hort. 80:73–89.

Liu, B. and R.D. Heins. 2002. Photothermal ratio affects plant quality in 'Freedom' poinsettia. J. Amer. Soc. Hort. Sci. 127:20–26.

Maceina, M.J. and D.L. Pereira. 2007. Recruitment, p. 121–185. In: Guy, C. and M.L. Brown (eds.). Analysis and interpretation of freshwater fisheries data. Amer. Fisheries Soc., Bethesda, MD.

Mattson, N. and J. Erwin. 2003. Temperature affects flower initiation and development rate of *Impatiens*, *Petunia*, and *Viola*. Acta Hort. 624:191–197.

Miller, A.M., M.W. van Iersel, and A.M. Armitage. 2001. Whole-plant carbon dioxide exchange responses of *Angelonia angustifolia* to temperature and irradiance. J. Amer. Soc. Hort. Sci. 126:606–610.

Moccaldi, L.A. and E.S. Runkle. 2007. Modeling the effects of temperature and photosynthetic daily light integral on growth and flowering of *Salvia splendens* and *Tagetes patula*. J. Amer. Soc. Hort. Sci. 132:283–288.

Moseley, P.L. 1997. Heat shock proteins and heat adaptation of the whole organism. J. Appl. Plant Physiol. 83:1413–1417.

Neilson, R.E., M.M. Ludlow, and P.G. Jarvis. 1972. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). II. Response to temperature. J. Appl. Ecol. 9:721–745.

Niu, G., R.D. Heins, A.C. Cameron, and W.H. Carlson. 2000. Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of pansy (*Viola ×wittrockiana*). J. Amer. Soc. Hort. Sci. 125:436–441.

Niu, G., R.D. Heins, A.C. Cameron, and W.H. Carlson. 2001. Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of *Campanula carpatica* 'Blue Clips'. Scientia Hort. 87:93–105.

Niu, G., D.S. Rodriguez, and Y.-T. Wang. 2006. Impact of drought and temperature on growth and leaf gas exchange of six bedding plant species under greenhouse conditions. HortScience 41:1408–1411.

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.

Pietsch, G.M., W.H. Carlson, R.D. Heins, and J.E. Faust. 1995. The effect of day and night temperature and irradiance on development of *Catharanthus roseus* (L.) 'Grape Cooler'. J. Amer. Soc. Hort. Sci. 120:877–881.

Pramuk, L.A. and E.S. Runkle. 2005. Modeling growth and development of celosia and impatiens in response to temperature and photosynthetic daily light integral. J. Amer. Soc. Hort. Sci. 130:813–818.

Reed, K.L., E.R. Hamerly, B.E. Dinger, and P.G. Jarvis. 1976. An analytical model for field measurement of photosynthesis. J. Appl. Ecol. 13:925–942.

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

Semeniuk, P. 1975. Effect of temperature on growth, flowering, and fruiting in 'Blue Troll' browallia. HortScience 10:480–481.

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

Summerfield, R.J., E.H. Roberts, R.H. Ellis, and R.J. Lawn. 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. Expt. Agr. 27:11–31.

van Iersel, M.W. 2003. Short-term temperature change affects the carbon exchange characteristics and growth of four bedding plant species. J. Amer. Soc. Hort. Sci. 128:100–106.

Volk, T. and B. Bugbee. 1991. Modeling light and temperature effects on leaf emergence in wheat and barley. Crop Sci. 31:1218–1224.

Wang, J.Y. 1960. A critique of the heat unit approach to plant response studies. Ecology 41:785–790.

Wang, C.-H., D.-M. Yeh, and C.-S. Sheu. 2008. Heat tolerance and flowering-heat-delay sensitivity in relation to cell membrane thermostability in chrysanthemum. J. Amer. Soc. Hort. Sci. 133:754–759.

Wang, S.-Y., 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.

Warner, R.M. and J.E. Erwin. 2005. Prolonged high temperature exposure and daily light integral impact growth and flowering of five herbaceous ornamental species. J. Amer. Soc. Hort. Sci. 130:319–325.

Warner, R.M. and J.E. Erwin. 2006. Prolonged high-temperature exposure differentially reduces growth and flowering of 12 *Viola* ×*wittrockiana* Gams. cvs. Scientia Hort. 108:295–302.

Yeh, D.M., J.G. Atherton, and J. Craigon. 1999. A thermal time model of post-initiation flower development in the shade plant, cineraria. Ann. Appl. Biol. 134:335–340.

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.

SECTION II

MODELING PLANT GROWTH AND DEVELOPMENT OF PETUNIA IN RESPONSE TO TEMPERATURE AND PHOTOSYNTHETIC DAILY LIGHT INTEGRAL

Modeling Plant Growth and Development of Petunia in Response to Temperature and Photosynthetic Daily Light Integral

Matthew G. Blanchard and Erik S. Runkle[1]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

Paul R. Fisher

Environmental Horticulture Department, University of Florida, Gainesville, FL 32611

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[1]Associate Professor of Horticulture and Extension Specialist and to whom reprint requests should be addressed (Email: runkleer@msu.edu).

Abstract

The effects of mean daily temperature (MDT) and photosynthetic daily light integral (DLI) on flowering during the finish stage of two petunia (*Petunia ×hybrida* Vilm.-Andr.) hybrids were quantified. Petunia 'Easy Wave Coral Reef' and 'Wave Purple' were grown in glass-glazed greenhouses at 14 to 26 °C and under 4 to 19 $mol \cdot m^{-2} \cdot d^{-1}$ with a 16-h photoperiod. The flower development rate was predicted using a model that included a linear MDT function with a base temperature multiplied by an exponential DLI saturation function. The flower development rate increased and time to flower decreased as MDT increased within the temperature range studied. For example, under a mean DLI of 12 $mol \cdot m^{-2} \cdot d^{-1}$, as MDT increased from 14 to 23 °C, time to flower of 'Easy Wave Coral Reef' and 'Wave Purple' decreased from 51 to 22 d and 62 to 30 d, respectively. Flower development rate increased as DLI increased until saturation at 14.1 to 14.4 $mol \cdot m^{-2} \cdot d^{-1}$. Polynomial response surfaces were generated for effects of MDT and DLI on flower bud number, leaf node number, plant height, and shoot length at flowering. The number of flower buds at flowering increased as MDT decreased and DLI increased. For example, at an MDT of 14 °C with 18 $mol \cdot m^{-2} \cdot d^{-1}$, plants had 3.1 to 3.4 times more flower buds than those grown at 23 °C and 4 $mol \cdot m^{-2} \cdot d^{-1}$. Models were validated with an independent data set and the predicted time to flower, flower bud number, and plant height were within 7 d, 20 flowers, and 5 cm, respectively, for 87 to 100% of the observations. The models could be used to predict the influence of MDT and DLI on crop scheduling and quality of these petunia hybrids.

Introduction

Efficient and predictable commercial production of greenhouse crops requires information on how species respond to the environment so that they can be accurately scheduled to finish for predetermined market dates. Scientific studies have been performed on many economically important ornamental greenhouse crops to quantify how light and temperature influence growth and development (Faust and Heins, 1994; Karlsson and Heins, 1986; Pramuk and Runkle, 2005; Steininger and Pasian, 2002). Data from these experiments have been used to generate crop models that predict how changing environmental factors, such as mean daily temperature (MDT) or photosynthetic daily light integral (DLI), affect the rate of plant development. Several analytical approaches have been described to model plant development rate in response to environmental conditions.

Temperature influences many biochemical, metabolic, and physiological processes that occur during crop production, including photosynthesis, respiration, transpiration, and plant development (Jones, 1992). Plant growth is defined as an irreversible increase in weight, height, or volume of a plant cell, tissue, organ, or whole plant, whereas development refers to a series of phenological stages that occur during the life cycle of an organism (Steininger et al., 2002). Although environmental factors interact and plant species exhibit differences in response, under typical horticultural conditions, plant development is primarily controlled by temperature whereas growth is largely influenced by DLI (Jones, 1992).

Plant developmental responses to temperature, such as flowering or leaf unfolding rate, are primarily controlled by the integrated MDT. The time required for the

completion of a developmental event can be converted to a rate by calculating the reciprocal of time (e.g., 1/d). The relationship between MDT and development rate has been described using linear, quadratic, cubic, and exponential models (Landsberg, 1977; Larson, 1990). In a linear model, development rate is related to MDT as:

$$\text{Rate} = b_0 + b_1 \times \text{MDT} \quad [1]$$

where rate (e.g., 1/d) is equal to the intercept (b_0) plus the product of the slope (b_1) and MDT (°C). The parameters of the model are specific to a genotype or a development stage (Summerfield et al., 1991). In this model, the relationship between MDT and development rate is linear between the base and optimum temperature. The base temperature (T_{min}) is the temperature at or below which the rate of progress towards a developmental stage is zero. T_{min} can be estimated as:

$$T_{min} = -b_0/b_1 \quad [2]$$

and can vary considerably among plant species. For example, T_{min} for the rate of flower development in black-eyed Susan [*Rudbeckia fulgida* (Ait.) 'Goldsturm'] was calculated to be −1.3 °C, compared with 12.2 °C in rose mallow (*Hibiscus moscheutos* L. 'Disco Belle Mixed') (Wang et al., 1998; Yuan et al., 1998).

An optimum temperature (T_{opt}) is defined as the temperature at which the rate of progress towards a developmental event is maximal. For example, T_{opt} for flower development rate in pansy (*Viola ×wittrockiana* Gams.) and vinca (*Catharanthus roseus*

L.) was calculated to be 21.7 °C and ≥35 °C, respectively (Adams et al., 1997b; Pietsch et al., 1995). Linear models relating MDT and the rate of development are only valid when $T_{min} \leq MDT \leq T_{opt}$.

Modeling development rate in different phases has been used to quantify temperature responses where data indicate non-linearity across the experimental range of temperatures. A linear equation for temperatures below T_{opt} can be combined with a negative linear function above T_{opt}. The linear function to describe the response above T_{opt} may or may not be symmetrical with the slope at temperatures $<T_{opt}$, or alternatively a constant development rate can be assumed to occur above T_{opt} (Pearson et al., 1993; Roberts and Summerfield, 1987).

Polynomial equations have also been used to describe the influence of MDT on development rate. Although these equations can provide a close empirical fit to data, the parameters tend to have limited biological meaning (Brøndum and Heins, 1993; Landsberg, 1977). In Rieger begonia (*Begonia ×hiemalis* Fotsch) grown under a 16-h photoperiod, a quadratic model predicted a maximum rate of 0.12 leaves·d^{-1} at 21 °C (Karlsson, 1992). A cubic model was developed to describe the relationship between MDT and the rate of leaf unfolding for cyclamen (*Cyclamen persicum* Mill.; Karlsson and Werner, 2001), Chinese hibiscus (*Hibiscus rosa-sinensis* L.), (Karlsson et al., 1991), and corn (*Zea mays* L.;Tollenaar et al., 1979).

Various exponential functions have been developed that incorporate parameters such as T_{min}, T_{opt}, and an upper temperature threshold at which development rate is zero (T_{max}) (Reed et al., 1976; Landsberg, 1977; Hidén and Larsen, 1994; Larsen and Hidén, 1995). For example, an asymmetrical exponential function (Reed et al., 1976;

Landsberg, 1977) has been used to model the influence of temperature on flower development rate in dahlia (*Dahlia pinnata* Cav.; Brøndum and Heins, 1993) and leaf unfolding and leaf expansion rate in African violet (*Saintpaulia ionantha* Wendl.; Faust and Heins, 1993, 1994).

The rate of plant development can also be secondarily influenced by other environmental factors and multiplicative models (Hidén and Larsen, 1994; Larsen and Persson, 1999) have been developed that combine factors such as MDT, photoperiod, and DLI (Larsen, 1990; Moccaldi and Runkle, 2007). In some species, factors such as MDT and DLI can interact to influence development and therefore, models that include more than one environmental parameter are adaptable to a range of conditions. Multiplicative models have been published for several ornamental crops including chrysanthemum [*Chrysanthemum ×grandiflorum* (Ramat.) Kitam.; Karlsson and Heins, 1986; Larsen and Persson, 1999], impatiens (*Impatiens walleriana* Hook.f.; Pramuk and Runkle, 2005), geranium (*Pelargonium ×hortorum* Bailey; White and Warrington, 1988), cineraria (*Pericallis ×hybrida* R. Nordenstam; Larson, 1988, 1989), pansy (Adams et al., 1997b), and red salvia (*Salvia splendens* F. Sello ex Roem & Schult.) (Moccaldi and Runkle, 2007).

The objectives of this study were to quantify and model the influence of MDT and DLI on flowering and plant quality during the finish stage of two petunia hybrids (*Petunia* × *hybrida* Vilm.-Andr. 'Easy Wave Coral Reef' and 'Wave Purple') under long-day conditions. Finish stage describes the production period from the time plugs are transplanted until plants are marketable. Petunia was selected because it is among the top 10 bedding plants produced in the United States, with a reported wholesale value of $120

million in 2008 (U.S. Department of Agriculture, 2009). Petunia flowering responses to temperature, DLI, and photoperiod have been previously described using response surface equations by Adams et al. (1997a, 1998, 1999); for temperature and DLI only using quadratic equations (Kaczperski et al., 1991); and for temperature only using a linear equation by Mattson and Erwin (2003). Calibration of models with data from 'Easy Wave Coral Reef' and 'Wave Purple' was necessary to develop decision-support tools for crop scheduling of these cultivars, because model parameters are generally cultivar-specific.

Materials and Methods

On 7 Dec. 2006 and 4 Apr. 2007, seeds of petunia 'Easy Wave Coral Reef' and on 10 Sept. 2007 and 21 Mar. 2008, seeds of petunia 'Wave Purple' were sown in plug trays [288-cell size (6-ml volume)] by a commercial greenhouse (C. Raker & Sons, Litchfield, MI). After germination, plugs were received at Michigan State University (MSU) and were grown in a controlled environmental growth chamber at a constant temperature set point of 20 °C. A 16-h photoperiod was provided by 215-W cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and 60-W incandescent lamps (INC; Philips), at a CWF:INC (by W) of 3.6, and at an intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Plants were irrigated as necessary with well water acidified with H_2SO_4 to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$ and containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively. The water was supplemented with a water-soluble fertilizer providing (in $mg \cdot L^{-1}$) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, Mn,

and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Greenhouse Environment

After 27 d and 34 d from seed sow, 6- to 8-leaf 'Easy Wave Coral Reef' and 'Wave Purple' seedlings, respectively, were transplanted into 10-cm round plastic containers (480-ml volume) filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). At transplant, plugs were thinned to one seedling per cell. Plants were randomly assigned to treatments and grown in glass-glazed greenhouses at constant air temperature set points of 14, 17, 20, 23, or 26 °C and under a 16-h photoperiod that consisted of natural photoperiods (43 °N lat.) with day-extension lighting from 0600 to 2200 HR provided by high-pressure sodium (HPS) lamps. 'Easy Wave Coral Reef' was not grown at 26 °C. At each temperature, plants were grown under two DLI treatments provided by ambient light and a combination of shade curtains (OLS 30, OLS 50; Ludvig Svensson Inc., Charlotte, NC) and different intensities (25 to 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of supplemental lighting from HPS lamps that were positioned above the shade curtains. Ten plants of each species were randomly assigned to each temperature and DLI combination. The HPS lamps were operated by an environmental computer (Priva Intégro 724; Priva, Vineland Station, Ontario) and were turned on when the outside light intensity was <290 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and turned off at >580 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Whitewash was applied to the greenhouse glazing during late Mar. each year, and removed in mid Oct. The experiment was performed twice under mean DLIs from transplant to flowering that ranged from 3.9 to 18.7 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 2.1).

Temperature in each greenhouse compartment was controlled by an environmental computer with steam heating, passive and active ventilation, and fan-and-pad evaporative cooling as needed. Air temperature was independently measured in each greenhouse by an aspirated, shielded thermocouple (0.13-mm type E; Omega Engineering, Stamford, CT) positioned 1.5 m above the floor (at plant level). At 30 cm above the bench, the photosynthetic photon flux (*PPF*) was measured by a line quantum sensor containing 10 photodiodes (Apogee Instruments, Inc., Logan, UT) under six DLI and temperature combinations. Environmental measurements were collected every 10 s and hourly means were recorded by a data logger (CR10; Campbell Scientific, Logan, UT). A vapor-pressure deficit of 1.2 kPa was maintained during the night by the injection of steam into the air. Horizontal airflow fans positioned 1.4 m above the growing surface operated if the ridge vent was <90% of the maximum opening and provided air movement at $\approx$0.1 $m \cdot s^{-1}$ at plant height [as measured with an air velocity transducer (8475; TSI, Inc., St. Paul, MN)]. Plants were irrigated with reverse osmosis water supplemented with a water-soluble fertilizer providing (in $mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc.).

Data Collection and Analysis

The date of first open flower per plant was recorded and time to first open flower was calculated for each plant. Plants were considered flowering when one flower had a fully open corolla. When each plant flowered, plant height and the total number of open flowers and closed flower buds were recorded. In 'Easy Wave Coral Reef', leaf number

on the primary shoot below the first open flower was also recorded. In 'Wave Purple', the first open flower occurred on either a lateral stem or on the primary shoot and therefore, leaf number below the flower could not be modeled. Plant height was measured from the soil surface to the tip of the uppermost leaf on the primary stem. In 'Wave Purple', the length of the longest lateral stem was measured at flowering by extending the stem and recording the distance from the axil to the shoot tip.

Flowering data were used to develop mathematical models to predict flower development rate, flower bud number, height, lateral stem length, and leaf number under different MDT and DLI conditions. Models for 'Easy Wave Coral Reef' and 'Wave Purple' were generated using 159 and 200 observations (individual plants), respectively. Data were analyzed using the calculated MDT and DLI for each plant from transplant to the date of flowering. DLI values for treatments that did not have a line quantum sensor were determined by calculating the mean irradiance among sensors that were positioned in other temperature treatments and under similar light conditions. Flowering time data were converted to developmental rates by calculating the reciprocal of days to flowering (1/d to flower). A multiplicative model was developed to describe the relationship between the rate of progress to flowering and MDT and DLI:

$$1/\text{d to flower} = f_{\text{MDT}} \times f_{\text{DLI}} \qquad [3]$$

where f_{MDT} and f_{DLI} are temperature and light functions, respectively. Models of this type have been previously used to describe the rate of flower development in chrysanthemum (Hidén and Larsen, 1994; Larsen and Persson, 1999) and cineraria

(Larsen, 1989). The response of flower development rate to MDT is described with a temperature function and can be quantified by algebraically rewriting equation [1] to include the base temperature:

$$1/\text{d to flower} = \begin{cases} 0 & \ldots \text{if MDT} \leq T_{min} \\ -1 \times T_{min} \times b_1 + b_1 \times \text{MDT} & \ldots \text{if } T_{min} < \text{MDT} \leq T_{opt} \end{cases} \quad [4]$$

where T_{min} and MDT are measured in °C and b_1 is a species-specific temperature constant. We used a linear function to quantify the MDT response because plots of the actual data showed that T_{opt} was not observed for both petunia hybrids. The influence of DLI on flower development rate was described with a light function (Larsen, 1990):

$$\text{DLI factor} = 1 - \text{EXP}(-e \times \text{DLI}) \quad [5]$$

where the light factor ranges from 0 to 1. The e value is a species-specific light constant and determines the skew of the curve and DLI is the mean ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) from transplant to flowering. This function indicates that the rate of progress towards flowering increases as DLI increases, until some saturating value.

The final model to predict the rate of development towards flowering in petunia consisted of equations [4] and [5] multiplied together:

$$1/\text{d to flower} = \begin{cases} 0 & \ldots \text{if MDT} \leq T_{min} \\ (-1 \times T_{min} \times b_1 + b_1 \times \text{MDT}) & \ldots \text{if } T_{min} < \text{MDT} \leq T_{opt} \\ \times (1 - \text{EXP}(-e \times \text{DLI})) & \end{cases} \quad [6]$$

Estimates for model coefficients were determined with the nonlinear regression procedure (NLIN) of SAS (version 9.1; SAS Institute, Cary, NC). T_{min} for 'Easy Wave Coral Reef' was estimated by using the NLIN procedure of SAS. A T_{min} of 5.5 °C was used for 'Wave Purple', which was obtained from unpublished experiments performed by the authors in environmental growth chambers at constant air temperature set points of 5 to 30 °C and under a DLI of 10 $mol \cdot m^{-2} \cdot d^{-1}$ and a constant 16-h photoperiod.

Data for flower bud and leaf number, plant height, and lateral stem length at first flowering were analyzed using the regression procedure (REG) of SAS to determine the influence of MDT and DLI. The flower bud and leaf number, plant height, and lateral stem length response surfaces equations are in the form:

$$y = y_0 + a\text{MDT} + b\text{MDT}^2 + c\text{DLI} + d\text{DLI}^2 + g\text{MDT} \times \text{DLI} \quad [7]$$

where y_0 is the y-axis intercept and a, b, c, d, and g are species-specific constants. Previous published studies that quantified the influence of MDT and DLI on flowering used a similar polynomial equation (Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005). The terms of the equation were only included if they were significant at $P \leq 0.05$.

Model Validation

On 15 Jan. 2009, seeds of each petunia hybrid were sown in 288-cell plug trays by a commercial greenhouse. After germination, trays were received at MSU and grown in an environmental growth chamber. Environmental conditions inside the chamber,

plant culture, and transplant schedules were the same as described for the previous experiments. Seedlings were transplanted into 10-cm round pots and 15 plants of each species were grown in glass-glazed greenhouses at constant temperature set points of 17, 20, or 23 °C and under a 16-h photoperiod and a mean DLI of 14 to 19 $mol \cdot m^{-2} \cdot d^{-1}$. In each greenhouse, air temperature and *PPF* were measured on each bench and data was recorded by a data logger as previously described. Photoperiod control, plant culture, and data collection were the same a previously described. Data collected from the validation study were used to test the accuracy and precision of model predictions.

Results

In both petunia hybrids, the rate of flower development increased and time to flower decreased as MDT increased. For example, under a mean DLI of 12 $mol \cdot m^{-2} \cdot d^{-1}$, as MDT increased from 14 to 23 °C, time to flower of 'Easy Wave Coral Reef' and 'Wave Purple' decreased from 51 to 22 d and 62 to 30 d, respectively (Figs. 2.1A and 2.2A). Base temperature (T_{min}) for the rate of flower development for 'Easy Wave Coral Reef' and 'Wave Purple' were estimated to be 7.3 °C and 5.5 °C, respectively, although the 95% asymptotic confidence intervals for T_{min} overlapped between cultivars (Table 2.2). The upper temperature at which non-linearity occurred, T_{opt}, was not determined because the rate of flower development continued to increase within the experimental range of temperature.

Time to flower decreased as DLI increased in both petunia hybrids. For example, at an MDT of 20 °C, time to flower of 'Easy Wave Coral Reef' and 'Wave Purple' decreased by 10 and 12 d, respectively, when DLI increased from 4 to 14 $mol \cdot m^{-2} \cdot d^{-1}$.

The influence of DLI, which was modeled as a multiplier of the temperature response, approached saturation (within 99% of maximum development rate) in 'Easy Wave Coral Reef' and 'Wave Purple' at 14.4 and 14.1 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. Values for *e* (Table 2.2) were not statistically different between cultivars, and estimates of Eq. [5] did not differ between cultivars by more than 0.01 between 3.9 and 18.7 $mol \cdot m^{-2} \cdot d^{-1}$. The flowering rate models predicted time to flower within 7 d for 96% and 100% of the 'Easy Wave Coral Reef' and 'Wave Purple' validation data sets, respectively (r^2 = 0.73 or 0.93) (Fig. 2.3). The slope and intercept for the relationship between predicted and observed 'Easy Wave Coral Reef' flower development rate had a 95% confidence interval of 1.2 ± 0.3 and −0.007 ± 0.012, respectively (data not presented). The slope and intercept for the relationship between predicted and observed 'Wave Purple' flower development rate had a 95% confidence interval of 1.4 ± 0.2 and −0.009 ± 0.003, respectively (data not presented).

Flower number (including open and closed flowers) increased as MDT decreased and DLI increased (Table 2.3 and Figs. 2.1B and 2.2B). For example, at 14 °C and 18 $mol \cdot m^{-2} \cdot d^{-1}$, plants had 3.1 to 3.4 times more flowers than those grown at 23 °C and 4 $mol \cdot m^{-2} \cdot d^{-1}$. The response surfaces predicted flower number for both hybrids within 20 flowers for 87% of the observations in the validation data sets (data not presented).

Plant height at flowering of both petunia hybrids increased as DLI decreased. In 'Easy Wave Coral Reef' and 'Wave Purple', MDT had a quadratic and linear influence, respectively, on height at flower (Figs. 2.1C and 2.2C). There was also an interaction between temperature and DLI on plant height; DLI had a greater effect at a high MDT (>20 °C) compared to a lower MDT (Table 2.3). Under the environmental conditions

tested in this study, plants of 'Easy Wave Coral Reef' were tallest (18.2 cm) when grown at 21.5 °C and 3.9 $mol \cdot m^{-2} \cdot d^{-1}$, whereas 'Wave Purple' were tallest (11.0 cm) when grown at 26 °C and 4.3 $mol \cdot m^{-2} \cdot d^{-1}$. Crop models for both hybrids predicted plant height within 5 cm for all of the observations in the validation data sets (data not presented).

The number of leaves that developed on the primary shoot before flowering in 'Easy Wave Coral Reef' decreased from a mean of 12 at 14 °C and 12.6 $mol \cdot m^{-2} \cdot d^{-1}$ to a mean of 7 at 19.2 °C and 4 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 2.1D). However, leaf number was highly variable and the model had a low coefficient of determination ($r^2 = 0.17$) (Table 2.3). The length of the longest lateral stem in 'Wave Purple' was primary influenced by DLI and not by MDT. As the DLI increased from 4 to 18 $mol \cdot m^{-2} \cdot d^{-1}$, lateral stem length decreased by 16.7 cm (Fig. 2.2D). The model predicted lateral stem length within 5 and 10 cm for 67 and 93% of the observations in the validation data set, respectively (data not presented).

Discussion

In both petunia hybrids, a simple linear relationship was adequate to describe the effect of MDT on development rate, indicating the range of temperature conditions (14.2 to 26.0 °C was between T_{min} and T_{opt}. Estimates of base temperature (T_{min}) for 'Easy Wave Coral Reef' and 'Wave Purple' of 7.3 °C and 5.5 °C, respectively, did not statistically differ in terms of 95% asymptotic confidence intervals (Table 2.2). These estimates of T_{min} were also similar to published T_{min} values under 22.3 $mol \cdot m^{-2} \cdot d^{-1}$ for petunia 'Avalanche Pink', 'Dreams Rose', and 'Wave Purple' of 4.5, 4.2, and 5.9 °C,

respectively (Mattson and Erwin, 2003), and petunia 'Sylvana Malve' of 5.7 °C (Adams et al., 1997a). Particularly considering that T_{min} was well outside the experimental range in this and other studies, results from different researchers are in close agreement and average 5.5 ± 1.1 °C (mean ± SD).

Adams et al. (1997a, 1998) reported that under long days, petunia 'Express Blush Pink', 'Sylvana Malve', and 'Sylvana White' had a predicted T_{opt} of 25.4, 26.0, and 25.2 °C, respectively. Similarly, T_{opt} in petunia 'Snow Cloud' grown under 13.5 $mol \cdot m^{-2} \cdot d^{-1}$ was predicted to be 25.0 °C (Kaczperski et al., 1991). Our model should not be extrapolated beyond the experimental range in temperatures (14 to 26 °C), particularly given that previous research suggests non-linearity in temperature response in petunia above 25 °C.

Adams et al. (1998) developed a model for petunia in which DLI had a positive linear effect on the rate of progress towards flowering (DLI range not reported). However, we observed that at each experimental temperature, development rate increased with increasing DLI in a diminishing returns relationship. Therefore, an exponential DLI function was used in our model based on that reported by Larsen and Persson (1999) for chrysanthemum, but with genotype-specific constants that showed saturation above 14 $mol \cdot m^{-2} \cdot d^{-1}$. Faust et al. (2005) reported that petunia 'Apple Blossom' flowered a mean of 6 d earlier under a DLI of $\geq$19 $mol \cdot m^{-2} \cdot d^{-1}$ versus 12 $mol \cdot m^{-2} \cdot d^{-1}$. In chrysanthemum, the estimated saturation DLI for the rate of flowering was 9.8 $mol \cdot m^{-2} \cdot d^{-1}$ (Hidén and Larsen, 1994), whereas geranium had a higher estimated saturation DLI of 17 $mol \cdot m^{-2} \cdot d^{-1}$ (White and Warrington, 1988). Adams et al. (1999) hypothesized that petunia flower development rate decreased at a low DLI because of an

increase in the duration of the photoperiod-insensitive juvenile phase and photoperiod-sensitive flower induction phase.

An advantage of using an exponential function to quantify the relationship between DLI and flower development rate is that above the saturation DLI, the equation predicts that rate does not increase with increasing DLI. Therefore, although the model was developed with data for plants grown under 4 to 19 $mol \cdot m^{-2} \cdot d^{-1}$, flowering predications could theoretically be made for plants grown under 25 or 30 $mol \cdot m^{-2} \cdot d^{-1}$ of light because petunia had an estimated saturation DLI of ≈ 14 $mol \cdot m^{-2} \cdot d^{-1}$. Polynomial models generated for other crops could inaccurately predict flowering if the crop is grown outside of the DLI range under which the model was produced. For example, a polynomial model for celosia (*Celosia argentea* L. var. *plumosa* Voss) grown under 8 to 26 $mol \cdot m^{-2} \cdot d^{-1}$ predicted that at 20 °C, as DLI increased from 10 to 25 $mol \cdot m^{-2} \cdot d^{-1}$ flowering time decreased by 3 d, and as DLI increased from 25 to 35 $mol \cdot m^{-2} \cdot d^{-1}$ flowering time increased by 9 d (Pramuk and Runkle, 2005).

Albert et al. (2009) determined that the light compensation and saturation *PPF* for photosynthesis in petunia 'Mitchell' was 28 and 590 μ $mol \cdot m^{-2} \cdot s^{-1}$, respectively, in plants grown at 22 °C and under a constant irradiance of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 14 $h \cdot d^{-1}$. These results reinforce that supplemental lighting during petunia crop production is most beneficial when the ambient DLI is low. For example, in 'Wave Purple' grown at an MDT of 20 °C, adding 4 $mol \cdot m^{-2} \cdot d^{-1}$ from supplemental lighting when the DLI from natural sunlight is 4 or 8 $mol \cdot m^{-2} \cdot d^{-1}$ is predicted to accelerate flowering by 10 and 2 d, respectively. Our flowering time models also indicate that DLI promoted petunia flower rate more at lower than higher MDT. For example, as DLI increased from 4 to 14

$mol \cdot m^{-2} \cdot d^{-1}$, predicted time to flower of 'Wave Purple' grown at 14 °C and 26 °C decreased by 22 d and 9 d, respectively. This response is in agreement with Kaczperski et al. (1991), who reported that petunia 'Snow Cloud' grown at 14 °C or 26 °C flowered 14 or 4 d earlier, respectively, as DLI increased from 6.5 to 13 $mol \cdot m^{-2} \cdot d^{-1}$.

Our flowering models assumed that T_{min} was not affected by DLI, but crop models developed for other bedding plants suggest that in some species, T_{min} could decrease with increasing DLI. For example, a polynomial flower rate model generated for impatiens calculated a T_{min} of 7.5 and 4.3 °C under 5 and 15 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Pramuk and Runkle, 2005). However, in French marigold (*Tagetes patula* L.) and red salvia, DLI had little or no effect on T_{min} (Moccaldi and Runkle, 2007). T_{min} for some species may be lower under a higher DLI because a higher DLI may increase plant temperature.

The flower development model could be used to predict time to flowering using a thermal time approach. Thermal time, calculated as $1/b_1$ from Eq. [6], describes the accumulated temperature that is required to reach a certain developmental event, with units of thermal time of degree-hour (°C·h) or degree-day (°C·d) (Pasian and Lieth, 1994; Roberts and Summerfield, 1987; Steininger et al., 2002; Wang et al., 1998). Commercial crop growers can use thermal time to predict the occurrence of a developmental event (e.g., first flowering) by subtracting T_{min} from the MDT and accumulating the amount of time, in units of °C·h or °C·d (Roberts and Summerfield, 1987; Steininger et al., 2002). For example, a model developed for miniature rose (*Rosa* L. 'Red Sunblaze') predicted the development phase from lateral bud break to open flower had a T_{min} of 8.1 °C and required 589 °C·d (Steininger et al., 2002). Using parameter estimates from Table 2.2,

thermal time to flowering would be 338 °C·d for 'Easy Wave Coral Reef' and 513 °C·d for Wave Purple. In our case, the model could be used with a one-day time step where T_{min} is subtracted from the MDT, and the (°C·d) is multiplied by the DLI factor (Eq. [5], between 0 and 1. For example, at 4, 11, and 18 $mol \cdot m^{-2} \cdot d^{-1}$, the DLI factor averaged across both cultivars would be 0.73, 0.97, and 1.00, respectively.

Photoperiod was not included as an experimental factor in our crop models partly because in many commercial greenhouses during the spring finishing phase, bedding plants are grown under an inductive photoperiod to reduce production time. Petunia hybrids have been classified as quantitative or qualitative long-day plants (Erwin, 2007). For example, Adams et al. (1998) reported that the rate of flower development in petunia 'Express Blush Pink' increased linearly as photoperiod increased from 8 h to 14.5 h, and further increases in photoperiod did not hasten flowering. Therefore, in this study, plants were grown under a 16-h photoperiod during the plug and finish stages to accelerate flowering and to make these models applicable for commercial production. Our models would not be valid for petunia grown under a noninductive photoperiod, but the approach of Adams et al. (1998) could be incorporated into an expanded version of the model.

In both hybrids studied, flower number at first flowering decreased as the MDT increased. For example, in 'Easy Wave Coral Reef' grown under a DLI of 4 to 18 $mol \cdot m^{-2} \cdot d^{-1}$, as MDT increased from 14 to 23 °C, the predicted flower bud number decreased by 49 to 62%. Our results are in agreement with Mattson and Erwin (2003) who reported that mean flower and lateral stem number in petunia 'Dreams Rose' decreased by 11 and 4, respectively, as MDT increased from 12 to 24 °C. This information indicates that there is a trade-off between a short production duration and

high plant quality. At a low MDT, the rate of flower development is slow, but plants have more time to harvest light and accumulate carbon before flowering. For example, in impatiens grown under 15 $mol \cdot m^{-2} \cdot d^{-1}$, as MDT decreased from 26 to 14 °C, time to flower, flower bud number, and dry weight increased by 15 d, 141%, and 52%, respectively (Pramuk and Runkle, 2005).

Our models illustrate that if a petunia crop is grown at a high MDT to accelerate flowering, plant quality can be improved by increasing the DLI. For example, in 'Easy Wave Coral Reef' grown at 23 °C, as DLI increased from 4 to 18 $mol \cdot m^{-2} \cdot d^{-1}$, flower bud number increased by 72% and plant height decreased by 68%. Lieth et al. (1991) reported that dry weight accumulation in petunia 'Snow Cloud' grown at an MDT of 23 °C increased by a mean of 25 $g \cdot m^{-2} \cdot d^{-1}$ as DLI increased from 5 to 25 $mol \cdot m^{-2} \cdot d^{-1}$. The models in the present study predicted that flower bud number in 'Easy Wave Coral Reef' and 'Wave Purple' would be greatest under a DLI of >18.7 and 14.7 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. These results demonstrate that in some crops, the saturation DLI for the greatest crop quality can be higher than the DLI that elicits the fastest flower development rate.

Leaf number below the first flower can be a useful morphological indication of timing of flower induction. Adams et al. (1999) reported that the duration of the juvenile phase in petunia increased at both low and high MDTs and was shortest at an optimum MDT of 21.3 °C (leaf number not reported). In our study, the number of leaves that developed on the primary shoot and below the first flower in 'Easy Wave Coral Reef' decreased by a mean of 3 as MDT increased from 14 to 19.2 °C and then increased by a mean of 2 as MDT increased to 23 °C. In comparison, Mattson and Erwin (2003) who

reported that under 22.3 $mol \cdot m^{-2} \cdot d^{-1}$, leaf number below the first open flower in petunia 'Avalanche', 'Dreams Rose', and 'Wave Purple' decreased by a mean of 6 to 8 as temperature increased from 12 to 24 °C, suggesting a higher optimum MDT.

Although 'Easy Wave Coral Reef' and 'Wave Purple' had similar development rates and growth responses to temperature and DLI, the models generated for one hybrid did not accurately predict flower development rate, flower number, or plant height for the other hybrid. The different models between hybrids could be caused by genetic differences and results from breeding selection criteria such as growth form, production time, and heat tolerance. For example, at an MDT of 14 to 23 °C and under a DLI of 4 to 18 $mol \cdot m^{-2} \cdot d^{-1}$, 'Easy Wave Coral Reef' flowered 7 to 12 d earlier, but had <28 fewer flowers buds than 'Wave Purple'. It is unknown whether the crop models developed for these two petunia hybrids could be used with other hybrids within the same Easy Wave or Wave petunia series. There is estimated to be over 360 petunia hybrids available commercially (Kelly, et al., 2007) and future research could determine similarities in flowering responses among other hybrids. Given the similarity in T_{min} for petunia between various studies and between estimates for the DLI factor (e) in the two cultivars evaluated here, the main cultivar-specific parameter for flower development rate would focus on estimating the slope (b_1). The slope could be estimated by growing plants at a single MDT, allowing for rapid model calibration to new cultivars.

Table 2.1. Mean daily air temperature (MDT) at the indicated set points and mean photosynthetic daily light integral (DLI) above benches, from transplant to flowering of each cultivar, in glass-glazed greenhouse compartments during experiments.

	MDT (°C)					DLI ($mol \cdot m^{-2} \cdot d^{-1}$)[z]	
Replication	14	17	20	23	26	Low	High
				'Easy Wave Coral Reef'			
1	14.2	17.0	19.9	22.7	–[y]	3.9	10.4
2	17.1	18.7	20.6	23.0	–	6.1	18.7
				'Wave Purple'			
1	14.7	17.2	20.3	22.9	25.9	4.3	10.5
2	16.3	18.0	20.4	22.6	26.0	5.9	16.4

[z]Light from natural photoperiods and supplemental light from high-pressure sodium lamps that were turned on when the outside photosynthetic photon flux was <290 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and turned off when >580 $\mu mol \cdot m^{-2} \cdot s^{-1}$.
[y]Temperature treatment not included.

Table 2.2. Parameters of nonlinear model relating rate of flowering of petunia 'Easy Wave Coral Reef' and 'Wave Purple' to mean daily air temperature [MDT (°C)] and daily light integral [DLI ($mol \cdot m^{-2} \cdot d^{-1}$)]. Models (Eq. [6]) are in the form of: 1/d to flower = $(-1 \times T_{min} \times b_1 + b_1 \times MDT) \times (1 - \exp(-e \times DLI))$. Coefficients for each petunia model were used to generate Figs. 2.1A and 2.2A. ACI = Asymptotic 95% confidence interval.

Parameter	Estimate	Lower ACI	Upper ACI	N[z]
		'Easy Wave Coral Reef'		
T_{min}	7.3 °C	5.9 °C	8.7 °C	159
b_1	2.96 E–03	2.62 E–03	3.31 E–03	
e	3.20 E–01	2.74 E–01	3.67 E–01	
		'Wave Purple'		
T_{min}	5.5 °C[y]	4.3 °C	6.6 °C	200
b_1	1.95 E–03	1.91 E–03	1.98 E–03	
e	3.28 E–01	3.04 E–01	3.53 E–01	

[z]Number of observations in data set.
[y]Estimated from unpublished data that included 77 observations.

Table 2.3. Parameters of stepwise regression analysis relating flower number, plant height, leaf number increase or lateral stem length for petunia 'Easy Wave Coral Reef' and 'Wave Purple' to mean daily air temperature [MDT (°C)] and daily light integral [DLI ($mol \cdot m^{-2} \cdot d^{-1}$)]. All models are in the form of: $y = y_0 + aMDT + bMDT^2 + cDLI + dDLI^2 + gMDT \times DLI$. Models for 'Easy Wave Coral Reef' and 'Wave Purple' were generated using 159 and 200 observations, respectively. Coefficients for each petunia model were used to generate Figs. 2.1B-D and 2.2B-D.

	'Easy Wave Coral Reef'			'Wave Purple'		
Regression parameter	Flower number	Height (cm)	Leaf number	Flower number	Height (cm)	Lateral stem length (cm)
y_0	257.3	−79.5	43.2	21.1	2.98	56.2
	(49.1)[z]	(16.7)	(8.88)	(6.93)	(2.12)	(1.57)
a	−20.6	9.32	−4.00	–[x]	3.76 E−01	–
	(5.26)	(1.79)	(9.36 E−01)		(1.12 E−01)	
b	4.44 E−01	−2.09 E−01	1.04 E−01	−5.38 E−02	–	–
	(1.39 E−01)	(4.78 E−02)	(2.46 E−02)	(6.88 E−03)		
c	1.18	–	6.55 E−01	9.02	–	−1.19
	(1.90 E−01)		(2.03 E−01)	(1.35)		(1.5 E−01)
d	–	4.13 E−02	−2.60 E−02	−3.08 E−01	–	–
		(1.42 E−02)	(8.69 E−03)	(6.33 E−02)		
g	–	−7.66 E−02	–	–	−1.62 E−02	–
		(1.68 E−02)			(3.73 E−03)	
r^2	0.48***	0.47***	0.17***	0.52***	0.10***	0.24***

[z]Standard errors are shown in parentheses.

[x]Parameter not significant at $P > 0.05$

***Parameter significant at $P \leq 0.001$.

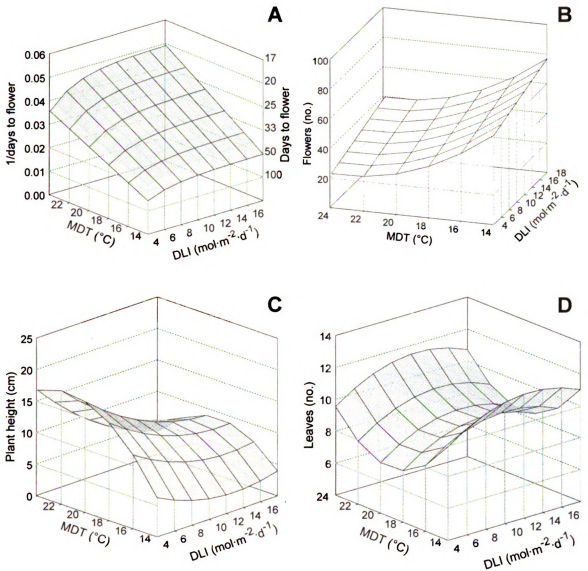

Fig. 2.1. The influence of mean daily temperature (MDT) and daily light integral (DLI) on petunia 'Easy Wave Coral Reef' predicted flowering rate (1/d to flowering) and time to flower (**A**), flower bud number (**B**), plant height (**C**), and leaf number increase at flowering (**D**). The response surfaces were generated using Eqs. [6] and [7] and coefficients in Tables 2.2 and 2.3. Each model was generated using 159 observations.

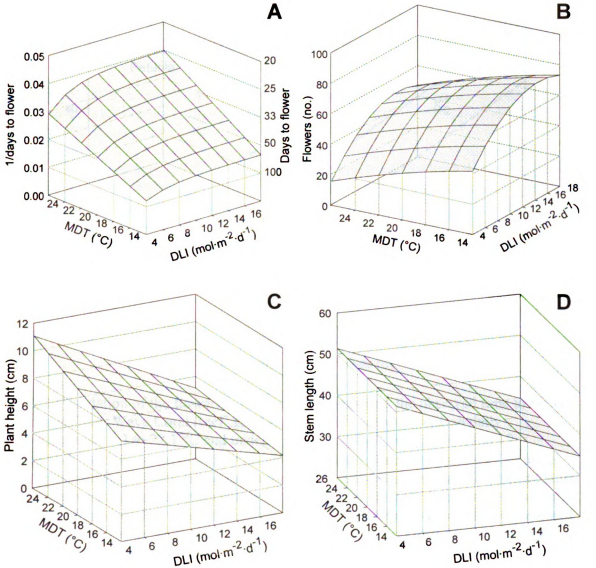

Fig. 2.2. The influence of mean daily temperature (MDT) and daily light integral (DLI) on petunia 'Wave Purple' predicted flowering rate (1/d to flowering) and time to flower (**A**), flower bud number (**B**), plant height (**C**), and lateral stem length at flowering (**D**). The response surfaces were generated using Eqs. [6] and [7] and coefficients in Tables 2.2 and 2.3. The models were generated using 200 observations.

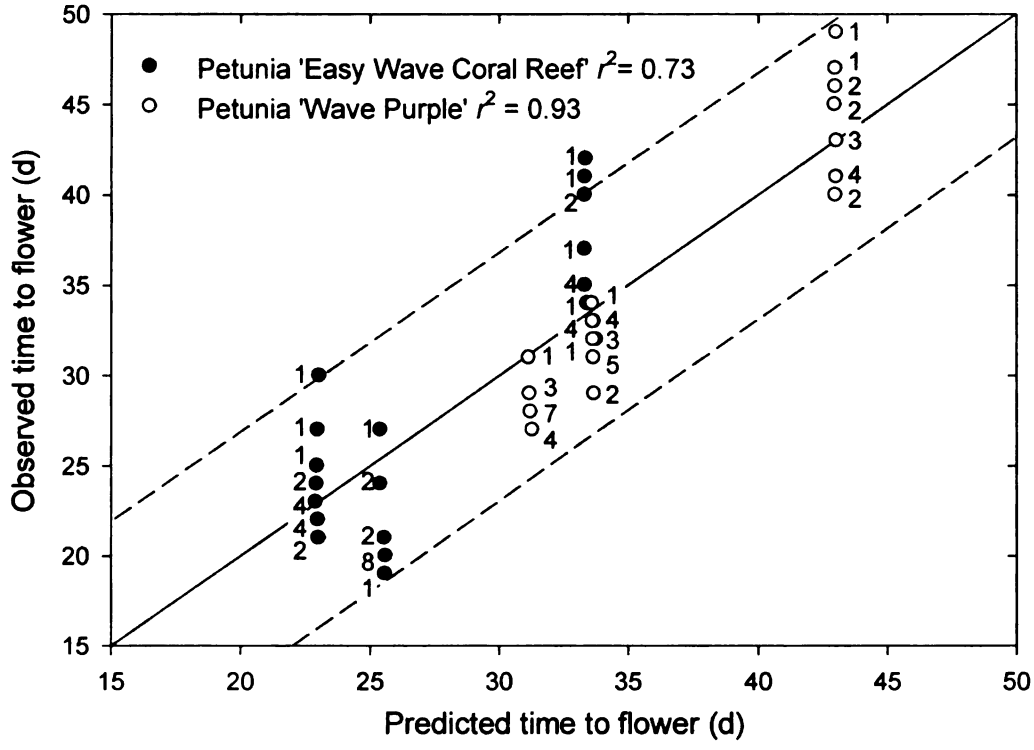

Fig. 2.3. Validation of the flowering rate models, comparing the observed time to flower of petunia 'Easy Wave Coral Reef' and 'Wave Purple' grown at a mean daily temperature of 17.3 to 22.1 °C and under a mean daily light integral of 14 to 19 $mol \cdot m^{-2} \cdot d^{-1}$ with those predicted by Eq. [6]. The dashed lines represent the 7-d lower and upper boundary. Forty-five observations for each hybrid were used for the validation study, where each symbol represents an individual plant. Numbers represent the quantity of observations at each symbol. Coefficients for the flowering rate models are presented in Table 2.2. r^2 values were generated by performing linear regression analysis on the predicted versus observed data.

Literature Cited

Adams, S.R., S. Pearson, and P. Hadley. 1997a. The effects of temperature and photoperiod on the flowering and morphology of trailing petunias. Acta Hort. 435:65–75.

Adams, S.R., S. Pearson, and P. Hadley. 1997b. The effects of temperature, photoperiod and light integral on the time to flowering of pansy cv. Universal Violet (*Viola* × *wittrockiana* Gams.). Ann. Bot. 80:107–112.

Adams, S.R., P. Hadley, and S. Pearson. 1998. The effects of temperature, photoperiod, and photosynthetic photon flux on the time to flowering of *Petunia* 'Express Blush Pink'. J. Amer. Soc. Hort. Sci. 123:577–580.

Adams, S.R., S. Pearson, P. Hadley, and W.M. Patefield. 1999. The effects of temperature and light integral on the phases of photoperiod sensitivity in *Petunia* × *hybrida*. Ann. Bot. 83:263–269.

Albert, N.W., D.H. Lewis, H. Zhang, L.J. Irving, P.E. Jameson, and K.M. Davies. 2009. Light-induced vegetative anthocyanin pigmentation in *Petunia*. 60:2191–2202.

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.

Erwin, J. 2007. Factors affecting flowering in ornamental plants, p. 7–48. In: N.O. Anderson (ed.). Flower breeding and genetics. Springer, The Netherlands.

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

Faust, J.E. and R.D. Heins. 1994. Modeling inflorescence development of the African violet (*Saintpaulia ionantha* Wendl.). J. Amer. Soc. Hort. Sci. 119:727–734.

Faust, J.E., V. Holcombe, N.C. Rajapakse, and D.R. Layne. 2005. The effect of daily light integral on bedding plant growth and flowering. HortScience 40:645–649.

Hidén, C. and R.U. Larsen. 1994. Predicting flower development in greenhouse grown chrysanthemum. Scientia Hort. 58:123–138.

Jones, H.G. 1992. Plants and microclimate. 2nd ed. Cambridge Univ. Press, New York, NY.

Kaczperski, M.P., W.H. Carlson, and M.G. Karlsson. 1991. Growth and development of *Petunia* × *hybrids* as a function of temperature and irradiance. J. Amer. Soc. Hort. Sci. 116:232–237.

Karlsson, M.G. and R.D. Heins. 1986. Response surface analysis of flowering in chrysanthemum 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253–259.

Karlsson, M.G., R.D. Heins, J.O. Gerberick, and M.E. Hackmann. 1991. Temperature driven leaf unfolding rate in *Hibiscus rosa-sinensis*. Scientia Hort. 45:323–331.

Karlsson, M.G. 1992. Leaf unfolding rate in *Begonia* × *hiemulis* [sic]. HortScience 27:109–110.

Karlsson, M. and J. Werner. 2001. Temperature affects leaf unfolding rate and flowering of cyclamen. HortScience 36:292–294.

Kelly, R.O., Z. Deng, and B. Harbaugh. 2007. Evaluation of 125 petunia cultivars as bedding plants and establishment of class standards. HortTechnology 17:386–396.

Landsberg, J.J. 1977. Some useful equations for biological studies. Expt. Agr. 13:273–286.

Larsen, R.U. 1988. A prediction model of the development rate of the pot plant *Senecio* × *hybridus* Hyl. a case study. Acta Hort. 230:381–388.

Larsen, R.U. 1989. A prediction model for floral development of *Senecio* × *hybridus* Hyl. 'Molls Stams'. Acta Hort. 248:247–254.

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

Larsen, R.U. and C. Hidén. 1995. Predicting leaf unfolding in flower induced shoots of greenhouse grown chrysanthemum. Scientia Hort. 63:225–239.

Larsen, R.U. and L. Persson. 1999. Modeling flower development in greenhouse chrysanthemum cultivars in relation to temperature and response group. Scientia Hort. 80:73–89.

Lieth, J.H., R.H. Merritt, and H.C. Kohl Jr. 1991. Crop productivity of petunia in relation to photosynthetically active radiation and air temperature. J. Amer. Soc. Hort. Sci. 116:623–626.

Mattson, N. and J. Erwin. 2003. Temperature affects flower initiation and development rate of *Impatiens*, *Petunia*, and *Viola*. Acta Hort. 624:191–197.

Moccaldi, L.A. and E.S. Runkle. 2007. Modeling the effects of temperature and photosynthetic daily light integral on growth and flowering of *Salvia splendens* and *Tagetes patula*. J. Amer. Soc. Hort. Sci. 132:283–288.

Pasian, C.C. and J.H. Lieth. 1994. Prediction of flowering rose shoot development based on air temperature and thermal units. Scientia Hort. 59:131–145.

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.

Pietsch, G.M., W.H. Carlson, R.D. Heins, and J.E. Faust. 1995. The effect of day and night temperature and irradiance on development of *Catharanthus roseus* (L.) 'Grape Cooler'. J. Amer. Soc. Hort. Sci. 120:877–881.

Pramuk, L.A. and E.S. Runkle. 2005. Modeling growth and development of celosia and impatiens in response to temperature and photosynthetic daily light integral. J. Amer. Soc. Hort. Sci. 130:813–818.

Reed, K.L., E.R. Hamerly, B.E. Dinger, and P.G. Jarvis. 1976. An analytical model for field measurement of photosynthesis. J. Appl. Ecol. 13:925–942.

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

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

Summerfield, R.J., E.H. Roberts, R.H. Ellis, and R.J. Lawn. 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. Expt. Agr. 27:11–31.

Tollenaar, M., T.B. Daynard, and R.B. Hunter. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. 19:363–366.

U.S. Department of Agriculture. 2009. Floriculture crops 2008 summary. Agr. Stat. Board, Washington D.C.

Wang, S.-Y., 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.

White, J.W. and I.J. Warrington. 1988. Temperature and light integral effects on growth and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 113:354–359.

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.

SECTION III

THE INFLUENCE OF DAY AND NIGHT TEMPERATURE FLUCTUATIONS ON GROWTH AND FLOWERING OF ANNUAL BEDDING PLANTS AND GREENHOUSE HEATING COST PREDICTIONS

The Influence of Day and Night Temperature Fluctuations on Growth and Flowering of Annual Bedding Plants and Greenhouse Heating Cost Predictions

Matthew G. Blanchard[1] and Erik S. Runkle[2]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

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[1]Ph.D. candidate.

[2]Associate Professor of Horticulture and Extension Specialist and to whom reprint requests should be addressed (Email: runkleer@msu.edu).

Abstract

Volatile energy costs and lower profit margins have motivated many flower growers in temperate climates to improve the energy efficiency of crop production. We performed experiments with dahlia (*Dahlia ×hybrida* Cav. 'Figaro Mix), French marigold (*Tagetes patula* L. 'Janie Flame'), and zinnia (*Zinnia elegans* Jacq. 'Magellan Pink') to quantify the effects of constant and fluctuating temperatures on growth and flowering during the finish stage. Plants were grown in glass-glazed greenhouses with a day/night (16 h/8 h) temperature of 20/14, 18/18, 16/22 (means of 18 °C), 24/18, 22/22, or 20/26 °C (means of 22 °C) with a 16-h photoperiod and under a photosynthetic daily light integral of 11 to 19 $mol \cdot m^{-2} \cdot d^{-1}$. Flowering times of dahlia, French marigold, and zinnia (Year 2 only) were similar among treatments with the same mean daily air temperature (MDT). All species grown at 20/14 °C were 10 to 41% taller than those grown at 16/22 °C. Crop timing data and computer software that estimates energy consumption for heating (Virtual Grower) were then used to estimate energy consumption for greenhouse heating on a per-crop basis. Energy costs to produce these crops in Charlotte, NC, Grand Rapids, MI, and Minneapolis, MN for a finish date of 15 Apr. or 15 May and grown at the same MDT were estimated to be 3 to 42% lower at a +6 °C day/night temperature difference (DIF) compared with a 0 °C DIF and 2 to 90% higher at a −6 °C DIF versus a 0 °C DIF. This information could be used by greenhouse growers to reduce energy inputs for heating on a per-crop basis.

Introduction

Plant developmental responses to temperature, such as flowering or leaf unfolding rate, are controlled by the integrated mean daily temperature (MDT) (Roberts and Summerfield, 1987). The rate of plant development is zero at or below a species-specific base temperature (T_{min}) and increases as MDT increases until a maximum rate at an optimum temperature (T_{opt}). Development rates between T_{min} and T_{opt} for different phenological stages have been estimated for several floriculture crops such as African violet (*Saintpaulia ionantha* Wendl.; Faust and Heins, 1994), chrysanthemum [*Chrysanthemum ×grandiflorum* (Ramat.) Kitam.; Hidén and Larsen, 1994; Karlsson et al., 1989a], Easter lily (*Lilium longiflorum* Thunb.; Erwin and Heins, 1990; Karlsson et al., 1988), poinsettia (*Euphorbia pulcherrima* Willd. ex Klotz; Berghage, 1990), and potted rose (*Rosa* L ; Steininger et al., 2002). Models developed for these species can be used to predict crop time in response to temperature and other environmental factors.

Temperature can also affect plant morphology; in many species, stem elongation is influenced by the difference between the day and night temperature (DIF) (Myster and Moe, 1995). Stem elongation is promoted when the day temperature is higher than the night temperature (+DIF) and suppressed when the day temperature is lower than the night temperature (−DIF). The effect of DIF on plant height has been studied in many common greenhouse crops, such as campanula (*Campanula isophylla* Moretti) (Moe et al., 1991), chrysanthemum (Karlsson et al., 1989b), fuchsia (*Fuchsia ×hybrida* hort. ex Sieb. and Voss) (Erwin et al., 1991), Easter lily (Erwin et al., 1989), and poinsettia (Berghage, 1989; Berghage and Heins, 1991). For example, Erwin et al. (1989) reported that plant height of Easter lily increased by 129% as DIF increased from −16 to +16 °C.

Similarly, internode length of chrysanthemum increased by 133% as DIF increased from −12 to +12 °C (Karlsson et al., 1989). Stem elongation responses to DIF occur primarily from changes in cellular elongation rather than cellular division, and gibberellins are likely involved (Grindal et al., 1998; Jensen et al., 1996; Myster and Moe, 1995). A −DIF is sometimes used by growers as a height control strategy in controlled environment production of floriculture crops (Myster and Moe, 1995).

In temperate climates, high energy inputs can be required to maintain a desirable greenhouse temperature, making fuel for heating one of the largest floriculture production expenses (Bartok, 2001). In the Netherlands, greenhouses account for 79% of the energy used by the agricultural sector and 7% of the country's total energy consumption (Lansink and Ondersteijn, 2006). In the U.S., the mean commercial price of natural gas increased by 119% from 1998 to 2008 (U.S. Department of Energy, 2009). Rising and volatile fuel costs for heating greenhouses have motivated many growers to improve energy conservation and to minimize energy inputs for crop production in controlled environments.

Greenhouse growers can reduce energy consumption by managing the greenhouse environment with dynamic temperature control (DTC) strategies (Körner et al., 2007; Lund et al., 2006). In DTC, instead of static temperature set points that are the same each day, heating set points are lowered during periods when the greenhouse energy-loss factor is high (e.g., outside temperature and incoming solar radiation are low) and increased when the energy-loss factor is low (Körner et al., 2004). This environmental control strategy integrates temperature and maintains a target MDT over a 1- to 7-d interval (Körner and Challa, 2003; Körner et al., 2004). Lund et al. (2006) reported that a

greenhouse in Denmark with DTC had 32 to 79% and 75 to 89% lower energy consumption for heating during winter and spring months, respectively, compared to a greenhouse with static temperature set points.

To achieve the greatest potential energy savings with temperature integration, a greenhouse environmental control computer with sophisticated software (e.g., DTC) is required (Aaslyng et al., 2003, 2005; Körner and Van Straten, 2008). However, not all greenhouses utilize environmental control computers, and of those that do, relatively few utilize DTC strategies. An alternative and simple energy-saving approach is to use a +DIF with static day and night heating and ventilation set points. With a +DIF, the heating set point is lowered during the night when energy consumption for heating is highest (Bartok, 2001). A low night temperature is compensated by increasing the day temperature so that the target MDT is achieved.

A DTC or DIF strategy to reduce energy consumption assumes that plant development is influenced by MDT, and crop time is similar at different day and night temperatures ($>T_{min}$ and $\leq T_{opt}$) that deliver the same MDT. However, studies with bedding plants that compared flowering times at DIF and constant temperatures regimens with the same MDT have reported different responses among species. For example, geranium (*Pelargonium* ×*hortorum* Bailey) grown at an MDT of 18 °C flowered similarly at day/night (12 h/12 h) set points of 18/18 or 27/9 °C (White and Warrington, 1988). In contrast, Mortensen and Moe (1992) reported that petunia 'Ultra Red' (*Petunia* ×*hybrida* Vilm.-Andr.) flowered 5 d earlier at a day/night (16 h/8 h) of 21/15 °C compared with 19/19 °C and 17/23 °C, while red salvia (*Salvia splendens* F. Sello ex Roem & Schult.) flowered 5 d later at 17/23 °C compared with 19/19 °C and 21/15 °C.

Therefore, the benefits of using DIF to reduce energy inputs or to suppress stem elongation may not be practical for all bedding plant species if crop time is delayed. The objectives of this research were to (1) quantify the effects of constant and fluctuating temperatures on growth and flowering during the finish stage of three bedding plant species and (2) predict greenhouse heating costs for different crop finish dates, at different locations in the United States, with different DIF regimens.

Materials and Methods

During Sept. 2008 (Year 1) and Mar. 2009 (Year 2), seeds of dahlia (*Dahlia ×hybrida* Cav. 'Figaro Mix'), French marigold (*Tagetes patula* L. 'Janie Flame'), and zinnia (*Zinnia elegans* Jacq. 'Magellan Pink') were sown in plug trays [288-cell size (6-ml volume)] by a commercial greenhouse (C. Raker & Sons, Litchfield, MI). In Year 1, zinnia received a foliar spray of paclobutrazol (Bonzi; Syngenta Crop Protection, Inc., Greensboro, NC) at an unreported rate and volume to suppress hypocotyl elongation. Ten to 17 d after seed sow, plugs were received at Michigan State University (MSU) and were grown in a controlled environmental growth chamber at a constant temperature set point of 20 °C. A 16-h photoperiod was provided by 215-W cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and 60-W incandescent lamps (INC; Philips), at a CWF:INC (by W) of 3.6, and at an intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Plants were irrigated as necessary with well water acidified with H_2SO_4 to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$ and containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively. The water was supplemented with a water-soluble fertilizer

providing ($mg \cdot L^{-1}$) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, Mn, and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Greenhouse Environment

After 26 d (dahlia), 19 or 23 d (French marigold), and 23 or 16 d (zinnia) from seed sow, seedlings were thinned to one seedling per cell and transplanted into 10-cm round plastic containers (480-ml volume) filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). At transplant, dahlia, French marigold, and zinnia had a mean of 3, 6, or 6 leaves, respectively. Fifteen plants of each species were randomly assigned to each of 6 glass-glazed greenhouse sections with constant temperature set points of 18 or 22 °C and fluctuating day/night (16 h/8 h) temperature set points of 20/14, 16/22, 24/18, or 20/26 °C. The temperature set points were chosen so that 3 treatments each had an MDT of 18 or 22 °C. In each greenhouse section, temperature set points were maintained by an environmental computer (Priva Intégro 724; Priva, Vineland Station, Ontario) that controlled steam heating, passive and active ventilation, and evaporative cooling pads when needed. The transition period between the day and night temperature set points was 3 $min \cdot °C^{-1}$. The experiment was performed twice with transplant dates beginning on 18 Oct. 2008 (Year 1) and 20 Mar. 2009 (Year 2).

The photoperiod was maintained at 16 h and consisted of natural photoperiods (43 °N lat.) with day-extension lighting from 0600 to 2200 HR provided by high-pressure sodium (HPS) lamps. The HPS lamps were operated by an environmental computer and were turned on when the outside light intensity was <290 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and turned off at

>580 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The photoperiod and skotoperiod paralleled the day and night temperature set points, respectively. In Year 2, whitewash was applied to the greenhouse glazing so that the maximum photosynthetic photon flux (*PPF*) was 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. A maximum vapor-pressure deficit of 1.2 kPa was maintained during the night by the injection of steam into the air. Horizontal airflow fans positioned 1.4 m above the growing surface operated if the ridge vent was <90% of the maximum opening and provided air movement at ≈ 0.1 $m \cdot s^{-1}$ at plant height [as measured with an air velocity transducer (8475; TSI, Inc., St. Paul, MN)].

Environmental Monitoring and Plant Culture

Air temperature was independently measured in each greenhouse by an aspirated, shielded thermocouple (0.13-mm type E; Omega Engineering, Stamford, CT) positioned at plant level. In each temperature treatment, the *PPF* was measured by a line quantum sensor containing 10 photodiodes (Apogee Instruments, Inc., Logan, UT) positioned at 30 cm above the bench. Environmental measurements were collected every 10 s and hourly means were recorded by a data logger (CR10; Campbell Scientific, Logan, UT). Temperature control during the experiment was within 1.3 °C of the greenhouse temperature set points for all treatments in both years and the actual MDT was 18.0 ±0.4 °C or 22.0 ±0.2 °C (Table 3.1). The mean photosynthetic daily light integral (DLI) from transplant to flowering ranged from 10.6 to 12.3 $mol \cdot m^{-2} \cdot d^{-1}$ in Year 1 and 15.7 to 19.1 $mol \cdot m^{-2} \cdot d^{-1}$ in Year 2.

Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe

and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc.).

Data Collection and Analysis

The date of first open inflorescence (flowering) was recorded and time to flower was calculated for each plant. Plants were considered flowering when each species had an inflorescence with at least 50% of the ray petals fully reflexed. When each plant flowered, plant height and the number of inflorescences were recorded. Plant height was measured from the soil surface to the base of the first whorl of flowers on an inflorescence.

A completely randomized block design was used during each year. Data were analyzed using SAS (SAS Institute, Inc., Cary, N.C.) mixed model procedure (PROC MIXED), and pairwise comparisons between treatments were performed using Tukey's honestly significant difference test at $P \leq 0.01$. Data were pooled between replications if the treatment ×year interaction was not significant at $P \leq 0.01$.

Heating Cost Estimation

The cost to heat a 1,991 m^2 greenhouse to produce a flowering crop grown at day/night (16 h/8 h) temperature set points of 18/18, 20/14, 16/22, 22/22, 24/18, or 20/26 °C for finish dates of 15 Mar., 15 Apr., or 15 May was estimated for Charlotte, NC, Grand Rapids, MI, and Minneapolis, MN using the Virtual Grower 2.5 software (Frantz et al., 2007; U.S. Department of Agriculture, 2009a). Production time for each species was calculated from the greenhouse experiments using the mean time to flower at an

MDT of 18 or 22 °C. Flowering time for zinnia was calculated based on data from Year 2 only. The greenhouse characteristics used to estimate heating costs included: 8 spans each 34.1 × 7.3 m, arched 3.7-m roof, 2.7-m gutter, polyethylene double layer roof, polycarbonate bi-wall ends and sides, forced air unit heaters burning natural gas, 50% heater efficiency, no energy curtain, an air infiltration rate of $1.0 \cdot h^{-1}$, and day temperature set points from 0600 to 2200 HR. These values and characteristics are typical of commercial greenhouses used to produce floriculture crops in the northern half of the United States. The heater efficiency was chosen based on the mean recorded values from several commercial greenhouses (Frantz et al., 2009). Cities were subjectively chosen from a list of the largest garden plant-producing states in the United States (U.S. Department of Agriculture, 2009b) and were selected if they had an outside MDT <10 °C during Jan., Feb., Mar., and Apr. (U.S. Department of Energy. 1995).

Results

In dahlia and French marigold, there were no differences in time to flower among plants grown at temperature treatments with a similar MDT (Fig. 3.1A and 3.2A). For example, French marigold flowered a mean of 26 d after transplant when grown at 18/18, 20/14, or 16/22 °C and a mean of 21 d when grown at 22/22, 24/18, or 20/26 °C. In zinnia, plants grown at temperature treatments that delivered a similar MDT flowered at the same time in Year 2, but not Year 1 (Fig. 3.3A). In Year 1, zinnia flowered 3 to 7 d earlier in plants grown at 20/14 °C compared with plants grown at 18/18 or 16/22 °C.

In dahlia, plants grown at 18/18 or 20/14 °C had a mean of 8 more inflorescences than plants grown at 22/22, 24/18, 20/26, or 16/22 °C (Fig. 3.1B). French marigold had a

similar inflorescence number among treatments, although those grown at 16/22 °C had a mean of 3 more than those at 24/18 °C (Fig. 3.2B). In Year 1, when the mean DLI was ≈11 $mol \cdot m^{-2} \cdot d^{-1}$, zinnia grown at an MDT of 22 °C developed 2 or 3 more inflorescences than plants grown at an MDT of 18 °C (Fig. 3.3B). In contrast, inflorescence number was similar among temperature treatments in Year 2, when the mean DLI was ≈17 $mol \cdot m^{-2} \cdot d^{-1}$.

Dahlia grown at a +6 °C DIF (20/14 or 24/18 °C) was 4.6 to 5.3 cm taller at flowering than plants grown at a −6 °C DIF (16/22 or 20/26 °C; Fig. 3.1C). In French marigold, plants were 11% taller when grown at 20/14 °C or 24/18 °C versus 16/22 °C. In Year 1, zinnia grown at 24/18 °C were 17 to 58 % taller than all other treatments, while in Year 2, plants grown at 20/14 were 13 to 32% taller than all other treatments (Fig. 3.3C). For all species, there were no differences in height between plants grown at a 0 °C DIF.

In all species and locations, energy for heating predictions to produce a flowering crop for 15 Apr. or 15 May were up to 41% lower when grown at a +6 °C DIF compared with a constant temperature (Table 3.2). As finish date progressed from 15 Mar. to 15 May, the relative difference in heating costs between a +6 °C DIF and 0 °C DIF increased. Heating costs per crop for all locations and finish dates were estimated to be greatest when grown at 16/22, 20/26, or 22/22 °C. For example, dahlia grown in Minneapolis, MN would consume 2 to 29% more energy if grown at 16/22 °C versus 18/18 or 20/14 °C. In nearly all instances, the least amount of energy consumed per crop of dahlia or French marigold occurred at 20/14 °C. In contrast, the lowest energy input for a crop of zinnia was 24/18 °C for 15 Mar. finish dates and a +6 °C DIF for the later

two finish dates. The estimated energy consumption for heating was greatest for dahlia grown at 20/26 °C or constant 22 °C, regardless of location or finish date. For French marigold and zinnia, greenhouse heating was greatest for a crop grown at a +6 °C DIF. As finish date increased from 15 Mar. to 15 May, heating costs at each temperature regimen decreased by 52 to 84%. For example, zinnia grown for 15 May at 20/14 °C would require 77% less energy inputs for heating than the same crop grown for 15 Mar.

Discussion

Flowering time of dahlia, French marigold, and zinnia (Year 2 only) was similar among temperature treatments with the same MDT. This response reinforces the paradigm that flowering rate is a function of the MDT and, within limits, the effects of day and night temperature on progress towards flowering are equal (Karlsson et al., 1988; Roberts and Summerfield, 1987; Steininger et al., 2002). Our results are in agreement with Mortensen and Moe (1992) who reported no difference in flowering time of fuchsia, geranium, impatiens (*Impatiens walleriana* Hook.f.), pocketbook plant (*Calceolaria ×herbeohybrida* Voss), potted rose, and tuberous begonia (*Begonia ×tuberhybrida pendula*) grown at day/night (16 h/8 h) temperature set points of 19/19, 21/15, or 17/23 °C. Similarly, flowering time was controlled by MDT and not DIF in pinnate dahlia (*Dahlia pinnata* Cav.; Brøndum and Heins, 1993), pansy (*Viola ×wittrockiana* Gams.; Niu et al., 2000), and vinca (*Catharanthus roseus* L.; Pietsch et al., 1995).

Crop models that predict flowering time under different environmental conditions have been developed for several bedding plants including celosia, French marigold, impatiens, pansy, petunia, pinnate dahlia, and red salvia (Adams et al., 1997, 1998;

Brøndum and Heins, 1993; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005). In many of these experiments, models were generated with data from plants that were grown at constant temperature set points. For example, flowering models predicted that as constant temperature set points increased from 14 to 26 °C, time to flower in celosia (*Celosia argentea* L. var. *plumosa* Voss) and impatiens grown under a DLI of 15 $mol \cdot m^{-2} \cdot d^{-1}$ decreased by 38 and 15 d, respectively (Pramuk and Runkle, 2005). Data from our study presenting similar flowering times at different day/night treatments with the same MDT indicates that these crop models could also be used to predict flowering time at fluctuating temperature set points. Caveats of many crop models that predict flowering time are that they are only valid if the day and night temperatures are $\geq T_{min}$ and $\leq T_{opt}$ (Summerfield et al., 1991).

In zinnia during Year 1, flowering time was different among treatments with an MDT of 18 °C. The actual MDT among these treatments varied by only 0.1 to 0.4 °C and plants received a DLI within 0.6 $mol \cdot m^{-2} \cdot d^{-1}$. Therefore, it is not clear why plants grown at a 20/14 °C flowered later than those grown at a constant 18 °C or 16/22 °C. At an MDT of 18 °C, zinnia flowered a mean of 2 to 9 d earlier and had a mean of 3 more inflorescences in Year 2 compared with Year 1. The differences between years could be because after transplant, plants in Year 2 received a DLI that was 6 $mol \cdot m^{-2} \cdot d^{-1}$ higher than in Year 1. In many species, flowering time decreases and flower number increases as DLI increases. For example, as DLI increased from 10 to 15 $mol \cdot m^{-2} \cdot d^{-1}$, time to flower in celosia grown at 20 °C decreased by 3 d and inflorescence number increased by 2 (Pramuk and Runkle, 2005). The flowering delay and reduced inflorescence number in zinnia during Year 1 could also be at least partially attributed to the paclobutrazol

application that was applied during the plug, which has been shown to delay flowering in some crops (Blanchard and Runkle, 2007).

Plant height at flower in all species generally increased as DIF increased from −6 °C to +6 °C. These results are in agreement with Myster and Moe (1995) that the relative promotion or suppression of stem elongation is influenced by the magnitude of DIF. Similar effects of DIF on plant height have been reported in other bedding plants including geranium (Mortensen and Moe, 1992), pinnate dahlia (Brøndum and Heins, 1993), impatiens (Mortensen and Moe, 1992), pansy (Niu et al., 2000), petunia (Kaczperski et al., 1991), red salvia (Mortensen and Moe, 1992), snapdragon (*Antirrhinum majus* L.; Neily et al., 1997), tall verbena (*Verbena bonariensis* L.; Shimizu and Heins, 2000), and zinnia (Neily et al., 1997). For example, stem elongation during the vegetative stage in snapdragon and zinnia increased by 38 and 13%, respectively, as DIF (13-h day/11-h night) increased from −5 to +5 °C (Neily et al., 1997).

Although a +DIF temperature regimen promoted stem elongation, greenhouse energy inputs to heat these bedding plants at these locations and finish dates were estimated to be lowest with a +DIF. For example, the estimated energy inputs to produce these three crops in Charlotte, NC, Grand Rapids, MI, and Minneapolis, MN for a finish date of 15 Mar. were similar or up to 11% lower if grown at +6 °C DIF instead of a constant temperature. In contrast, for a finish date of 15 May, energy inputs at the same MDT were estimated to be 9 to 42% lower at a +6 °C DIF compared with a 0 °C DIF. Similar results were reported in a simulated greenhouse study in the Netherlands: total annual energy consumption was 9%, 13%, and 23% lower during Feb., Mar., and Apr., respectively, with a +6 °C DIF compared with a −2 °C DIF (Körner et al., 2004).

These results collectively indicate that for many locations, a +DIF temperature regimen is an energy efficient-production strategy and the energy-savings with +DIF increases with later production dates. Because plants grown at some +DIF treatments were taller than those grown at a constant or −DIF temperature regimen, the advantages and disadvantages of DIF should be considered. If a +DIF temperature regimen is used to save energy, growers may need to utilize an alternative height control strategy to suppress stem elongation. An example of a height control strategy could be the application of a chemical plant growth retardant (Blanchard and Runkle, 2007). Plants grown under a −DIF had suppressed stem elongation, but were estimated to require the highest energy inputs to produce. An economic analysis could determine if it is more cost-effective to deliver a +DIF to save energy and use different height control strategies or to deliver a −DIF with more energy inputs, but less height control requirements.

Dahlia had a mean of 42% more inflorescences when grown at a day/night of 18/18 and 20/14 °C compared with the other treatments. Plants grown at a lower MDT could have more inflorescences at flowering than those grown at a higher MDT because they had more time to harvest photosynthetic light and accumulate dry matter before flowering. For example, Moccaldi and Runkle (2007) reported that as MDT decreased from 26 to 14 °C, time to flower, inflorescence number, inflorescence diameter, and dry weight at flowering increased. Dahlia grown at 16/22 °C had a mean of 7 fewer inflorescences than plants grown at the same MDT but at 18/18 and 20/14 °C. The lower flower number at a night temperature of 22 °C could be attributed to a higher respiration rate during the night that could decrease available carbon. van Iersel (2003) reported that as temperature increased from 6 to 36 °C, whole-plant dark respiration in French

marigold, geranium, pansy, and petunia increased exponentially and daily carbon gain decreased quadratically.

The production of these species at different MDTs would require that crops are transplanted on different dates so that they are finished on the same market date. For example, dahlia grown for a market date of 15 May would need to be transplanted on 25 Mar. if grown at a constant 18 °C and on 30 Mar. if grown at a constant 22 °C. In this example, the crop transplanted earlier and grown at 18 °C would develop 8 more inflorescences before flowering than the crop grown at 22 °C.

Some greenhouse growers have lowered the MDT in an attempt to conserve energy for heating. Although this strategy can decrease the heating requirement on a daily basis, time to flower increases. For some locations and crops, the longer production time at a low MDT could require more total energy inputs per crop than a shorter production time at a higher MDT (Blanchard et al., in press; Shimizu et al., 2003). We estimated that to produce flowering zinnia for 15 Mar. or 15 Apr. in Grand Rapids, MI or Minneapolis, MN, energy consumption for heating per crop would be similar or 4 to 14% lower at 22/22 or 24/18 °C instead of 18/18 or 20/14 °C. However, to produce French marigold for the same finish date at these locations, energy consumption is estimated to be 2 to 13% higher at 22/22 or 24/18 °C compared with 18/18 or 20/14 °C. Therefore, energy-efficient production temperatures depend on the crop grown, time of year, and location. When selecting a growing temperature, other production factors such as the number of crop turns, irrigation frequency, and disease and insect control could also be considered.

Table 3.1. Mean daily air temperature and daily light integral during experiments in Year 1 and 2. The day and night were 16 and 8 h, respectively.

Day/night temperature set point (°C)	Actual day/night temperature (°C)		Actual mean daily temperature (°C)		Daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$)	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
18/18	18.4/16.7	18.1/17.8	17.9	18.0	11.6	15.9
20/14	20.4/14.1	19.7/15.0	18.3	18.2	11.0	16.3
16/22	16.5/21.4	16.8/21.8	18.1	18.4	11.0	16.9
22/22	22.3/21.1	22.3/21.5	21.9	22.1	10.7	19.1
24/18	24.0/18.6	24.0/18.7	22.2	22.2	12.3	15.7
20/26	20.7/25.1	20.3/25.7	22.2	22.1	10.6	18.3

Table 3.2. Predicted relative amount of energy used for greenhouse heating to produce three annual species grown at different day and night temperature set points in different locations and finish dates. Heating inputs were estimated using Virtual Grower software (U.S. Department of Agriculture, 2009a) and include time from transplant to first flowering on 15 Mar., 15 Apr., or 15 May. Production time for each species was calculated from greenhouse experiments using the mean time to flower at 18/18, 20/14, and 16/22 °C or 22/22, 24/18, and 20/26 °C. Percentages were calculated by dividing heating input by the highest input for each location and species. See materials and methods for greenhouse and heating parameter inputs.

Day/night temperature set point (°C)	Greenhouse location and finish date								
	Charlotte, NC			Grand Rapids, MI			Minneapolis, MN		
	15 Mar.	15 Apr.	15 May	15 Mar.	15 Apr.	15 May	15 Mar.	15 Apr.	15 May
	Dahlia 'Figaro Mix'								
18/18	0.83	0.45	0.22	0.91	0.62	0.35	0.96	0.55	0.26
20/14	0.79	0.39	0.17	0.91	0.60	0.32	0.96	0.53	0.24
16/22	0.90	0.55	0.34	0.93	0.65	0.41	0.98	0.59	0.31
22/22	0.96	0.62	0.38	1.00	0.70	0.44	1.00	0.61	0.35
24/18	0.91	0.55	0.29	0.98	0.67	0.40	0.98	0.58	0.31
20/26	1.00	0.67	0.45	1.00	0.71	0.48	1.00	0.63	0.37
	French marigold 'Janie Flame'								
18/18	0.76	0.43	0.18	0.97	0.60	0.32	0.96	0.44	0.26
20/14	0.68	0.35	0.11	0.95	0.57	0.27	0.95	0.42	0.21
16/22	0.88	0.58	0.35	1.00	0.65	0.39	1.00	0.50	0.32
22/22	0.94	0.60	0.30	0.95	0.63	0.36	0.99	0.48	0.27
24/18	0.86	0.49	0.18	0.92	0.59	0.30	0.97	0.44	0.23
20/26	1.00	0.67	0.40	0.96	0.65	0.40	1.00	0.50	0.31
	Zinnia 'Magellan Pink'								
18/18	0.91	0.51	0.27	0.97	0.64	0.38	0.97	0.55	0.27
20/14	0.86	0.44	0.20	0.97	0.62	0.33	0.97	0.53	0.24
16/22	1.00	0.63	0.40	1.00	0.68	0.43	1.00	0.59	0.33
22/22	0.89	0.61	0.35	0.93	0.64	0.39	0.87	0.49	0.30
24/18	0.83	0.53	0.26	0.91	0.62	0.35	0.85	0.46	0.26
20/26	0.93	0.66	0.43	0.94	0.66	0.42	0.87	0.51	0.33

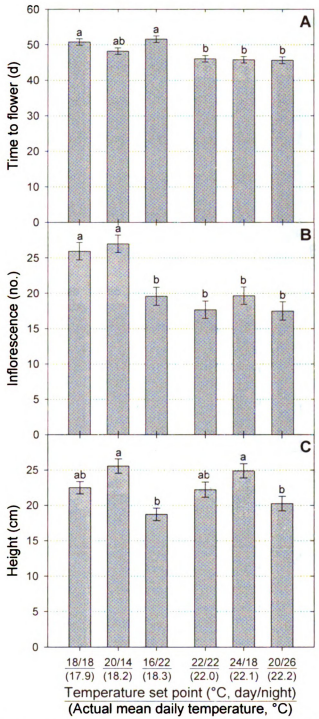

Fig. 3.1. The influence of temperature on time to flower (**A**), and inflorescence number (**B**) and height (**C**) at flowering, in dahlia 'Figaro Mix' at constant and fluctuating day/night (16 h/8 h) temperature set points. Vertical bars indicate standard errors of treatment means. Mean separation by Tukey's honestly significant difference test at $P \leq 0.01$.

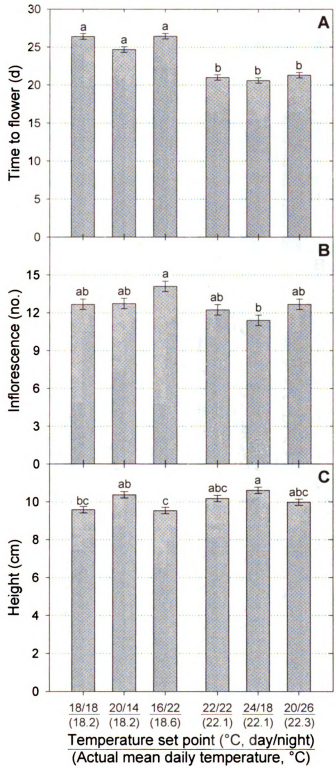

Fig. 3.2. The influence of temperature on time to flower (**A**), and inflorescence number (**B**) and height (**C**) at flowering, in French marigold 'Janie Flame' at constant and fluctuating day/night (16 h/8 h) temperature set points. Vertical bars indicate standard errors of treatment means. Mean separation by Tukey's honestly significant difference test at $P \leq 0.01$.

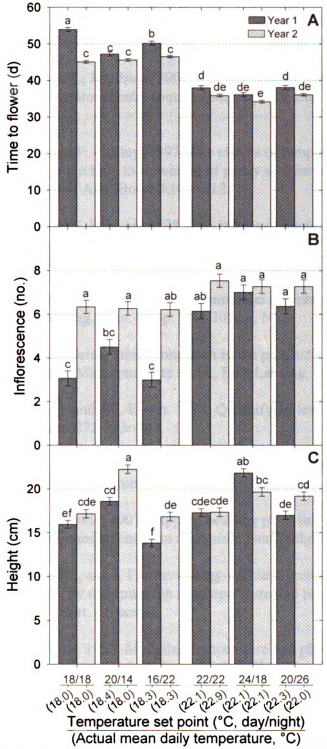

Fig. 3.3. The influence of temperature on time to flower (**A**), and inflorescence number (**B**) and height (**C**) at flowering, in zinnia 'Magellan Pink' at constant and fluctuating day/night (16 h/8 h) temperature set points. Vertical bars indicate standard errors of treatment means. Mean separation by Tukey's honestly significant difference test at $P \leq 0.01$.

Literature Cited

Aaslyng, J.M., J.B. Lund, N. Ehler, and E. Rosenqvist. 2003. IntelliGrow: A greenhouse component-based climate control system. Environ. Model. Software 18:657–666.

Aaslyng, J.M., N. Ehler, and L. Jakobsen. 2005. Climate control software integration with a greenhouse environmental control computer. Environ. Model. Software 20:521–527.

Adams, S.R., S. Pearson, and P. Hadley. 1997. The effects of temperature, photoperiod and light integral on the time to flowering of pansy cv. Universal Violet (*Viola* ×*wittrockiana* Gams.). Ann. Bot. 80:107–112.

Adams, S.R., P. Hadley, and S. Pearson. 1998. The effects of temperature, photoperiod, and photosynthetic photon flux on the time to flowering of *Petunia* 'Express Blush Pink'. J. Amer. Soc. Hort. Sci. 123:577–580.

Bartok, J.W. Jr. 2001. Energy conservation for commercial greenhouses. Natural Resource, Agr., and Eng. Serv. Coop. Ext., Ithaca, NY.

Berghage, R.D. Jr. 1989. Modeling stem elongation in the poinsettia. Ph.D. Dissertation, Dept. of Horticulture, Michigan State Univ., East Lansing, MI.

Berghage, R.D., R.D. Heins, and J.E. Erwin. 1990. Quantifying leaf unfolding in the poinsettia. Acta Hort. 272:243–247.

Berghage, R.D. and R.D. Heins. 1991. Quantification of temperature effects on stem elongation in poinsettia. J. Amer. Soc. Hort. Sci. 116:14–18.

Blanchard, M.G. and E.S. Runkle. 2007. Dipping bedding plant liners in paclobutrazol or uniconazole inhibits subsequent stem extension. HortTechnology 17:178–182.

Blanchard, M.G., E.S. Runkle, and J. Frantz. Energy-efficient greenhouse production of *Petunia* and *Tagetes* by manipulation of temperature and photosynthetic daily light integral. Acta Hort. (in press).

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.

Erwin, J.E., R.D. Heins, and M.G. Karlsson. 1989. Thermomorphogenesis in *Lilium longiflorum*. Amer. J. Bot. 76:47–52.

Erwin, J.E. and R.D. Heins. 1990. Temperature effects on lily development rate and morphology from the visible bud stage until anthesis. J. Amer. Soc. Hort. Sci. 115:644–646.

Erwin, J.E., R.D. Heins, and R. Moe. 1991. Temperature and photoperiod effects on *Fuchsia* × *hybrida* morphology. J. Amer. Soc. Hort. Sci. 116:955–960.

Frantz, J., E. Runkle, M. Blanchard, L. Locke, and C. Krause. 2007. Virtual Grower: Estimating greenhouse energy costs and plant growth using new computer software. HortScience 42:1018 (abstr.).

Frantz, J., B. Hand, and L. Buckingham. 2009. Virtual Grower software user manual (Version 2.51). U.S. Dept. Agr., Agr. Res. Serv., Washington D.C.

Faust, J.E. and R.D. Heins. 1994. Modeling inflorescence development of the African violet (*Saintpaulia ionantha* Wendl.). J. Amer. Soc. Hort. Sci. 119:727–734.

Grindal, G., A. Ernstsen, J.B. Reid, O. Junttila, B. Lindgard, and R. Moe. 1998. Endogenous gibberellin A_1 levels control thermoperiodic stem elongation in *Pisum sativum*. Physiol. Plant. 102:523–531.

Hidén, C. and R.U. Larsen. 1994. Predicting flower development in greenhouse grown chrysanthemum. Scientia Hort. 58:123–138.

Jensen, E., S. Eilertsen, A. Ernsten, O. Juntilla, and R. Moe. 1996. Thermoperiodic control of stem elongation and endogenous gibberellins in *Campanula isophylla*. J. Plant Growth Regul. 15:167–171.

Jones, H.G. 1992. Plants and microclimate. 2nd ed. Cambridge Univ. Press, New York, NY.

Kaczperski, M.P., W.H. Carlson, and M.G. Karlsson. 1991. Growth and development of *Petunia* × *hybrids* as a function of temperature and irradiance. J. Amer. Soc. Hort. Sci. 116:232–237.

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

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

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

Körner, O. and H. Challa. 2003. Temperature integration and DIF in cut chrysanthemum. J. Hort. Sci. Biotechnol. 78:335–342.

Körner, O., M.J. Bakker, and E. Heuvelink. 2004. Daily temperature integration: A simulation study to quantify energy consumption. Biosystems Eng. 87:333–343.

Körner, O., J.M. Aaslyng, A.U. Andreassen, and N. Holst. 2007. Microclimate prediction for dynamic greenhouse climate control. HortScience 42:272–279.

Körner, O. and G. Van Straten. 2008. Decision support for dynamic greenhouse climate control strategies. Comput. Electron. Agr. 60:18–30.

Lansink, A.O. and C. Ondersteijn. 2006. Energy productivity growth in the Dutch greenhouse industry. Amer. J. Agr. Econ. 88:124–132.

Lund, J.B., A. Andreassen, C.-O. Ottosen, and J.M. Aaslyng. 2006. Effect of a dynamic climate on energy consumption and production of *Hibiscus rosa-sinensis* L. in greenhouses. HortScience 41:384–388.

Moccaldi, L.A. and E.S. Runkle. 2007. Modeling the effects of temperature and photosynthetic daily light integral on growth and flowering of *Salvia splendens* and *Tagetes patula*. J. Amer. Soc. Hort. Sci. 132:283–288.

Moe, R., R.D. Heins, and J. Erwin. 1991. Stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti in response to day and night temperature alternations and light quality. Scientia Hort. 48:141–151.

Mortensen, L.M. and R. Moe. 1992. Effects of various day and night temperature treatments on the morphogenesis and growth of some greenhouse and bedding plant species. Acta Hort. 327:77–86.

Myster, J. and R. Moe. 1995. Effect of diurnal temperature alternations on plant morphology in some greenhouse crops—a mini review. Scientia Hort. 62:205–215.

Neily, W.G., P.R. Hicklenton, and D.N. Kristie. 1997. Temperature and developmental stage influence diurnal rhythms of stem elongation in snapdragon and zinnia. J. Amer. Soc. Hort. Sci. 122:778–783.

Niu, G., R.D. Heins, A.C. Cameron, and W.H. Carlson. 2000. Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of pansy (*Viola ×wittrockiana*). J. Amer. Soc. Hort. Sci. 125:436–441.

Pietsch, G.M., W.H. Carlson, R.D. Heins, and J.E. Faust. 1995. The effect of day and night temperature and irradiance on development of *Catharanthus roseus* (L.) 'Grape Cooler'. J. Amer. Soc. Hort. Sci. 120:877–881.

Pramuk, L.A. and E.S. Runkle. 2005. Modeling growth and development of celosia and impatiens in response to temperature and photosynthetic daily light integral. J. Amer. Soc. Hort. Sci. 130:813–818.

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

Shimizu, H. and R.D. Heins. 2000. Photoperiod and the difference between day and night temperature influence stem elongation kinetics in *Verbena bonariensis*. J. Amer. Soc. Hort. Sci. 125:576–580.

Shimizu, H., R.D. Heins, and E. Runkle. 2003. Simulation study of total energy consumption required to produce a mature plant at different greenhouse temperatures. J. Soc. High Tech. in Agr. 15:123–129.

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

Summerfield, R.J., E.H. Roberts, R.H. Ellis, and R.J. Lawn. 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. Expt. Agr. 27:11–31.

U.S. Department of Agriculture. 2009a. Application technology research unit: Virtual Grower. Agr. Res. Serv., Washington, DC. 23 Sept. 2009. <http://www.virtualgrower.net>.

U.S. Department of Agriculture. 2009b. Floriculture crops 2008 summary. Agr. Stat. Board, Washington, DC.

U.S. Department of Energy. 1995. National solar radiation data base 1961-1990: Typical meteorological Year 2. Natl. Renewable Energy Lab., Golden, CO.

U.S. Department of Energy. 2009. Monthly energy review August 2009. Energy Info. Admin., Washington, DC.

van Iersel, M.W. 2003. Short-term temperature change affects the carbon exchange characteristics and growth of four bedding plant species. J. Amer. Soc. Hort. Sci. 128:100–106.

White, J.W. and I.J. Warrington. 1988. Temperature and light integral effects on growth and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 113:354–359.

SECTION IV

MODELING THE INFLUENCE OF GREENHOUSE SCREENS ON PLANT SHOOT-TIP TEMPERATURE OF NEW GUINEA IMPATIENS

Modeling the Influence of Greenhouse Screens on Plant Shoot-tip Temperature of New Guinea Impatiens

Matthew G. Blanchard and Erik S. Runkle[1]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

A.J. Both

Bioresource Engineering, Department of Environmental Sciences, Rutgers University, New Brunswick, NJ 08901

Hiroshi Shimizu

Division of Environmental Science & Technology, Kyoto University, Kyoto 606-8502, Japan

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[1]Associate Professor of Horticulture and Extension Specialist and to whom reprint requests should be addressed (Email: runkleer@msu.edu).

Abstract

The effect of retractable nighttime screens on plant shoot-tip temperature of New Guinea impatiens (*Impatiens hawkeri* Bull.) was quantified in glass-glazed greenhouses during winter. An energy balance model was developed that predicts shoot-tip temperature using cover (glazing or screen) emissivity and five environmental measurements: dry-bulb, wet-bulb, and cover temperature; transmitted shortwave radiation (SWR, 300 to 3,000 nm); and air velocity. Plants under a screen extended at night had a shoot-tip temperature 0.5 to 2.3 °C higher and absorbed 70 to 125% more net radiation (250 to 60,000 nm) than plants without a screen. Shoot-tip temperature was 0.9 to 1.4 °C lower under a shading screen with open-weave construction (high air permeability) compared with closed-weave constructed screens (e.g., blackout). Under an air vapor-pressure deficit (VPD) of 0.4 to 0.9 kPa, plant shoot-tip temperature was up to 1.5 °C closer to dry-bulb temperature than plants under a VPD of 1.4 to 1.8 kPa. During the day, shoot-tip temperature was 1.2 °C lower than dry-bulb temperature when SWR was <100 $W \cdot m^{-2}$, and a mean of 1.6 °C higher than dry-bulb temperature when SWR was >100 $W \cdot m^{-2}$. The model predicted shoot-tip temperature within 1 °C for 62% and 91% of the actual shoot-tip temperature during the day and night, respectively (13,824 observations). Thus, a screen extended at night over a crop of New Guinea impatiens could increase plant shoot-tip temperature and accelerate development.

Introduction

The commercial production of ornamental greenhouse crops demands that plants are accurately scheduled for predetermined market dates (Heins et al., 2000). The ability

to schedule crops requires knowledge of how environmental factors (e.g., temperature and light) influence plant growth and development. The rate of plant development and the time required to complete a phenological stage (e.g., unfold leaves or flower) is controlled by the mean daily temperature (MDT) of the apical meristem (e.g., shoot-tip) (Faust and Heins, 1993; Niu et al., 2001; Roberts and Summerfield, 1987). For example, as shoot-tip MDT increased from 16 to 24 °C, flower development rate in campanula (*Campanula carpatica* Jacq.) increased from 0.018 to 0.024 (Niu et al., 2001).

Many published crop models use ambient air MDT to predict the completion of a developmental stage rather than actual shoot-tip temperature (Adams et al., 1998; Erwin and Heins, 1990; Moccaldi and Runkle, 2007). However, shoot-tip temperature is often different from air temperature. Faust and Heins (1998) reported that shoot-tip MDT in vinca (*Catharanthus roseus* L.) grown at 15 and 20 °C was within 2 °C of the air MDT, while plants grown at 35 °C had a shoot-tip MDT 4 to 6 °C below the air MDT. Crop models that are based on actual shoot-tip MDT can be more accurate than those that use air MDT. For example, in African violet (*Saintpaulia ionantha* Wendl.), the mean deviation between predicted and observed leaf number was 63% higher when air temperature was used instead of plant temperature (Faust and Heins, 1993).

Plant temperature is determined by the transfer of energy between the plant and the surrounding environment and can be calculated using an energy balance equation (Nobel, 2005). Under steady-state conditions, plant temperature is equal to the sum of the total radiation absorbed by the plant, emitted longwave radiation (LWR, 3,000 to 100,000 nm), convection, and transpiration (Nobel, 2005). Plant energy balance models have been developed that predict shoot-tip temperature under different greenhouse

conditions (Faust and Heins, 1998; Shimizu et al., 2004). During the day, shortwave radiation (SWR, 300 to 3,000 nm) and transpiration have the largest influence on energy transfer between the plant and the surrounding environment (Faust and Heins, 1998). During the night, convection and the transfer of LWR between the plant and the greenhouse structure often have the greatest influence on plant temperature.

The exchange of LWR between plants and the surrounding environment is influenced by the temperature and emissivity of radiating objects. In temperate climates during winter nights, outside temperatures are low and the greenhouse glazing temperature can be considerably lower than inside air temperature. As glazing temperature decreases, LWR emitted by the glazing material decreases, and LWR emitted by the plant can become greater than incoming LWR. This net loss of LWR can cause plant temperature to be below air temperature. For example, as glazing temperature at night decreased from 2 to 16 °C below air temperature, vinca shoot-tip temperature decreased from 1 to 5 °C below air temperature (Faust and Heins, 1998).

In response to increasing and volatile fuel costs, some commercial growers have made greenhouse structural improvements to reduce energy losses, such as the installation of retractable thermal screens (Dieleman and Kempkes, 2006; Korner et al., 2004; Lund et al., 2006). Thermal screens are commonly extended over a greenhouse crop from sunset to sunrise and retracted during the day (Bailey, 1988; Lund et al., 2006). A thermal screen that has a closed-weave construction (low air permeability) and seals tightly with the greenhouse sidewalls creates a barrier between the heated and non-heated space above and below the screen, respectively (Öztürk and Basçetinçelik, 1997; Zabeltitz and Meyer, 1984). Energy requirements for greenhouse heating can decrease

with a thermal screen because the volume of heated air below the screen is reduced. Brajeul et al. (2005) and Le Quillec et al. (2005) reported that a greenhouse with a thermal screen closed at night consumed 22 to 41% less energy than a greenhouse without a thermal screen.

Another benefit of retractable screens is the potential to increase LWR absorbed by the crop (Kittas et al., 2003). During the night, the interior surface temperature of a thermal screen is often higher than glazing temperature. Therefore, when a screen is extended over a crop, plants receive more incoming LWR than without a screen. The higher net LWR (LWR_{net}) exchange can increase plant temperature. For example, a rose (*Rosa hybrida* L.) crop grow under a greenhouse thermal screen with 75% SWR transmission had 100% higher absorbed LWR and 1 to 3 °C higher canopy temperature at night than a crop grown without a screen (Kittas et al., 2003). Studies with other crops such as African violet, tomato (*Lycopersicon esculentum* Mill.), and vinca have also reported higher canopy, leaf, or shoot-tip temperatures under screens compared with no screens (Bailey, 1977 and 1981a; Faust, 1994). However, to our knowledge, crop models that predict the influence of thermal screens on plant shoot-tip temperature during the night have not been published.

The objective of this study was to quantify the effect of different screen materials on shoot-tip temperature of New Guinea impatiens (*Impatiens hawkeri* Bull.) during cold nights. Our goal was to develop a shoot-tip temperature model using environmental factors that can be measured in commercial greenhouses. New Guinea impatiens was selected because it is among the top 10 bedding plants produced in the United States, with a reported wholesale value of $54 million in 2008 (U.S. Department of Agriculture,

2009). Since plant development of New Guinea impatiens is delayed considerably at a low temperature (Erwin, 1995), a model that predicts shoot-tip temperature could improve production scheduling and management of the greenhouse environment.

Materials and Methods

Greenhouse Experiment

Plant material. On 26 Nov. 2008, rooted vegetative cuttings of New Guinea impatiens 'Supersonic Flame' grown 50-cell trays (2.5 × 2.5 cm; 27.2-ml volume) were received from a commercial greenhouse (Raker's Acres, Inc., Litchfield, MI). Plants were subsequently transplanted into 11-cm round plastic containers (600-ml volume) filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI) and were grown at a constant temperature set point of 23 °C. The photoperiod was a constant 16 h that consisted of natural photoperiods (42.7 °N lat.) with day-extension lighting from 0600 to 2200 HR provided by high-pressure sodium (HPS) lamps that delivered a photosynthetic photon flux of 75 to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height (as measured with a line quantum sensor [Apogee Instruments, Inc., Logan, Utah]).

Ethephon (Florel; Bayer CropScience LP, Research Triangle Park, NC) with a surfactant (Capsil; Aquatrols, Paulsboro, NJ) was applied as a foliar spray at 300 $mg \cdot L^{-1}$ and 0.2 $L \cdot m^{-2}$ every 2 to 3 weeks to abort flower buds. Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing ($mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

After 7.5 weeks, leaf canopy exceeded the container diameter and plants were transferred to different greenhouses for the screen study.

Greenhouse environment. The research facility for the screen experiment consisted of a row of six connected (4.8 × 4.1 m) glass-glazed greenhouse compartments oriented east-west. Compartments were separated by a glass wall orientated north-south. Only the middle four compartments were used for the experiment. In each compartment, 25 plants were grown on a bench that was positioned in the middle of the greenhouse. Plants were spaced so that leafs of adjacent plants touched and hence formed a full canopy.

In three compartments, a screen located horizontally at eave height was manually extended over plants at 1700 HR and retracted at 0800 HR. Screens were closed so that they contacted the greenhouse sidewalls. Control plants were grown in one compartment without a screen. Six 4-d experiments were performed during Jan. and Feb. with different screens and under different air vapor-pressure deficits (VPD_{air}). The screens used in the study were obtained from Ludvig Svensson, Inc. (Charlotte, NC) and included: (1) blackout with aluminized (AL) polyester and 0% light transmission (blackout AL); (2) blackout with black polyester and 0% light transmission (blackout BL); (3) closed-weave screen with alternating 5-mm wide AL and transparent plastic (TP) strips and 46% light transmission (energy AL/TP); (4) open-weave screen composed of alternating 5-mm wide AL, TP, and no strips with 50% light transmission (shade AL/TP/X); (5) closed-weave screen with 5-mm wide TP strips and 88% light transmission (energy TP1); and (6) closed-weave screen with 5-mm wide TP strips and 83% light transmission (energy TP2) (Table 4.1).

Temperature in each greenhouse compartment was controlled by an environmental computer (Priva Intégro 724; Priva, Vineland Station, Ontario) that controlled steam heating and passive and active ventilation when needed. The air temperature set point in each compartment was a constant 20 °C and the actual mean daily dry-bulb temperature was 19.9 ± 0.7 °C (± SD). The greenhouse was heated with steam-heating units located below the benches along the knee wall of each compartment. During the screen study, plants were grown without HPS lamps and under natural photoperiods. The calculated time from sunrise to sunset ranged from 9 to 11 h. Plants were grown with minimal overhead obstructions and were irrigated as previously described without water stress.

In each compartment, dry-bulb and wet-bulb temperature were independently measured by aspirated, shielded thermocouples (0.13-mm type E; Omega Engineering, Stamford, CT) positioned at plant level and adjacent to the canopy. Shoot-tip temperatures was independently measured on three plants in each compartment by inserting fine-wire thermocouples (Type E; Omega Engineering) ≈0.3 cm below the shoot apex. Thermocouples were reinserted every 4 d as plants unfolded leaves. At 15 cm above the canopy in each compartment, a pyranometer (LI-200SA; LI-COR, Lincoln, NE) measured shortwave radiation (SWR, 300 to 3,000 nm). At the same height, net radiation was measured in two compartments using total hemispherical radiometers (THR) [(250 to 60,000 nm) THRDS7.1; Radiation and Energy Balance Systems, Inc., Seattle, WA] and in one compartment using a net radiometer [(300 to 50,000 nm) CNR1; Kipp & Zonen USA Inc., Bohemia, NY]. Prior to the study, radiation measurements from the two THRs were collected over 2 days (307 measurements per instrument) and

compared against the net radiometer (reference) and a calibration equation was developed. The equation was subsequently applied to data from the THRs and adjusted values were calculated.

In each compartment, canopy temperature and cover temperature were recorded with infrared (IR, 6,500 to 14,000 nm) sensors (Type K, OS36-01; Omega Engineering Inc.) positioned 15 cm above the canopy and oriented vertically upward (cover) or downward (canopy). Cover temperature represented the greenhouse glazing and superstructure temperature when the screen was retracted and the surface temperature of the screen when it was extended over the crop. In two compartments, air velocity transducers (8470 and 8475; TSI, Inc., St. Paul, MN) positioned 2 cm from the shoot-tip measured air velocity and was 0 to 0.1 $m \cdot s^{-1}$. Active ventilation with fans did not occur during the study. In the two compartments in which air velocity was not measured continuously, air velocity was measured instantaneously at the same location and was found to be ± 0.05 $m \cdot s^{-1}$ of the other compartments.

Environmental greenhouse measurements were collected every 10 s and 10-min means were recorded by two data loggers (CR10; Campbell Scientific, Logan, UT). Outside air temperature was measured every 5 min by a Priva weather station located 2 m above the greenhouse peak and data was recorded by the greenhouse environmental-control computer. During three experimental periods, VPD_{air} was maintained at 0.4 to 0.8 kPa by the injection of steam into the air. During the other three experimental periods, VPD_{air} was not controlled and ranged from 1.4 to 1.8 kPa.

Data analysis. Data for cover temperature, net LWR, and the difference between shoot-tip and dry bulb temperature were analyzed for each 4-d experimental period by

using the 10-min means for each recorded parameter from each treatment. Data were analyzed using SAS (SAS Institute, Inc., Cary, NC) mixed model procedure (PROC MIXED), and pairwise comparisons between treatments were performed using Tukey's honestly significant difference test at $P \leq 0.01$.

Model Development

Plant shoot-tip temperature (T_{shoot}) is determined by the balance of incoming and outgoing energy. Incoming energy must equal outgoing energy or T_{shoot} will increase or decrease until an equilibrium is obtained. The relationship between the energy gained and the energy lost from a plant shoot-tip can be described as (Monteith and Unsworth, 2008) (Fig. 4.1):

Shortwave radiation + longwave radiation + convection + transpiration = 0 [1]

We developed a model to predict New Guinea impatiens T_{shoot} using the following equations to describe the individual components of the energy balance equation (Eq. [1]):

Shortwave radiation. SWR absorbed (SWR_{abs}) by the shoot-tip can be described as:

$$SWR_{abs} = a_{SWR} \times SWR_{mes} \quad [2]$$

where a_{SWR} is the shoot-tip absorptivity for SWR and SWR_{mes} is incident SWR on the shoot-tip. A typical mean absorbance value for plants of 0.5 was used for a_{SWR} (Nobel, 2005).

Longwave radiation. In greenhouses, closely spaced plants (as in this study) form a horizontal surface and exchange LWR with the greenhouse ceiling (e.g., glazing or screen) (Jones, 1994). The net flux of LWR (LWR_{net}) absorbed by a shoot-tip is the sum of incoming and outgoing radiation and can be described as (Holman, 1997):

$$LWR_{net} = (SF_{LWRnet}) \times \left(\frac{E_{Bc} - E_{Bshoot}}{\frac{1}{\varepsilon_c} + \frac{1}{\varepsilon_{shoot}} - 1} \right) \quad (\mathrm{W \cdot m^{-2}}) \qquad [3]$$

where $\frac{1}{\varepsilon_c} + \frac{1}{\varepsilon_{shoot}} - 1$ [4]

is resistance to LWR_{net} and is calculated with the emissivity of the cover (ε_c) and shoot-tip (ε_{shoot}). The emissivity for the bottom surface (facing downward towards crop) of each screen used in the experiment is presented in Table 4.1. An emissivity value of 0.9 and 0.96 was used for the glass-glazing and shoot-tip, respectively (Nijskens et al., 1984; Nobel, 2005). The emissive power of a black body at a cover temperature (E_{Bc}) and at T_{shoot} (E_{Bshoot}) is calculated as:

$$E_B = \sigma \times T^4 \quad (\mathrm{W \cdot m^{-2}}) \qquad [5]$$

where σ is the Stephan-Boltzmann constant (5.67 E−8) and T is the surface temperature of the cover or shoot-tip in Kelvin. The shape factor for LWR_{net} (SF_{LWRnet}) can be described as (Shimizu et al., 2004):

$$SF_{LWRnet} = \frac{d1}{d1 + (4 \times h1)} \quad [6]$$

where $d1$ and $h1$ are the diameter (m) and height (m) of the shoot-tip, respectively. New Guinea impatiens plants used in this experiment had a $d1$ and $h1$ of 0.0032 and 0.003 m, respectively, which were means of ten measurements made with a digital caliper.

Convection. Two types of convection (*Conv*) can be described as (Gates, 2003):

$$\begin{aligned} &\text{Free convection: } Gr > Re^2 \\ &\text{Forced convection: } Gr < Re^2 \end{aligned} \quad [7]$$

The Grashof (*Gr*) and Reynolds (*Re*) numbers are calculated as:

$$Gr = \frac{\left(\beta \times g \times d^3\right) \times \left(\left| T_{db} - T_{shoot} \right|\right)}{\nu^2} \quad [8]$$

$$Re = \frac{V \times d}{\nu} \quad [9]$$

where β is the coefficient of volumetric thermal expansion [for air, β equals the inverse of the dry-bulb temperature (T_{db}) in Kelvin], g is the acceleration of gravity (9.80 $m \cdot s^{-2}$), V is the air velocity ($m \cdot s^{-1}$), ν is the kinematic viscosity of air ($m^2 \cdot s^{-1}$) at the T_{db}, and d is the characteristic dimension of the shoot-tip:

$$d = \left(\frac{1}{d1} + \frac{1}{h1}\right)^{-1} \text{ (m)} \qquad [10]$$

Free *Conv* can be classified as laminar or turbulent flow based on the value of *Gr* multiplied by the Prandtl number [(*Pr*), 0.71] (Holman, 1997):

[11]

$$\text{Laminar flow: } 10^4 < (Gr \times Pr) < 10^9 \longrightarrow h_c = 1.42 \times \left(\frac{|T_{db} - T_{shoot}|}{d}\right)^{\frac{1}{4}} (\text{W}\cdot\text{m}^{-2}\cdot\text{K}^{-1})$$

$$\text{Turbulent flow: } 10^9 < (Gr \times Pr) \longrightarrow h_c = 1.31 \times (|T_{db} - T_{shoot}|)^{\frac{1}{3}} \ (\text{W}\cdot\text{m}^{-2}\cdot\text{K}^{-1}) \qquad [12]$$

where h_c is the *Conv* heat-transfer coefficient.

Forced *Conv* across a cylinder (e.g., plant shoot-tip) can be described as:

$$h_c = \left(\frac{\kappa}{d}\right) \times (C) \times \left(\frac{V \times d}{\nu}\right)^N \times Pr^{\frac{1}{3}} \ (\text{W}\cdot\text{m}^{-2}\cdot\text{K}^{-1}) \qquad [13]$$

where κ is the thermal conductivity of air (0.024 $\text{W}\cdot\text{m}^{-2}\cdot\text{K}^{-1}$) and *C* and *N* are constants that depend on *Re* (Table 4.3).

Using the calculated h_c value for free *Conv* (Eqs. [11] or [12]) or forced *Conv* (Eq. [13]), the total energy exchange by *Conv* is described as (Gates, 2003):

$$Conv = h_c \times (T_{db} - T_{shoot}) \ (\text{W}\cdot\text{m}^{-2}) \qquad [14]$$

Transpiration. The conductance of water vapor from the plant to the air (λE) is described as (Monteith and Unsworth, 2008):

$$\lambda E = \left(\frac{\rho \times C_p \times (e_s(T_{shoot}) - e(T_{db}))}{\gamma \times (R_b + R_c)} \right) \ (\mathrm{W \cdot m^{-2}}) \qquad [15]$$

where ρ is the density of air at the mean temperature of T_{db} and T_{shoot} in Kelvin, C_p is the specific heat of air (1010 $\mathrm{J \cdot kg^{-1} \cdot K^{-1}}$), $e_s(T_{shoot})$ is the saturation vapor pressure at T_{shoot}, $e(T_{db})$ is the vapor pressure at T_{db}, γ is the psychrometer value (0.0663 $\mathrm{kPa \cdot K^{-1}}$), R_b is the boundary layer resistance for water vapor, and R_c is the cuticle resistance of the shoot tip. R_b has been reported to be 0.93 times that of convective heat transfer resistance and can be calculated as (Monteith and Unsworth, 2008):

$$R_b = 0.93 \times \left(\frac{\rho \times C_p}{h_c} \right) \ (\mathrm{s \cdot m^{-1}}) \qquad [16]$$

Shoot-tip R_c is species dependent and must be experimentally calculated (Shimizu and Heins, 2000). Leaf R_c for New Guinea impatiens at a T_{db} of 18 to 24 °C and under SWR_{mes} of 30 to 450 $\mathrm{W \cdot m^{-2}}$ has been reported to range from 20 to 350 $\mathrm{s \cdot m^{-1}}$ (Al-Faraj et al., 1994; Mankin et al., 1998). To our knowledge, there is no published information on shoot-tip R_c for New Guinea impatiens. Therefore, measured environmental data and New Guinea impatiens T_{shoot} data from the validation study were used to generate equations that predict R_c. Equations were developed by first calculating SWR_{abs}, LWR_{net}, and $Conv$ from measured greenhouse data and solving Eq. [1] for λE. R_c was then estimated by rearranging Eq. [15]:

$$R_c = \left(\frac{\rho \times C_p \times (e_s(T_{shoot}) - e(T_{db}))}{\gamma \times \lambda E} \right) - R_b \qquad [17]$$

During the night, R_c was found to be related to shoot-tip vapor-pressure deficit (VPD_{shoot}) and LWR_{net}. Therefore, when SWR_{mes} is <5 W·m^{-2}, R_c was described with the following equations:

$$\begin{aligned} LWR_{net} < 0: \; R_c &= 257.4 + (445.3 \times (e_s(T_{shoot}) - e(T_{db}))) + (84.4 \times LWR) \\ LWR_{net} \geq 0: \; R_c &= 354.1 + (649.1 \times (e_s(T_{shoot}) - e(T_{db}))) + (84.8 \times LWR) \end{aligned} \qquad [18]$$

where R_c is always ≥0.

The environmental conditions used to generate these equations included 8,694 observations for R_c at a T_{db} of 18.3 to 22.3 °C, under a VPD_{shoot} of 0.1 to 1.6 kPa, and under LWR_{net} of −10.0 to 3.9 W·m^{-2}. During the day when SWR_{mes} was 5 to 530 W·m^{-2}, LWR_{net} was −17.9 to 5.2 W·m^{-2}, T_{db} was 15.0 to 23.4 °C, and VPD_{shoot} was 0.2 to 2.6 kPa, we found no relationship between R_c and VPD_{shoot}, VPD_{air}, SWR_{mes}, LWR_{net}, $T_{db}-T_{shoot}$, or T_{shoot}. Therefore, a constant R_c during the day was assumed and was calculated from the median of 5,114 observations (373 s·m^{-2}).

The complete model to predict New Guinea impatiens T_{shoot} under different greenhouse conditions was developed by substituting the components of Eq. [1] with Eqs. [2], [3], [14], and [15]. A similar modeling approach was used to predict poinsettia T_{shoot} (Shimizu and Heins, 2004). The model for New Guinea impatiens can predict T_{shoot} using five greenhouse environmental factors: T_{db}, T_{wb}, T_{cover}, SWR_{mes}, and V. The model also requires values for the diameter and height of the plant shoot-tip, SWR

absorptivity of the shoot-tip, and emissivity of the glazing or screen and the shoot tip. Since the model can not be analytically solved, a computer program was written and compiled in Microsoft Visual Basic 6.5 (Microsoft Corp., Redmond, WA) that used the root bisection technique (Wainwright and Mulligan, 2005) to find a value for shoot-tip temperature that satisfied [Eq. 1].

Results and Discussion

Model Validation

Environmental data (dry-bulb, wet-bulb, and cover temperature, measured SWR, and air velocity) from the greenhouse experiment and the emissivities of the glazing, screens, and plant were entered into the New Guinea impatiens shoot-tip model and the simulated shoot-tip temperatures were compared with the measured temperatures. The validation included measured data from 24 d and consisted of 5,184 observations for the day (screens open from 0800 to 1700 HR) and 8,640 observations for night (screens extended over crop). The night period for plants without a screen was considered to be from 1700 to 0800 HR during which the maximum measured SWR was 20.2 $W \cdot m^{-2}$. The actual sunset ranged from 1736 to 1815 HR and the actual sunrise ranged from 0729 to 0803 HR. During the night under all treatments, the simulated shoot-tip temperature was within 1 °C and 2 °C of the measured temperature 91% and 100% of the time, respectively (Fig. 4.2 to 4.3). During the day, the simulated shoot-tip temperature was within 1 °C and 2 °C of the measured temperature 63% and 89% of the time, respectively.

Influence of the Greenhouse Environment on Shoot-tip Temperature

During each experimental period and under all treatments, the measured mean shoot-tip temperature during the night was 0.6 to 3.8 °C lower than the mean dry-bulb temperature (Table 4.4 and Figs. 4.4 to 4.6). This shoot-tip temperature depression at night is in agreement with a poinsettia model that predicted shoot-tip temperature to be 4.2 °C lower than dry-bulb temperature at an air velocity of 0.05 $m \cdot s^{-1}$ and a dry-bulb, wet-bulb, and glazing temperature of 25, 22, and 0 °C, respectively (Shimizu et al., 2004). During the night, shoot-tip temperature depression occurs because energy losses from the plant exceed energy gains. Shoot-tip temperature at night can never be greater than air temperature without an infrared heat source (Rotz and Heins, 1982).

After the screens were retracted at 0800 HR, dry-bulb and shoot-tip temperature decreased on some days by up to 1.8 and 5.4 °C, respectively (Figs. 4.4 to 4.6). This temperature drop generally lasted for 30 to 60 min. During the day, plants had a measured mean shoot-tip temperature 1.2 °C lower than dry-bulb temperature when SWR was <100 $W \cdot m^{-2}$, and a mean of 1.6 °C higher than dry-bulb temperature when SWR was >100 $W \cdot m^{-2}$. Linear regression analysis performed on measured data predicted that as SWR increased from 5 to 250 $W \cdot m^{-2}$, the difference between shoot-tip and dry-bulb temperature increased linearly from −2.0 to 3.3 °C (data not shown). In African violet, shoot-tip temperature was up to 4 °C above the dry-bulb temperature on a sunny day (100 to 150 $W \cdot m^{-2}$) and 1 to 3 °C below the dry-bulb temperature on a cloudy day (≤50 $W \cdot m^{-2}$) (Faust and Heins, 1993).

Within each experimental period, plants under a screen extended during a cold night had a shoot-tip temperature 0.5 to 2.3 °C higher than plants without a screen (Table

4.4 and Figs. 4.4 to 4.6). This is in agreement with Faust (1994) who reported that at a nighttime glazing temperature of −1.5 °C, vinca had a mean shoot-tip temperature 2.9 °C higher under a screen compared to without a screen. Similarly, tomato grown under a thermal screen at night had a leaf temperature 0.5 °C higher than unscreened plants (Bailey, 1977).

The lower shoot-tip temperature in unscreened plants can be at least partially attributed to a net loss of LWR from the plant to the glazing at night (Bailey, 1977; Kittas et al., 2003). In a greenhouse, plants exchange LWR with the superstructure and sky above (Silva et al., 1991). According to the Stephan-Boltzmann law, emission of radiation from an object decreases as the surface temperature of the object decreases (Nobel, 2005). During the experimental period, plants that had a screen extended over them during the night had a cover temperature 0.8 to 6.9 °C higher than plants that were exposed to the glazing (Table 4.4). As cover temperature at night decreased, emitted LWR from the screen or glazing decreased and LWR_{net} absorbed by the plant decreased (data not shown). For example, LWR_{net} decreased from 5.7 to −22.9 $W \cdot m^{-2}$ and shoot-tip temperature decreased by 1.6 °C as cover temperature decreased from 20.1 to 14.4 °C during period 1.

Plants under a high air VPD (1.4 to 1.8 kPa) had a similar or up to 1.5 °C lower shoot-tip temperature at night than plants under a low VPD (0.4 to 0.9 kPa) (Table 4.4). If substrate moisture is not limiting, plant water uptake and transpiration increase as VPD increases (Mankin et al., 1998). Since the evaporation of water is an endothermic process, transpiration represents the loss of latent energy from a plant (Nobel, 2005). The simulation model predicted that at a T_{db}, T_{cover}, and V of 20 °C, 19 °C, and 0.1 $m \cdot s^{-1}$,

respectively, energy lost through transpiration at night would increase by 78% and shoot-tip temperature would decrease by 0.4 °C as air VPD increased from 0.5 to 2.0 kPa. Under the same environmental conditions, but with a T_{cover} of 14 °C, the model predicted energy lost through transpiration at night would increase by 24% and shoot-tip temperature would decrease by 0.2 °C as air VPD increased from 0.5 to 2.0 kPa Similarly, vinca shoot-tip temperature decreased by 1 °C when the VPD at night increased from 0.5 to 3.0 kPa (Faust and Heins, 1997). Mankin et al. (1998) also reported that New Guinea impatiens leaf temperature during the day decreased by 1 °C as air VPD increased from 0.5 to 1.5 kPa.

Shoot-tip temperature depression at night can also be caused by the convection of energy between the air and the plant. The amount of convection is influenced by the resistance of the boundary layer around the shoot-tip or leaf (Nobel, 2005). As air velocity decreases, boundary layer thickness and resistance to convective heat transfer increase. In this study, boundary layer resistance during the night was probably high because horizontal airflow fans (HAF) were turned off and mean air velocity was 0 $m \cdot s^{-1}$. New Guinea impatiens shoot-tip temperature at night could have been closer to air temperature with air movement. The simulation model predicted that at a T_{db}, T_{wb}, and T_{cover} of 20 °C, 14 °C, 19 °C, respectively, shoot-tip at night would increase from 18.2 to 19.5 °C if air velocity increased from 0 to 0.5 $m \cdot s^{-1}$. These results reinforce the importance of operating HAF fans at night in commercial greenhouses to increase convective heat transfer and thus plant temperature (Bartok, 2005).

Greenhouse screens are available from several manufacturers and are constructed of materials with different thermal and radiometric transmission properties (Bailey,

1981b; Cohen and Fuchs, 1999; Winspear and Bailey, 1978). A characteristic that can vary among screens is the emissivity. Emissivity is the ratio of radiation emitted from a material to the radiation emitted by a black body at the same temperature and ranges from 0 to 1 (Gates, 2003). As the emissivity of a material decreases, reflectivity and emitted radiation increase. The screens used in this study had a bottom emissivity that ranged from 0.5 to 0.88. In the present study, plants under closed-weave screens constructed of aluminized blackout (blackout AL), blackout with black polyester (blackout BL), and alternating AL and TP strips (energy AL/TP) had a shoot-tip temperature within 0.4 °C of each other (Table 4.4). Among these screens, there were no consistent trends between experimental periods in which screen elicited the greatest shoot-tip temperature. Similarly, vinca shoot-tip temperature under various closed-weave black or aluminized blackout screens was within 0.7 °C (Faust, 1994). The simulation model predicted that at a T_{db}, T_{wb}, T_{cover}, and V of 20 °C, 13 °C, 16 to 20 °C, and 0 to 0.5 $m \cdot s^{-1}$, respectively, shoot-tip temperature would be within 0.3 °C under a screen with an emissivity of 0.1 versus 1.0. Therefore, at the screen surface temperatures observed in this study, screen emissivity had little influence on shoot-tip temperature.

Although some of the screens had a similar emissivity, they had different bottom surface temperatures and different effects on plant shoot-tip temperature. For example, during periods 5 and 6, screens constructed of all transparent strips (energy TP1 and energy TP2; emissivity= 0.5 to 0.54) had a nighttime bottom surface temperature 1.7 to 2.6 °C lower than plants under Blackout AL (emissivity= 0.6) (Table 4.4 and Fig. 4.6). Under these same screens, plants had a shoot-tip temperature under 0.2 to 1.0 °C lower than plants under Blackout AL. The lower surface temperatures of some screens could

be related to differences in thermal conductivity, permeability, and thickness of the screen materials (Miguel et al., 1997; Nijskens et al., 1984; Winspear and Bailey, 1978). Materials that are thick or have low conductivity for heat transfer can elicit a high temperature gradient between the material surfaces (Nijskens et al., 1984). Therefore, a screen with high thermal conductivity can have a similar temperature on the upper surface exposed to the glazing as that of the lower surface exposed to the canopy. One strategy to increase screen temperature could be to utilize multiple horizontal shading or blackout screens (Heins and Runkle, 2004). The extension of two screens over a crop at night could increase the surface temperature of the lower screen and increase LWR absorbed by the plant.

Some greenhouse growers operate internal shading systems during the day when solar irradiance and outdoor temperature are high to reflect SWR and to prevent high temperature stress on crops (Heins and Runkle, 2004; Hoffmann and Waaijenberg, 2002). In this study, plants under a 50% shade screen with open-weave construction (shade AL/TP/X) had a nighttime shoot-tip temperature 0.2 to 0.6 °C higher than plants without a screen, but 0.9 to 1.4 °C lower than plants under Blackout AL or Shade CW (Table 4.4 and Fig. 4.4). These results indicate that the operation of an open-weave shade screen to reduce SWR transmission during the day can also increase shoot-tip temperature at night. However, there is a tradeoff between the shading percentage of a screen and its potential to reduce energy inputs for greenhouse heating. As the light transmission and air permeability of a screen increase, its insulative value decreases (Ludvig Svennson, 2009).

If a screen is constructed of a material with a very low emissivity (e.g., aluminum) and the heat permeability is high, then its surface temperature could decrease

below the dew-point temperature (Bailey, 1981b; Meijer, 1980). At surface temperatures lower than the dew-point temperature, water can condense on the screen and drip onto the crop below. In this study, screen temperature was always above the dew-point temperature and condensation did not occur. To minimize condensation in a greenhouse environment with high relative humidity, the screen surface with the lowest emissivity (i.e., high reflectivity of SWR) could be oriented upward and the surface with highest emissivity (high LWR absorption) could be orientated downward (Bailey, 1981b; Cohen and Fuchs, 1999).

The New Guinea impatiens shoot-tip model underestimated temperatures by up to 7.7 °C during the day when SWR was >100 $W \cdot m^{-2}$. The deviation between simulated and measured shoot-tip temperature during the day could be at least partially explained if the shoot-tip SWR absorptivity factor for New Guinea impatiens is greater than 50%. When a simulation was performed with a SWR absorbtivity factor of 80%, the model accuracy slightly improved between 1200 to 1400 HR, but was worse during the morning and late afternoon. Alternatively, the lower temperature predictions of the model during the day could be caused by over estimating the energy lost from transpiration. If transpiration decreased under high SWR, then shoot-tip temperature would increase. When the model was simulated with a very high cuticle transpiration resistance of 3,000 $s \cdot m^{-1}$ (i.e., low stomatal conductance), simulated shoot-tip temperatures increased and became closer to actual temperatures only when SWR was >150 $W \cdot m^{-2}$. However, published research on transpiration in New Guinea impatiens does not indicate that stomata would close during the day under these environmental conditions (Al-Faraj et al., 1994; Mankin et al., 1998; Pang, 1992).

The energy balance model used in this study is similar to the one developed by Shimizu et al. (2004) to predict poinsettia shoot-tip temperature. However, our model did not include a SWR shape factor to describe the ratio of shoot-tip surface area exposed to direct SWR to the total surface area. When a SWR factor was included in the model, simulated shoot-tip temperatures throughout the day were often greater than 2 °C below that measured. The accuracy of the model during the day improved when SWR absorbed by the shoot-tip was calculated based on the shoot-tip absorptivity for SWR and measured SWR (Faust and Heins, 1994).

Another difference between our model and the one for poinsettia is that we assumed that shoot-tip cuticle resistance for transpiration is not constant during the night (Al-Faraj et al., 1994; Mankin et al., 1998). The New Guinea impatiens model predicted cuticle resistance at night to increase as LWR_{net} increased and as the VPD between the shoot-tip and air increased. This response is in agreement with Mankin (1994) who also determined a positive relationship between increasing leaf VPD and New Guinea impatiens cuticle resistance. The shoot-tip model predicted that plants grown under a screen at night would have higher absorbed LWR_{net} and greater cuticle resistance than plants grown without a screen. For example, at a T_{db}= 20 °C, T_{wb}= 12 °C, T_{cover}= 19 °C, ε_{gs}= 0.9, and V= 0.1 $m \cdot s^{-1}$, shoot-tip temperature and cuticle resistance at night would be 19.1 °C and 849 $s \cdot m^{-1}$, respectively. Under the same environmental conditions, but with T_{cover}= 14 °C, shoot-tip temperature and cuticle resistance would be 18.3 °C and 442 $s \cdot m^{-1}$, respectively.

Several C_3 and C_4 annual and herbaceous perennial species, including New Guinea impatiens, maintain stomatal conductance and transpiration at night (Mankin et

al., 1998; Pang, 1992; Snyder et al., 2003). Therefore, nighttime transpiration and cuticle resistance represent important components of the energy balance model for New Guinea impatiens. The model predicted that shoot-tip transpiration would occur under any VPD. To prevent a shoot-tip temperature depression at night, the energy lost from transpiration must be balanced with the energy gained from convection and absorbed LWR. During winter in temperate climates, VPD at night can increase considerably because of infiltration of outside air containing little water vapor and the subsequent heating of this air (Hanan, 1990). These results indicate that during production of New Guinea impatiens, injecting water vapor into the air to decrease VPD would reduce transpiration and increase plant temperature.

In this study, plants exposed to the glazing had a measured mean nighttime shoot-tip temperature 2.4 to 4.4 °C lower than the greenhouse temperature set point of 20 °C. At temperatures below ≈17 °C, New Guinea impatiens development is severely delayed and there is greater variability in flowering (Erwin, 1995; Runkle 2008). Therefore, increased shoot-tip temperature at night under a screen can accelerate plant development. For example, time to flower of New Guinea impatiens 'Celebrette Peach' decreased by 3 d for every 1 °C increase in mean daily air temperature between 18 to 26 °C (Whitman et al., 2000). Assuming the cultivar in this study had a similar developmental response to mean daily shoot-tip temperature, a crop grown under a screen extended at night would flower up to 5 d earlier than a crop grown without a screen. These results support that a retractable greenhouse screen has the potential to decrease energy costs for heating (Brajeul et al., 2005) and also increase plant temperature and reduce production time.

Table 4.1. Characteristics of greenhouse screens used in experiment. Information obtained from manufacturer (Ludvig Svensson, Inc., Charlotte, NC). The bottom side of each screen was orientated towards the crop. Control plants were grown in a greenhouse without a screen and were exposed to glass glazing (emissivity= 0.9). SWR= shortwave radiation, 300 to 3,000 nm; AL= aluminum; BL= black; E= Empty space crossed with polyester threads; TP= transparent polyethylene.

Screen treatment	Description	SWR transmission (%)	Energy savings (%)	Emissivity bottom	Product name
Blackout AL	BL woven polyester; Top: polished AL coating with TP threads; Bottom: dull AL coating with BL threads	0	75	0.61	XLS Revolux FB A/A
Blackout BL	BL woven polyester with BL threads on both sides	0	75	0.88	XLS Obscura Revolux B/B
Energy AL/TP	AL-TP strips[z] woven with TP threads; Top: polished AL; Bottom: dull AL	46	57	0.54	XLS 15 FB
Shade AL/TP/X	AL-TP-AL-E-AL-E strips[z] woven with TP threads; Top: polished AL; Bottom: dull AL	50	20	0.50	XLS 15 F FB
Energy TP1	TP-TP strips[z] woven with TP threads	88	43	0.50	SLS 10 Ultra Plus
Energy TP2	TP-TP strips[z] woven with TP threads	83	47	0.54	XLS 10 Ultra Revolux

[z]5-mm wide parallel strips with different materials.

Table 4.2. Abbreviations, symbols, descriptions, and units of parameters in the New Guinea impatiens shoot-tip temperature model described in Eqs. [1–18].

Abbreviation or symbol	Description	Unit
β	Coefficient of volumetric thermal expansion	K^{-1}
γ	Psychrometer value (6.63 E–2)	$kPa \cdot K^{-1}$
λE	Transpiration	$W \cdot m^{-2}$
κ	Thermal conductivity of air (2.4 E–2)	$W \cdot m^{-2} \cdot K^{-1}$
ρ	Density of air	$Kg \cdot m^{-3}$
σ	Stefan-Boltzmann constant (5.67 E–8)	$W \cdot m^{-2} \cdot K^{-4}$
ε_c	Greenhouse glazing or screen emissivity	
ε_{shoot}	Plant shoot-tip emissivity	
a	Coefficient of thermal expansion rate of air	K^{-1}
a_{SWR}	Plant shoot-tip absorptivity	
C	Constant for calculating convection heat-transfer coefficient	
$Conv$	Convection	$W \cdot m^{-2}$
C_p	Specific heat of air	$J \cdot kg^{-1} \cdot K^{-1}$
d	Plant shoot-tip characteristic dimension	m
$d1$	Plant shoot-tip diameter	m
$e(T_{db})$	Vapor pressure at dry-bulb temperature	kPa
$e_s(T_{shoot})$	Saturation vapor pressure at shoot-tip temperature	kPa
E_B	Emmisive power of a black body	$W \cdot m^{-2}$
E_{Bc}	E_B at cover temperature	$W \cdot m^{-2}$
E_{Bshoot}	E_B at shoot-tip temperature	$W \cdot m^{-2}$
g	Acceleration of gravity	$m \cdot s^{-2}$
Gr	Grashof number	
$h1$	Plant shoot-tip height	m
h_c	Convection heat-transfer coefficient	$W \cdot m^{-2} \cdot K^{-1}$
LWR_{net}	Net longwave radiation	$W \cdot m^{-2}$
N	Constant for calculating convection heat-transfer coefficient	
Pr	Prandtl number (0.71)	
R_b	Boundary layer resistance for mass transfer	$s \cdot m^{-1}$
R_c	Cuticle resistance of shoot-tip	$s \cdot m^{-1}$
Re	Reynolds number	
SF_{LWRnet}	Shape factor for longwave radiation	
SWR_{abs}	Shortwave radiation absorbed by shoot-tip	$W \cdot m^{-2}$
SWR_{mes}	Measured shortwave radiation	$W \cdot m^{-2}$
T	Temperature	K
T_{db}	Dry-bulb temperature	°C
T_{cover}	Cover (glazing and superstructure or screen) temperature	°C
T_{shoot}	Shoot-tip temperature	°C
T_{wb}	Wet-bulb temperature	°C
ν	Kinematic viscosity of air	$m^2 \cdot s^{-1}$

Table 4.2 (cont'd).

Abbreviation or symbol	Description	Unit
V	Air velocity	$m \cdot s^{-1}$
VPD_{shoot}	Shoot vapor-pressure deficit $[e_s(T_{shoot}) - e(T_{db})]$	kPa

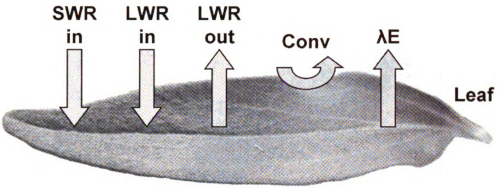
Table 4.3. C and N (unitless) with Eq. [13] (Gates, 2003).

Reynolds number (Re)	C	N
0.4 to 4	0.989	0.330
4 to 40	0.911	0.385
40 to 4,000	0.683	0.466
4,000 to 40,000	0.193	0.618
40,000 to 400,000	0.0266	0.805

Table 4.4. The effects of different screens on measured net longwave radiation (LWR_{net}) exchange between New Guinea impatiens shoot-tip and the cover (glazing and superstructure or screen) and the difference between measured shoot-tip temperature (T_{shoot}) and dry-bulb temperature (T_{db}) in glass-glazed greenhouses during the night (1700 to 0800 HR) in winter in East Lansing, MI (lat. 43 °N) under different air vapor-pressure deficits (VPD_{air}). Each experimental period was 4 d. The mean T_{db} during the experiments was 19.5 to 20.2 °C. See Table 4.1 for a description of screen materials. $T_{outside}$= outside air temperature; T_{cover}= cover (glazing and superstructure or screen temperature).

Expt. period (no.)	Mean $T_{outside}$ (°C)	Screen	VPD_{air} (kPa)	Mean T_{cover} (°C)	LWR_{net} ($W \cdot m^{-2}$)	Mean $T_{shoot}-T_{db}$ (°C)
1	−6.8	Blackout AL	1.6	20.1 a[z]	5.7 a	−2.1 b
		Energy AL/TP	1.5	18.9 b	1.3 b[y]	−1.9 a
		Shade AL/TP/X	1.6	17.1 c	−2.8 c	−2.3 c
		None	1.8	14.4 d	−22.9 d	−3.7 d
2	−9.8	Blackout AL	0.5	19.5 a	2.7 a	−1.2 a
		Energy AL/TP	0.5	18.5 b	−0.8 b[y]	−1.3 a
		Shade AL/TP/X	0.6	16.4 c	−5.2 c	−1.8 b
		None	0.7	14.0 d	−23.5 d	−2.7 c
3	−4.7	Blackout AL	1.4	19.1 b	1.3 b	−1.5 a
		Blackout BL	1.5	20.1 a	2.2 a	−1.7 a
		Energy AL/TP	1.4	18.6 c	0.2 c[y]	−1.9 b
		None	1.5	13.2 d	−25.4 d	−3.8 c
4	−10.8	Blackout AL	0.6	18.4 a	−0.1 a	−1.6 b
		Blackout BL	0.4	18.6 a	−2.2 b	−1.4 a
		Energy AL/TP	0.5	17.8 b	−1.5 b[y]	−1.3 a
		None	0.9	13.0 c	−27.7 c	−3.2 c
5	−2.9	Blackout AL	1.4	19.4 a	2.1 a	−1.3 a
		Energy TP1	1.4	16.8 c	−4.2 c	−2.3 c
		Energy TP2	1.4	17.7 b	−2.5 b[y]	−1.5 b
		None	1.4	15.0 d	−22.4 d	−3.1 d
6	0.5	Blackout AL	0.6	19.3 a	−0.3 a	−0.6 a
		Energy TP1	0.5	17.3 c	−4.5 c[y]	−0.9 b
		Energy TP2	0.5	17.5 b	−3.3 b	−1.1 c
		None	0.5	16.5 d	−14.8 d	−1.6 d

[z]Means within columns and experimental period followed by the same letter are not significantly different by Tukey's honestly significant difference test at $P \leq 0.01$.
[y]LWR_{net} not measured; calculated using Eq. [3] with cover and leaf temperature and screen and plant emissivity, but omitting the shape factor for LWR_{net}.



Energy balance: SWR + LWR + Conv + λE = 0

Fig. 4.1. Schematic illustration of the components of a leaf energy balance which include shortwave radiation (SWR), longwave radiation (LWR), convective heat transfer (Conv), and evaporative heat loss through transpiration (λE).

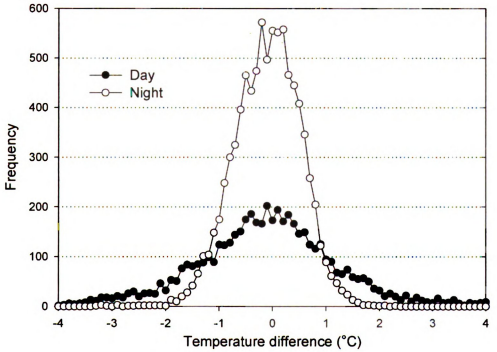


Fig. 4.2. Frequency of the difference between simulated New Guinea impatiens shoot-tip temperature and measured shoot-tip temperature for day and night using data from 24 d (13,824 observations). Plants were grown in glass-glazed greenhouses during winter in East Lansing, MI (lat. 43 °N) under different vapor-pressure deficits and with different screens extended over plants during the night (1700 to 0800 HR). Control plants were grown without a screen above.

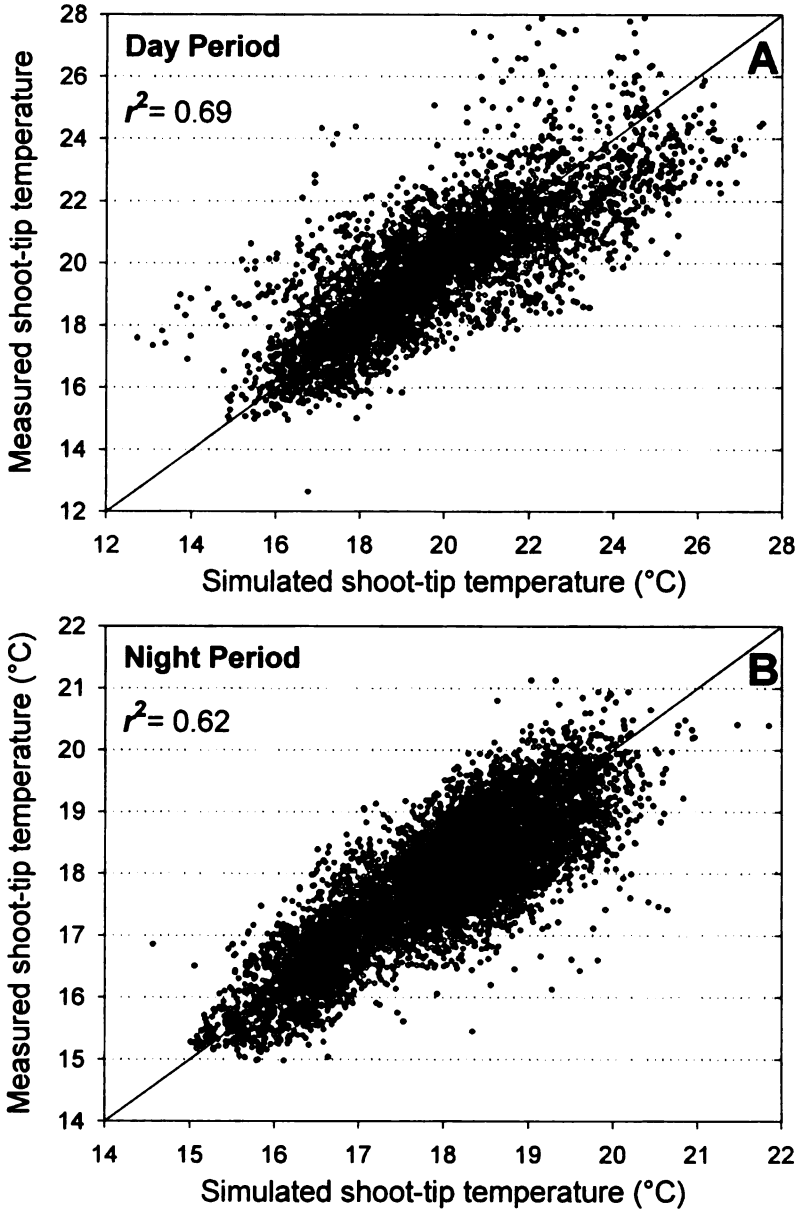


Fig. 4.3. Validation of the energy balance model, comparing simulated New Guinea impatiens shoot-tip temperature with measured shoot-tip temperature for the day [0800 to 1700 HR (**A**)] and night [1700 to 0800 (**B**)]. The validation included measured data from 24 d and consisted of 5,184 observations for the day and 8,640 observations for night. Plants were grown in glass-glazed greenhouses during winter in East Lansing, MI (lat. 43 °N) under different vapor-pressure deficits and with different screens extended over plants during the night. Control plants were grown without a screen above. r^2 values were generated by performing linear regression analysis on the simulated versus predicted data.

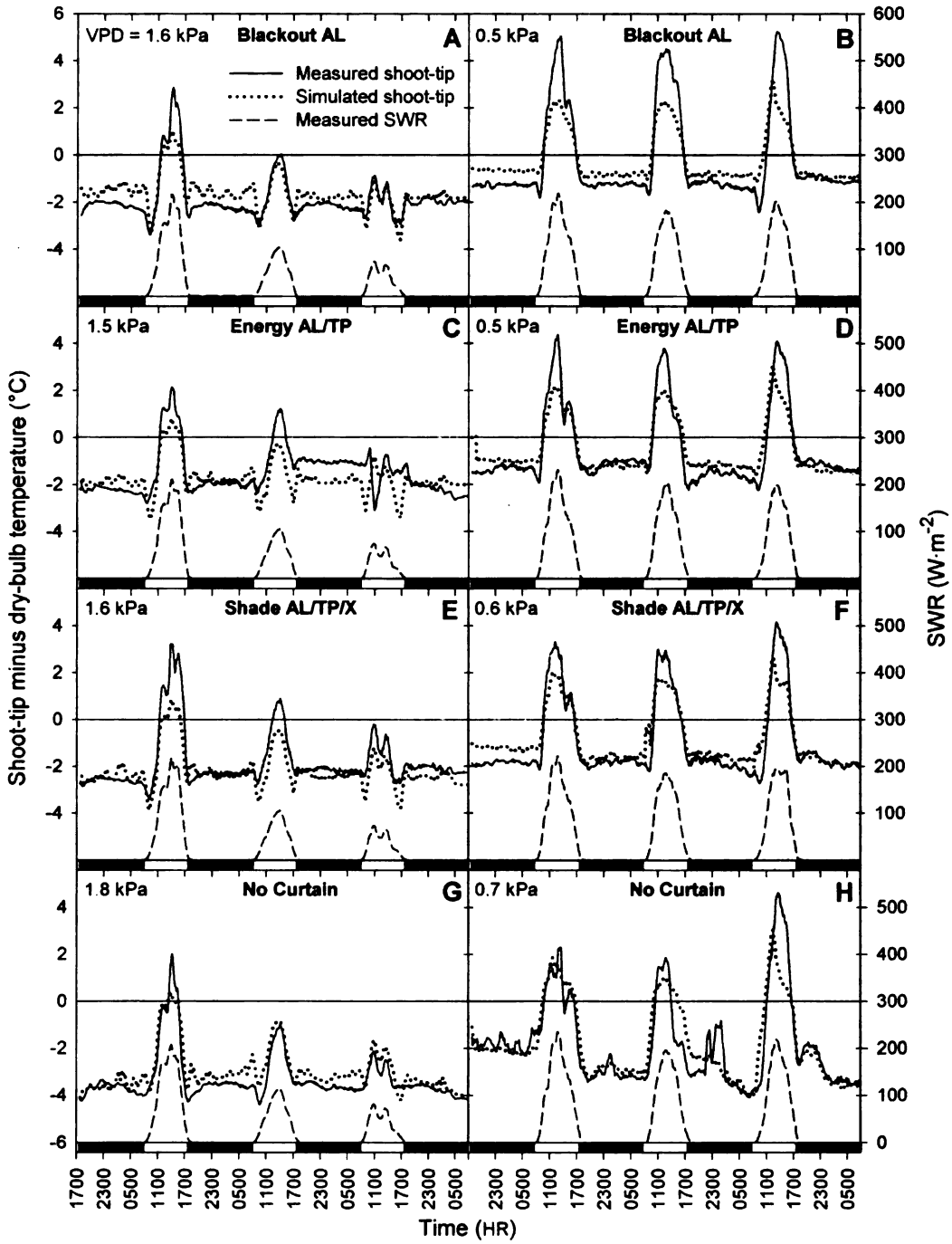


Fig. 4.4. Measured and simulated difference between New Guinea impatiens shoot-tip and dry-bulb temperature in glass-glazed greenhouses during winter in East Lansing, MI (lat. 43 °N) under different air vapor-pressure deficits (VPD) and with different screens extended over plants from1700 to 0800 HR. Control plants were grown without a screen above. The air temperature set point was 20 °C. See Table 4.1 for a description of screen materials. Data in panels A, C, E, and G and panels B, D, F, and H were collected during 20 to 24 Jan. and 25 to 29 Jan., respectively. Black bars represent night from actual sunset to sunrise. SWR= shortwave radiation (300 to 3,000 nm).

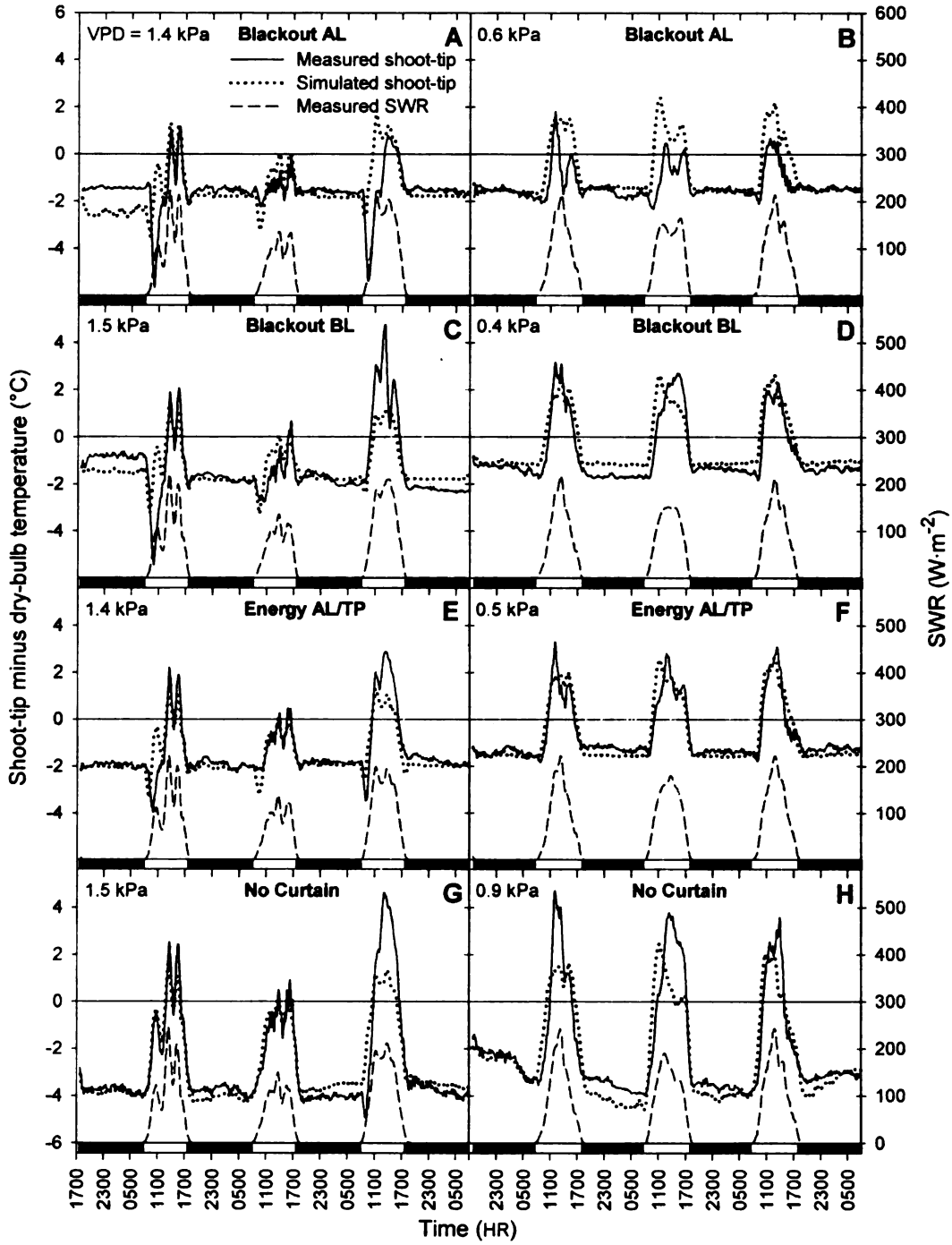


Fig. 4.5. Measured and simulated difference between New Guinea impatiens shoot-tip and dry-bulb temperature in glass-glazed greenhouses during winter in East Lansing, MI (lat. 43 °N) under different air vapor-pressure deficits (VPD) and with different screens extended over plants from 1700 to 0800 HR. Control plants were grown without a screen above. The air temperature set point was 20 °C. See Table 4.1 for a description of screen materials. Data in panels A, C, E, and G and panels B, D, F, and H were collected during 29 Jan. to 2 Feb. and 2 to 6 Feb., respectively. Black bars represent night from actual sunset to sunrise. SWR= shortwave radiation (300 to 3,000 nm).

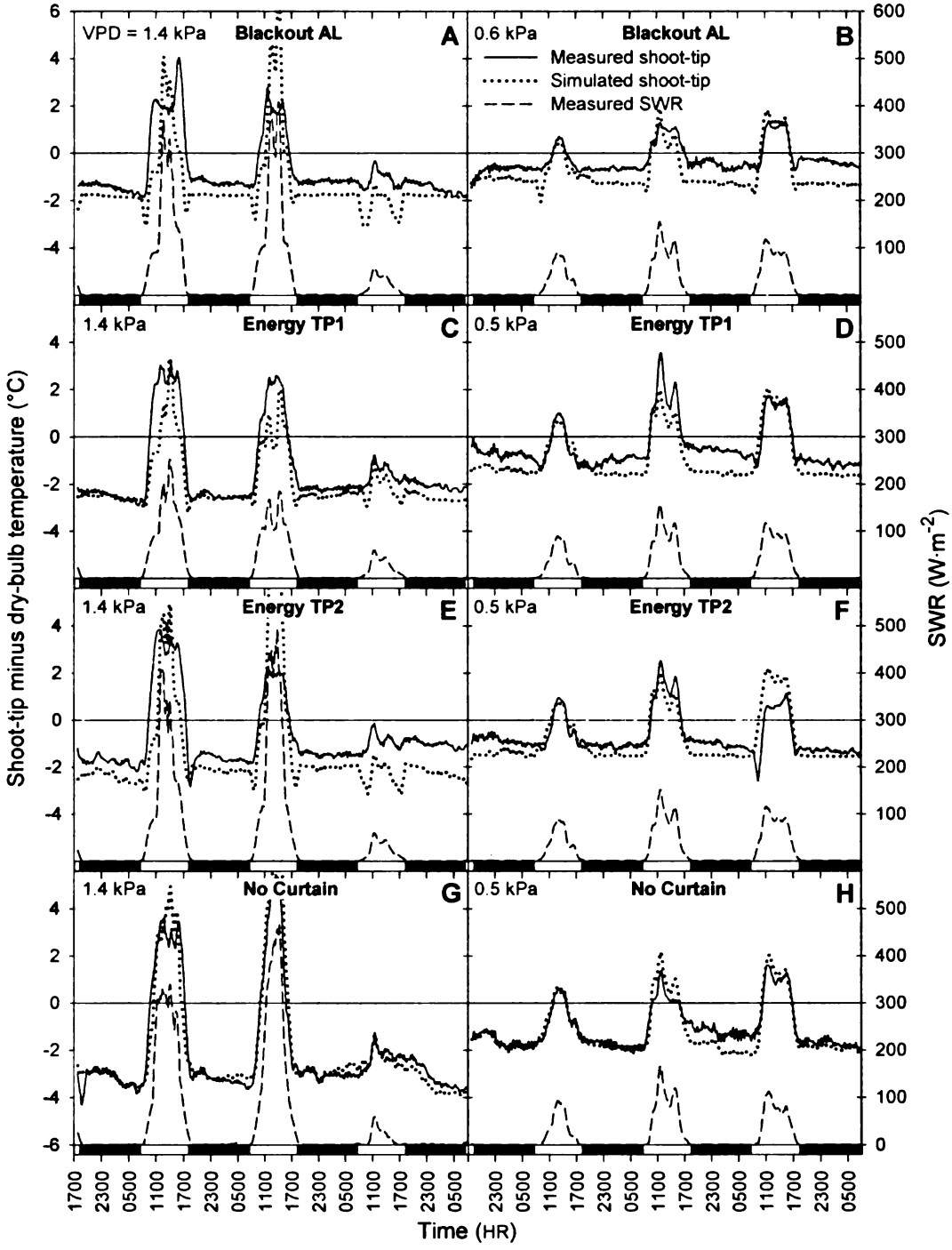


Fig. 4.6. Measured and simulated difference between New Guinea impatiens shoot-tip and dry-bulb temperature in glass-glazed greenhouses during winter in East Lansing, MI (lat. 43 °N) under different air vapor-pressure deficits (VPD) and with different screens extended over plants from 1700 to 0800 HR. Control plants were grown without a screen above. The air temperature set point was 20 °C. See Table 4.1 for a description of screen materials. Data in panels A, C, E, and G and panels B, D, F, and H were collected during 15 to 19 Feb. and 11 to 15 Feb., respectively. Black bars represent night from actual sunset to sunrise. SWR= shortwave radiation (300 to 3,000 nm).

Literature Cited

Adams, S.R., P. Hadley, and S. Pearson. 1998. The effects of temperature, photoperiod, and photosynthetic photon flux on the time to flowering of *Petunia* 'Express Blush Pink'. J. Amer. Soc. Hort. Sci. 123:577–580.

Al-Faraj, A., G.E. Meyer, and J.B. Fitzgerald. 1994. Simulated water use and canopy resistance of New Guinea Impatiens (*Impatiens* X *hb.*) in single pots using infrared heating. Trans. ASAE 37:1973–1980.

Bailey, B.J. 1977. Thermal screens for reducing heat losses from glasshouses. Acta Hort. 70:26–34.

Bailey, B.J. 1981a. The evaluation of thermal screens in glasshouses on commercial nurseries. Acta Hort. 115:663–670.

Bailey, B.J. 1981b. The reduction of thermal radiation in glasshouses by thermal screens. J. Agr. Eng. Res. 26:215–224.

Bailey, B.J. 1988. Improved control strategies for greenhouse thermal screens. Acta Hort. 230:485–492.

Bartok Jr., J. 2005. Grower 101: Horizontal air flow. Greenhouse Product News 15(9):26–28.

Brajeul, E., D. Lesourd, and D. Loda. 2005. Thermal screen evaluation in soilless cucumber crop under glasshouse. Acta Hort. 691:679–686.

Cohen, S. and M. Fuchs. 1999. Measuring and predicting radiometric properties of reflective shade nets and thermal screens. J. Agr. Eng. Res. 73:245–255.

Dieleman, J.A. and F.L.K. Kempkes. 2006. Energy screens in tomato: Determining the optimal opening strategy. Acta Hort. 718:599–606.

Erwin, J.E. and R.D. Heins. 1990. Temperature effects on lily development rate and morphology from the visible bud stage until anthesis. J. Amer. Soc. Hort. Sci. 115:644–646.

Erwin, J.E. 1995. Light and temperature, p. 41–54. In: W. Banner and M. Klopmeyer (eds.), New Guinea impatiens: A Ball guide. Ball Publ., Batavia, IL.

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

Faust, J.E. 1994. Modeling and managing shoot-tip temperatures in the greenhouse environment. Ph.D. Dissertation, Dept. of Horticulture, Michigan State Univ., East Lansing, MI.

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.

Faust, J.E. and R.D. Heins. 1998. Modeling shoot-tip temperature in the greenhouse environment. J. Amer. Soc. Hort. Sci. 123:208–214.

Gates, D.M. 2003. Biophysical ecology. Dover Publ. Mineola, NY.

Hanan, J.J. 1990. The influence of greenhouses on internal climate with special reference to Mediterranean regions. Acta Hort. 287:23–34.

Heins, R.D., B. Liu, and E.S. Runkle. 2000. Regulation of crop growth and development based on environmental factors. Acta Hort. 514:13–22.

Heins, R.D. and E. Runkle. 2004. Materials and strategies for greenhouse shade, p. 39–42. In: P. Fisher and E. Runkle (eds.), Lighting up profits: Understanding greenhouse lighting. Meister Media Worldwide, Willoughby, OH.

Hoffmann, S. and D. Waaijenberg. 2002. Tropical and subtropical greenhouses – a challenge for new plastic films. Acta Hort. 578:163–170.

Holman, J.P., 1997. Heat transfer. 8th ed. McGraw Hill, New York, NY.

Jones, H.G. 1992. Plants and microclimate. 2nd ed. Cambridge Univ. Press, New York, NY.

Kittas, C., N. Katsoulas, and A. Baille. 2003. Influence of an aluminized thermal screen on greenhouse microclimate and canopy energy balance. Trans. ASAE 46:1653–1663.

Korner, O., M.J. Bakker, and E. Heuvelink. 2004. Daily temperature integration: a Simulation study to quantify energy consumption. Biosystems Eng. 87:333–343.

Le Quillec, S., E. Brajeul, D. Lesourd, and D. Loda. 2005. Thermal screen evaluation in soilless tomato crop under glasshouse. Acta Hort. 691:709–716.

Ludvig Svensson, Inc. 2009. Cloth, firebreak, screens - Svensson screens. Ludvig Svensson, Inc. <http://www.ludvigsvensson.com> (last accessed October 29, 2009).

Lund, J.B., A. Andreassen, C.-O. Ottosen, and J.M. Aaslyng. 2006. Effect of a dynamic climate on energy consumption and production of *Hibiscus rosa-sinensis* L. in greenhouses. HortScience 41:384–388.

Mankin, K.R. 1994. Modeling nutrient and water uptake responses to the environment by New Guinea impatiens. Ph.D. Dissertation, Dept. of Agr. Eng., The Ohio State Univ., Columbus, OH.

Mankin, K.R., R.P. Fynn, and T.H. Short. 1998. Water uptake and transpiration characterization of New Guinea impatiens. Trans. ASAE 41:219–226.

Meijer, J. 1980. Reduction of heat losses from greenhouses by means of internal blinds with low thermal emissivity. J. Agr. Eng. Res. 25:381–390.

Miguel, A.F., N.J. van de Braak, and G.P.A. Bot. 1997. Analysis of the airflow characteristics of greenhouse screening materials. J. Agr. Eng. Res. 67:105–112.

Moccaldi, L.A. and E.S. Runkle. 2007. Modeling the effects of temperature and photosynthetic daily light integral on growth and flowering of *Salvia splendens* and *Tagetes patula*. J. Amer. Soc. Hort. Sci. 132:283–288.

Monteith, J.L. and M.H. Unsworth. 2008. Principles of environmental physics. 3rd ed. Academic Press, Burlington, MA.

Nijskens, J., J. Deltour, S. Coutisse, and A. Nisen. 1984. Heat transfer through covering materials of greenhouses. Agr. Forest Meteorol. 33:193–214.

Niu, G., R.D. Heins, A.C. Cameron, and W.H. Carlson. 2001. Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of *Campanula carpatica* 'Blue Clips'. Scientia Hort. 87:93–105.

Nobel, P.S. 2005. Physiochemical and environmental plant physiology. 3rd ed. Academic Press, Burlington, MA.

Öztürk, H.H. and A. Basçetinçelik. 1997. The nocturnal heat loss and internal temperatures in plastic tunnel greenhouses. Acta Hort. 443:79–84.

Pang, T. 1992. Dynamic analysis of water and nutrient uptake for New Guinea impatiens. Ph.D. Dissertation, Dept. of Agr. Eng., The Ohio State Univ., Columbus, OH.

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

Rotz, C.A. and R.D. Heins. 1982. Evaluation of infrared heating in a Michigan greenhouse. Trans. ASAE 25:402–407.

Runkle, E. 2008. Technically speaking: Overcoming New Guinea impatiens stall. Greenhouse Product News 18(2):62.

Shimizu, H. and R.D. Heins. 2000. Estimating cuticle resistance of seeding shoot tips based on the Penman Monteith model, p. 59–62. In: C. Kubota and C. Chun (eds.). Transplant production in the 21st century. Kluwer Academic Publ., Dordrecht, The Netherlands.

Shimizu, H., E.S. Runkle, and R.D. Heins. 2004. A steady-state model for prediction of poinsettia plant shoot-tip temperature. J. Amer. Soc. Hort. Sci. 129:303–312.

Silva, A.M., A. Miguel, and R. Rosa. 1991. Thermal radiation inside a single span greenhouse with a thermal screen. J. Agr. Eng. Res. 49:285–298.

Snyder, K.A., J.H. Richards, and L.A. Donovan. 2003. Night-time conductance in C_3 and C_4 species: Do plants lose water at night? J. Expt. Bot. 54:861–865.

U.S. Department of Agriculture. 2009. Floriculture crops 2008 summary. Agr. Stat. Board, Washington D.C.

Wainwright, J. and M. Mulligan. 2005. Environmental modeling: Finding simplicity in complexity. Wiley & Sons, England.

Whitman, C., D. Tschirhart, D. Joeright, and R. Heins. 2000. New Guinea impatiens: Flowers on time. Greenhouse Grower 18(10):48–60.

Winspear, K.W. and B.J. Bailey. 1978. Thermal screens for greenhouse energy effectiveness. Acta Hort. 87:111–118.

Zabeltitz, C.V. and J. Meyer. 1984. Evaluation of movable thermal screens in commercial greenhouses. Acta Hort. 148:437–442.

APPENDIX A

MODELING PLANT GROWTH AND DEVELOPMENT OF 29 BEDDING PLANT SPECIES AND CULTIVARS IN RESPONSE TO TEMPERATURE AND PHOTOSYNTHETIC DAILY LIGHT INTEGRAL

Research Objective

The objectives of this study were to quantify and model the influence of mean daily temperature (MDT) and photosynthetic daily light integral (DLI) on flowering during the finish stage of bedding plants under long-day conditions.

Materials and Methods

During Dec. 2006, Apr. 2007, Sept. 2007, or Mar. 2008, seeds of 29 bedding plant species and cultivars were sown in plug trays [288-cell size (6-ml volume)] by a commercial greenhouse (C. Raker & Sons, Litchfield, MI). After germination, plugs were received at Michigan State University (MSU) and were grown in a controlled environmental growth chamber at a constant temperature set point of 20 °C. A 16-h photoperiod was provided by 215-W cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and 60-W incandescent lamps (INC; Philips), at a CWF:INC (by W) of 3.6, and at an intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Plants were irrigated as necessary with well water acidified with H_2SO_4 to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$ and containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively. The water was supplemented with a water-soluble fertilizer providing (in $mg \cdot L^{-1}$) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, Mn, and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Greenhouse Environment

When seedlings were ready for transplant [16 to 45 d after seed sow, depending on species (Table 5.1)], they were transplanted into 10-cm round plastic containers (480-ml volume) filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). At transplant, plugs were thinned to one seedling per cell. Plants were randomly assigned to treatments and grown in glass-glazed greenhouses at constant air temperature set points of 14, 17, 20, 23, or 26 °C and under a 16-h photoperiod that consisted of natural photoperiods (43 °N lat.) with day-extension lighting from 0600 to 2200 HR provided by high-pressure sodium (HPS) lamps. At each temperature, plants were grown under two DLI treatments provided by ambient light and a combination of shade curtains (OLS 30, OLS 50; Ludvig Svensson Inc., Charlotte, NC) and different intensities (25 to 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of supplemental lighting from HPS lamps that were positioned above the shade curtains. Ten plants of each species were randomly assigned to each temperature and DLI combination. The HPS lamps were operated by an environmental computer (Priva Intégro 724; Priva, Vineland Station, Ontario) and were turned on when the outside light intensity was <290 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and turned off at >580 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Whitewash was applied to the greenhouse glazing during late Mar. each year, and removed in mid Oct. The experiment was performed twice under mean DLIs from transplant to flowering that ranged from 3.2 to 19.6 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 5.2).

Temperature in each greenhouse compartment was controlled by an environmental computer with steam heating, passive and active ventilation, and fan-and-pad evaporative cooling as needed. Air temperature was independently measured in each greenhouse by an aspirated, shielded thermocouple (0.13-mm type E; Omega

Engineering, Stamford, CT) positioned 1.5 m above the floor (at plant level). At 30 cm above the bench, the photosynthetic photon flux (*PPF*) was measured by a line quantum sensor containing 10 photodiodes (Apogee Instruments, Inc., Logan, UT) under six DLI and temperature combinations. Environmental measurements were collected every 10 s and hourly means were recorded by a data logger (CR10; Campbell Scientific, Logan, UT). A vapor-pressure deficit of 1.2 kPa was maintained during the night by the injection of steam into the air. Horizontal airflow fans positioned 1.4 m above the growing surface operated if the ridge vent was <90% of the maximum opening and provided air movement at ≈0.1 $m \cdot s^{-1}$. Plants were irrigated with reverse osmosis water supplemented with a water-soluble fertilizer providing (in $mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc.).

Data Collection and Analysis

The date of first open flower per plant was recorded and time to first open flower was calculated for each plant. The date of first open flower was recorded and time to flower was calculated for each plant. Plants were considered in flower according to individual flowering characteristics for each species (Table 5.1). When each plant flowered, plant height and the total number of open flowers and closed flower buds were recorded.

Flowering data were used to develop mathematical models to predict flower development rate under different MDT and DLI conditions. Models were generated using 155 to 200 observations (individual plants) for each species. Data were analyzed

using the calculated MDT and DLI for each plant from transplant to the date of flowering. DLI values for treatments that did not have a line quantum sensor were determined by calculating the mean irradiance among sensors that were positioned in other temperature treatments and under similar light conditions. Flowering time data were converted to developmental rates by calculating the reciprocal of days to flowering (1/d to flower). For all species except *Dahlia ×hybrida*, the following multiplicative model was developed to describe the relationship between the rate of progress to flowering and MDT and DLI:

$$1/\text{d to flower} = f_{\text{MDT}} \times f_{\text{DLI}} \qquad [3]$$

where f_{MDT} and f_{DLI} are temperature and light functions, respectively. Models of this type have been previously used to describe the rate of flower development in chrysanthemum (Hidén and Larsen, 1994; Larsen and Persson, 1999) and cineraria (Larsen, 1989). The response of flower development rate to MDT is described with a temperature function and can be quantified by algebraically rewriting equation [1] to include the base temperature:

$$1/\text{d to flower} = \begin{cases} 0 & \ldots \text{if MDT} \leq T_{\text{min}} \\ -1 \times T_{\text{min}} \times b_1 + b_1 \times \text{MDT} & \ldots \text{if } T_{\text{min}} < \text{MDT} \leq T_{\text{opt}} \end{cases} \qquad [4]$$

where T_{min} and MDT are measured in °C and b_1 is a species-specific temperature constant. We used a linear function to quantify the MDT response because plots of the

actual data showed that T_{opt} was not observed for all species except *Dahlia ×hybrida*. The influence of DLI on flower development rate was described with a light function (Larsen, 1990):

$$\text{DLI factor} = 1 - \text{EXP}(-e \times \text{DLI}) \quad [5]$$

where the light factor ranges from 0 to 1. The *e* value is a species-specific light constant and determines the skew of the curve and DLI is the mean ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) from transplant to flowering. This function indicates that the rate of progress towards flowering increases as DLI increases, until some saturating value.

The final model to predict the rate of development towards flowering consisted of equations [4] and [5] multiplied together:

$$\text{1/d to flower} = \begin{cases} 0 & \ldots \text{if MDT} \le T_{min} \\ (-1 \times T_{min} \times b_1 + b_1 \times \text{MDT}) \times & \ldots \text{if } T_{min} < \text{MDT} \le T_{opt} \\ (1 - \text{EXP}(-e \times \text{DLI})) & \end{cases} \quad [6]$$

A nonlinear model was used to describe the relationship between flowering rate and MDT for *Dahlia ×hybrida* (Landsberg, 1977; Reed et al., 1976):

$$\text{1/d to flower} = A \times (\text{MDT} - T_{min}) \times (T_{max} - \text{MDT})^B \quad [7]$$

$$\text{where } A = R_{max} / ((T_{opt} - T_{min}) \times (T_{max} - T_{opt})^B) \quad [8]$$

and $B = (T_{max} - T_{opt}) / (T_{opt} - T_{min})$ [9]

where MDT = mean daily air temperature (°C), T_{min} and T_{max} are the minimum and maximum temperatures, respectively. When MDT is $\leq T_{min}$ or $\geq T_{max}$, development rate is zero. T_{opt} is the temperature where the maximum development rate occurs (R_{max}) and the "B" value defines the skew of the function. This asymmetrical model describes a temperature-dependent promotion of development when $T_{min} < MDT \leq T_{opt}$ and a temperature-dependent inhibition of development when $T_{opt} < MDT < T_{max}$ (Larsen, 1990). This function has been used to model the influence of temperature on flowering rate in *Dahlia pinnata* Cav. (Brøndum and Heins, 1993) and leaf unfolding and leaf expansion rate in *Saintpaulia ionantha* Wendl. (African violet) (Faust and Heins, 1993, 1994). The complete multiplicative model to describe the flowering rate of *Dahlia ×hybrida* was generated by multiplying Eq. [5] with Eq. [7].

Estimates for model coefficients were determined with the nonlinear regression procedure (NLIN) of SAS (version 9.1; SAS Institute, Cary, NC). T_{min} for *Ageratum houstonianum* 'High Tide Blue', *Begonia semperflorens-cultorum* 'Sprint Blush', *Catharanthus roseus* 'Viper Grape', *Cleome hassleriana* 'Queen Mix', *Lobelia erinus* 'Riviera Midnight Blue', *Osteospermum ecklonis* 'Passion Mix', *Pelargonium ×hortorum* 'Florever Violet', *Petunia ×hybrida* 'Easy Wave Coral Reef', *Petunia ×hybrida* 'Fantasy Blue', *Tagetes erecta* 'Moonstruck Orange', and *Verbena ×hybrida* 'Obsession Lilac' was estimated by using the NLIN procedure of SAS. Estimates of T_{min} for all other species were obtained from Table 1.2.

Data for flower bud or inflorescence number at first flowering were analyzed using the regression procedure (REG) of SAS to determine the influence of MDT and DLI. The flower bud and inflorescence number response surfaces equations are in the form:

$$y = y_0 + a\text{MDT} + b\text{MDT}^2 + c\text{DLI} + d\text{DLI}^2 + g\text{MDT} \times \text{DLI} \quad [10]$$

where y_0 is the y-axis intercept and a, b, c, d, and g are species-specific constants. Previous published studies that quantified the influence of MDT and DLI on flowering used a similar polynomial equation (Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005). The terms of the equation were only included if they were significant at $P \leq 0.05$.

Model Validation

During fall 2008 and spring 2009, seeds of each species were sown in 288-cell plug trays by a commercial greenhouse. After germination, trays were received at MSU and grown in an environmental growth chamber. Environmental conditions inside the chamber, plant culture, and transplant schedules were the same as described for the previous experiments. Seedlings were transplanted into 10-cm round pots and 15 plants of each species were grown in glass-glazed greenhouses at constant temperature set points of 17, 20, or 23 °C and under a 16-h photoperiod and a mean DLI of 10 to 19 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. In each greenhouse, air temperature and *PPF* were measured on each bench and data was recorded by a data logger as previously described. Photoperiod control, plant culture, and data collection were the same a previously described. Data

collected from the validation study were used to test the accuracy and precision of model predictions. Validation experiments were not performed with *Begonia semperflorens-cultorum* 'Sprint Blush', *Catharanthus roseus* 'Viper Grape', *Osteospermum ecklonis* 'Passion Mix', *Pelargonium ×hortorum* 'Florever Violet', and *Tagetes erecta* 'Moonstruck Orange' because plants were not available from the commercial plug producer.

A separate validation experiment was performed with *Petunia ×hybrida* 'Dreams Neon Rose' and *Antirrhinum majus* 'Montego Burgundy Bicolor' to validate the flower development rate models and to determine the variation in flowering time among a population of plants grown under the same environmental conditions. On 1 April and 28 March 2009, seedlings of *Petunia* and *A. majus*, respectively, grown in 288-cell plug trays were transplanted into 10-cm round pots and 150 plants of each species were grown in a glass-glazed greenhouse at a MDT of 21 °C and under a 16-h photoperiod and a mean DLI of 21 $mol \cdot m^{-2} \cdot d^{-1}$. Plants of each species were grown on the same bench.

Air temperature and *PPF* were measured on each bench and data was recorded by a data logger as previously described. Photoperiod control, plant culture, and data collection were the same a previously described. *Petunia* was considered flowering when individual plants had one flower with a fully open corolla. *A. majus* was considered flowering when individual plants had 2 flowers open on an inflorescence.

Table 5.1. Time from seed sow to transplant (TP), mean node number at TP, and characteristics used to determine flowering date of bedding plants used in modeling experiments.

Species	Time from seed sow to TP (d)	Mean node no. at TP	Flowering characteristic
Ageratum houstonianum 'High Tide Blue'	27	3.2	2 flowers open on an inflorescence
Angelonia angustifolia 'Serena Purple'	40	5.8	3 flowers open on an inflorescence
Antirrhinum majus 'Montego Burgundy'	41	3.1	2 flowers open on an inflorescence
Begonia semperflorens-cultorum 'Sprint Blush'	38	3.9	1 flower open on an inflorescence
Browallia speciosa 'Bells Marine'	40	5.9	1 flower open
Catharanthus roseus 'Viper Grape'	38 or 45	2.2	1 flower open
Cleome hassleriana 'Queen Mix'	28	4.3	6 flowers open on an inflorescence
Cosmos sulphureus 'Cosmic Orange'	23	2.6	1 inflorescence with 1 whorl of petals reflexed
Dahlia ×hybrida 'Figaro Mix'	26	3.2	1 inflorescence with 1 whorl of petals reflexed
Dianthus chinensis 'Super Parfait Raspberry'	38	5.3	1 inflorescence with 1 whorl of petals reflexed
Gazania rigens 'Daybreak Bronze'	31	4.7	1 inflorescence with petals reflexed
Lobelia erinus 'Riviera Midnight Blue'	45	3.1	1 flower open
Osteospermum ecklonis 'Passion Mix'	28	4.6	1 inflorescence with 1 whorl of petals reflexed
Pelargonium ×hortorum 'Florever Violet'	28	3.8	5 flowers open on an inflorescence
Pentas lanceolata 'Graffiti Lavender'	40	3.9	8 flowers open on an inflorescence
Petunia ×hybrida 'Dreams Neon Rose'	31	6.2	1 flower with fully open corolla
Petunia ×hybrida 'Easy Wave Coral Reef'	27	6.7	1 flower with fully open corolla
Petunia ×hybrida 'Fantasy Blue'	34	11.2	1 flower with fully open corolla
Petunia ×hybrida 'Wave Purple'	33	7.2	1 flower with fully open corolla

Table 5.1 (cont'd).

Portulaca grandiflora 'Margarita Apricot'	44	18.8	1 flower open
Rudbeckia hirta 'Becky Cinnamon Bicolor'	31	5.5	1 inflorescence with 1 whorl of petals reflexed
Salvia farinacea 'Blue Bedder'	29	4.3	3 flowers open on an inflorescence
Tagetes erecta 'Antigua Primrose'	19 or 23	6.0	1 inflorescence with ≥50% of petals reflexed
Tagetes erecta 'Moonstruck Orange'	25	6.0	1 inflorescence with ≥50% of petals reflexed
Tagetes patula 'Janie Flame'	19 or 23	6.4	1 inflorescence with ≥50% of petals reflexed
Verbena ×hybrida 'Obsession Lilac'	28	4.5	6 flowers open on an inflorescence
Verbena ×hybrida 'Quartz Waterfall Mix'	32	3.6	6 flowers open on an inflorescence
Viola cornuta 'Sorbet Plum Velvet'	38	6.5	1 flower open
Zinnia elegans 'Dreamland Coral'	16	3.5	1 inflorescence with 1 whorl of petals reflexed

Table 5.2. Mean daily air temperature (MDT) at the indicated set points and mean photosynthetic daily light integral (DLI) above benches, from transplant to flowering of each species, in glass-glazed greenhouse compartments during experiments.

		MDT (°C)					DLI (mol·m^{-2}·d^{-1})[z]	
Species	Expt.	14	17	20	23	26	Low	High
Ageratum houstonianum 'High Tide Blue'	1	14.4	17.1	19.9	22.7	–[y]	4.1	11.1
	2	17.4	18.9	20.7	23.1	–	6.0	18.7
Angelonia angustifolia 'Serena Purple'	1	–	17.1	18.7	22.7	26.0	5.4	14.7
	2	–	17.2	19.4	23.0	–	–	10.4
Antirrhinum majus 'Montego Burgundy'	1	14.2	17.0	19.9	22.7	–	4.0	10.3
	2	17.1	18.6	20.6	23.0	–	6.0	18.6
Begonia semperflorens-cultorum 'Sprint Blush'	1	–	17.2	19.9	22.8	25.6	4.2	11.4
	2	–	19.2	21.1	23.3	26.2	6.2	19.1
Browallia speciosa 'Bells Marine'	1	14.5	17.1	20.1	22.8	25.9	4.6	10.5
	2	17.1	18.8	21.0	23.1	26.2	5.4	14.6
Catharanthus roseus 'Viper Grape'	1	–	17.2	19.9	22.8	25.7	4.4	11.8
	2	–	17.0	20.0	22.8	25.9	4.6	10.1
Cleome hassleriana 'Queen Mix'	1	14.6	17.1	20.3	22.8	25.9	4.6	10.4
	2	16.7	18.4	20.7	22.8	26.1	6.2	17.2
Cosmos sulphureus 'Cosmic Orange'	1	14.3	17.0	19.9	22.7	–	3.2	9.3
	2	16.8	18.4	20.6	23.1	–	5.8	17.9
Dahlia ×hybrida 'Figaro Mix'	1	14.7	17.2	20.3	22.8	25.9	4.3	10.3
	2	16.1	18.0	20.6	22.8	26.2	6.1	17.0
Dianthus chinensis 'Super Parfait Raspberry'	1	14.5	17.2	19.9	22.8	–	4.9	12.4
	2	17.4	18.9	20.9	23.2	–	6.0	18.2
Gazania rigens 'Daybreak Bronze'	1	–	17.3	19.9	22.9	25.7	5.2	12.1
	2	–	19.4	21.1	23.3	26.1	6.6	19.0
Lobelia erinus 'Riviera Midnight Blue'	1	14.3	17.1	19.9	22.8	–	4.7	11.9
	2	–	–	–	–	–	–	–
Osteospermum ecklonis 'Passion Mix'	1	14.6	17.2	20.3	22.8	25.9	4.4	10.2
	2	16.4	18.3	20.8	22.9	26.2	5.8	16.5

Table 5.2 (cont'd).

Species	Expt.	MDT (°C) 14	17	20	23	26	DLI (mol·m^{-2}·d^{-1})^z Low	High
Pelargonium ×hortorum 'Florever Violet'	1	–	17.3	19.9	22.8	25.6	4.9	11.6
	2	–	19.3	21.2	23.3	26.1	6.4	18.4
Pentas lanceolata 'Graffiti Lavender'	1	–	17.0	20.1	22.8	25.9	4.9	10.3
	2	17.0	19.0	21.0	23.2	26.2	5.4	14.6
Petunia ×hybrida 'Dreams Neon Rose'	1	14.4	16.2	19.0	21.1	23.5	4.1	10.5
	2	15.7	16.6	18.2	20.6	23.1	6.6	17.9
Petunia ×hybrida 'Fantasy Blue'	1	14.9	17.4	20.6	22.9	26.0	4.1	10.8
	2	15.3	17.6	20.5	22.5	26.1	6.3	18.7
Petunia ×hybrida 'Easy Wave Coral Reef'	1	14.2	17.0	19.9	22.7	–	3.9	10.4
	2	17.1	18.7	20.6	23.0	–	6.1	18.7
Petunia ×hybrida 'Wave Purple'	1	14.7	17.2	20.3	22.9	25.9	4.3	10.5
	2	16.3	18.0	20.4	22.6	26.0	5.9	16.4
Portulaca grandiflora 'Margarita Apricot'	1	–	17.4	19.8	23.0	25.6	5.6	13.5
	2	–	19.6	21.2	23.4	26.3	6.5	19.1
Rudbeckia hirta 'Becky Cinnamon Bicolor'	1	13.8	17.3	19.8	22.8	–	4.9	12.7
	2	17.9	19.3	21.2	23.3	–	6.5	19.4
Salvia farinacea 'Blue Bedder'	1	–	17.3	19.9	22.8	25.6	4.6	11.8
	2	–	18.7	20.7	23.1	25.9	5.9	17.9
Tagetes erecta 'Antigua Primrose'	1	14.6	17.2	20.3	22.8	25.9	4.2	10.4
	2	16.5	18.3	20.9	22.9	26.1	6.0	16.7
Tagetes erecta 'Moonstruck Orange'	1	14.4	17.2	19.9	22.8	–	4.6	11.9
	2	17.9	19.3	21.1	23.3	–	6.5	19.2
Tagetes patula 'Janie Flame'	1	14.1	16.4	19.5	21.4	23.9	3.8	10.7
	2	15.1	17.1	18.7	21.0	23.7	6.9	19.6
Verbena ×hybrida 'Obsession Lilac'	1	–	17.1	19.9	22.7	25.7	3.6	9.8
	2	–	18.9	20.7	23.1	25.9	6.3	19.2
Verbena ×hybrida 'Quartz Waterfall Mix'	1	14.7	17.2	20.3	22.8	25.9	4.4	10.4
	2	16.0	18.3	20.7	22.8	26.1	5.8	16.3

Table 5.2 (cont'd).

Species	Expt.	MDT (°C) 14	17	20	23	26	DLI (mol·m^{-2}·d^{-1})[z] Low	High
Viola cornuta 'Sorbet Plum Velvet'	1	14.2	17.0	19.9	22.8	–	4.2	10.6
	2	–	17.7	19.6	23.4	–	–	11.2
Zinnia elegans 'Dreamland Coral'	1	–	17.0	19.9	22.7	25.5	3.5	8.8
	2	–	18.7	20.7	23.1	25.9	5.9	17.9

[z]Light from natural photoperiods and supplemental light from high-pressure sodium lamps that were turned on when the outside photosynthetic photon flux was <290 μmol·m^{-2}·s^{-1} and turned off when >580 μmol·m^{-2}·s^{-1}.
[y]Temperature treatment not included.

Table 5.3. Parameter estimates for nonlinear model (Eq. [6] relating flowering rate to mean daily air temperature [MDT (°C)] and daily light integral [DLI (mol·m^{-2}·d^{-1})]. Models are in the form of: 1/d to flower = (−1 × T_{min} × b_1 + b_1 × MDT) × (1 − exp(−e × DLI)). CI= confidence interval.

Species	T_{min} (°C)	b_1	b_1 95% CI	e	e 95% CI	r^{2z}
Ageratum houstonianum 'High Tide Blue'	7.8	2.48 E−03	3.60 E−04	5.28 E−01	1.33 E−01	0.58
Angelonia angustifolia 'Serena Purple'	9.9	2.31 E−03	5.00 E−05	5.60 E−01	1.14 E−01	0.90
Antirrhinum majus 'Montego Burgundy'	2.0	2.12 E−03	9.00 E-05	2.54 E−01	3.93 E−02	0.65
Begonia semperflorens-cultorum 'Sprint Blush'	6.1	2.07 E−03	2.80 E−04	4.41 E−01	8.85 E−02	0.61
Browallia speciosa 'Bells Marine'	8.9	1.81 E−03	6.00 E−05	2.84 E−01	3.21 E−02	0.81
Catharanthus roseus 'Viper Grape'	11.4	3.08 E−03	1.20 E−04	9.63 E−01	0	0.60
Cleome hassleriana 'Queen Mix'	7.5	1.93 E−03	1.60 E−04	1.69 E−01	1.83 E−02	0.91
Cosmos sulphureus 'Cosmic Orange'	7.2	2.09 E−03	4.00 E−05	7.56 E−01	1.22 E−01	0.80
Dianthus chinensis 'Super Parfait Raspberry'	3.9	1.33 E−03	3.00 E−05	4.71 E−01	1.41 E−01	0.60
Gazania rigens 'Daybreak Bronze'	4.8	1.48 E−03	9.00 E−05	1.54 E−01	2.34 E−02	0.73
Lobelia erinus 'Riviera Midnight Blue'	5.0	2.77 E−03	4.80 E−04	5.62 E−01	2.23 E−01	0.67
Osteospermum ecklonis 'Passion Mix'	1.4	1.06 E−03	5.00 E−05	2.53 E−01	3.52 E−02	0.57
Pelargonium ×hortorum 'Florever Violet'	5.0	1.21 E−03	8.00 E−05	2.59 E−01	1.61 E−02	0.89
Pentas lanceolata 'Graffiti Lavender'	9.3	1.58 E−03	4.00 E−05	4.17 E−01	5.46 E−02	0.84
Petunia ×hybrida 'Dreams Neon Rose'	2.8	2.50 E−03	6.00 E−05	4.37 E−01	5.83 E−02	0.87
Petunia ×hybrida 'Fantasy Blue'	3.0	3.55 E−03	2.80 E−04	1.83 E−01	3.95 E−02	0.49
Petunia ×hybrida 'Easy Wave Coral Reef'	7.3	2.96 E−03	3.50 E−04	3.20 E−01	4.70 E−02	0.72
Petunia ×hybrida 'Wave Purple'	5.5	1.95 E−03	3.00 E−05	3.28 E−01	2.50 E−02	0.92
Portulaca grandiflora 'Margarita Apricot'	8.9	2.63 E−03	9.00 E−05	3.84 E−01	0	0.52
Rudbeckia hirta 'Becky Cinnamon Bicolor'	4.6	1.25 E−03	5.00 E−05	4.43 E−01	1.20 E−01	0.59
Salvia farinacea 'Victoria Blue'	9.4	2.01 E−03	1.30 E−04	2.92 E−01	6.83 E−02	0.41
Tagetes erecta 'Antigua Primrose'	4.4	1.22 E−03	3.00 E−05	5.60 E−01	1.28 E−01	0.74
Tagetes erecta 'Moonstruck Orange'	2.9	1.21 E−03	1.00 E−04	3.75 E−01	4.06 E−02	0.80
Tagetes patula 'Janie Flame'	1.1	2.32 E−03	1.00 E−04	5.40 E−01	1.79 E−01	0.45
Verbena ×hybrida 'Obsession Lilac'	6.5	2.57 E−03	2.90 E−04	3.18 E−01	4.24 E−02	0.75
Verbena 'Quartz Waterfall Mix'	5.1	1.53 E−03	6.00 E−05	2.36 E−01	2.92 E−02	0.76

Table 5.3 (cont'd).

Species	T_{min} (°C)	b_1	b_1 95% CI	e	e 95% CI	r^{2z}
Viola cornuta 'Sorbet Plum Velvet'	4.1	3.34 E−03	3.10 E−04	1.84 E−01	4.48 E−02	0.77
Zinnia elegans 'Dreamland Coral'	7.8	1.97 E−03	5.00 E−05	3.69 E−01	4.12 E−02	0.76

[z]Generated by performing linear regression analysis on the predicted versus observed data.

Table 5.4. Parameter estimates for the nonlinear model (Eq. [5] × Eq. [7]) relating flowering rate in *Dahlia* ×*hybrida* 'Figaro Mix' to mean daily air temperature [MDT (°C)] and daily light integral [DLI ($mol \cdot m^{-2} \cdot d^{-1}$)]. CI= confidence interval.

Parameter	Estimate	95% CI (±)	r^{2z}
T_{min}	5.6	5.00 E−01	0.56
T_{opt}	22.3	6.20 E−01	
T_{max}	31.0	5.67	
R_{max}	2.37 E−02	9.00 E−04	
e	2.81 E−01	3.33 E−02	

[z]Generated by performing linear regression analysis on the predicted versus observed data.

Table 5.5. Parameters of stepwise regression analysis relating flower bud or inflorescence number to mean daily air temperature [MDT (°C)] and daily light integral [DLI ($mol \cdot m^{-2} \cdot d^{-1}$)]. All models are in the form of: $y = y_0 + aMDT + bMDT^2 + cDLI + dDLI^2 + gMDT \times DLI$.

Species	Parameter	y_0	a	b	c	d	g	r^2
Ageratum houstonianum 'High Tide Blue'	Inflorescences (n)	28.79	−6.75 E−01	–[z]	–	–	–	0.15
Angelonia angustifolia 'Serena Purple'	Inflorescences (n)	−73.79	8.26	−2.07 E−01	–	4.01 E−02	–	0.61
Antirrhinum majus 'Montego Burgundy'	Inflorescences (n)	126.03	−11.62	2.95 E−01	1.95	–	−8.74 E−02	0.50
Begonia semperflorens-cultorum 'Sprint Blush'	Inflorescences (n)	6.74	–	−9.69 E−03	–	−1.45 E−02	2.16 E−02	0.30
Browallia speciosa 'Bells Marine'	Flowers (n)	10.92	–	−3.24 E−02	6.39	−3.39 E−01	–	0.18
Catharanthus roseus 'Viper Grape'	Flowers (n)	−4.40	–	3.04 E−03	2.79	−1.66 E−01	–	0.17
Cleome hassleriana 'Queen Mix'	Inflorescences (n)	–	–	–	–	–	–	–
Cosmos sulphureus 'Cosmic Orange'	Inflorescences (n)	−89.83	11.08	−3.01 E−01	1.48	–	–	0.54
Dahlia ×hybrida 'Figaro Mix'	Inflorescences (n)	16.17	–	−2.00 E−02	8.52 E−01	–	–	0.40
Dianthus chinensis 'Super Parfait Raspberry'	Inflorescences (n)	154.98	−13.61	2.80 E−01	3.69	−1.17 E−01	–	0.59
Gazania rigens 'Daybreak Bronze'	Inflorescences (n)	57.10	−4.40	9.08 E−02	–	1.02 E−02	–	0.48
Lobelia erinus 'Riviera Midnight Blue'	Flowers (n)	–	–	–	–	–	–	–
Osteospermum ecklonis 'Passion Mixed'	Inflorescences (n)	189.43	−17.11	3.81 E−01	2.53	–	−9.05 E−02	0.70

Table 5.5 (cont'd).

Species	Parameter	y_0	*a*	*b*	*c*	*d*	*g*	r^2
Pelargonium ×hortorum 'Florever Violet'	Inflorescences (n)	5.36	–	−2.24 E−03	1.08 E−01	–	–	0.26
Pentas lanceolata 'Graffiti Lavender'	Inflorescences (n)	21.95	–	−2.43 E−02	−1.96	4.79 E−02	6.57 E−02	0.38
Petunia ×hybrida 'Dreams Neon Rose'	Flowers (n)	−17.28	3.69	−1.17 E−01	–	–	3.64 E−02	0.48
Petunia ×hybrida 'Fantasy Blue'	Flowers (n)	15.44	–	–	9.36 E−01	–	−4.3 E−02	0.04
Petunia ×hybrida 'Easy Wave Coral Reef'	Flowers (n)	257.30	−20.60	4.44 E−01	1.18	–	–	0.48
Petunia ×hybrida 'Wave Purple'	Flowers (n)	21.10	–	−5.38 E−02	9.02	−3.08 E−01	–	0.52
Portulaca grandiflora 'Margarita Apricot'	Inflorescences (n)	38.83	−2.91	6.79 E−02	1.57 E−01	–	–	0.10
Rudbeckia hirta 'Becky Cinnamon Bicolor'	Inflorescences (n)	62.79	−5.35	1.12 E−01	2.30	−8.43 E−02	–	0.33
Salvia farinacea 'Blue Bedder'	Inflorescences (n)	19.71	−6.06 E−01	–	−9.05 E−01	–	5.68 E−02	0.36
Tagetes erecta 'Antigua Primrose'	Inflorescences (n)	−10.73	4.04	−1.39 E−01	1.14	–	–	0.57
Tagetes erecta 'Moonstruck Orange'	Inflorescences (n)	−24.64	3.79	−1.02 E−01	2.06	–	−6.90 E−02	0.58
Tagetes patula 'Janie Flame'	Inflorescences (n)	6.70	–	–	9.52 E−01	–	−2.84 E−02	0.42
Verbena ×hybrida 'Obsession Lilac'	Inflorescences (n)	10.78	–	−8.64 E−03	2.89 E−01	–	–	0.33
Verbena ×hybrida 'Quartz Waterfall Mix'	Inflorescences (n)	78.60	−6.42	1.22 E−01	3.00	−1.11 E−01	–	0.59

Table 5.5 (cont'd).

Species	Parameter	y_0	*a*	*b*	*c*	*d*	*g*	r^2
Viola cornuta 'Sorbet Plum Velvet'	Flowers (n)	12.17	−4.00 E−01	–	–	1.62 E−02	–	0.14
Zinnia elegans 'Dreamland Coral'	Inflorescences (n)	−11.00	1.71	−4.66 E−02	–	–	1.83 E−02	0.64

[z]Parameter not significant at $P > 0.05$.

Table 5.6. Validation of the flowering rate models, comparing the observed time to flower with those predicted. Coefficients for the models are presented in Tables 5.3.and 5.4. r^2 values and the slope and intercept were determined by performing linear regression analysis on the predicted versus observed flowering rates.

Species	±5 d (%)	±7 d (%)	r^2	Slope= 1	Intercept= 0	N[z]
Ageratum houstonianum 'High Tide Blue'	84	98	0.60	*	*	49
Angelonia angustifolia 'Serena Purple'	78	91	0.83	*	*	45
Antirrhinum majus 'Montego Burgundy'	86	93	0.84	*	*	57
Begonia semperflorens-cultorum 'Sprint Blush'	–[y]	–	–	–	–	–
Browallia speciosa 'Bells Marine'	31	47	0.92	*	*	45
Catharanthus roseus 'Viper Grape'	–	–	–	–	–	–
Cleome hassleriana 'Queen Mix'	73	96	0.68	*	*	45
Cosmos sulphureus 'Cosmic Orange'	93	96	0.79	*	*	45
Dahlia ×hybrida 'Figaro Mix'	29	49	0.26	*	*	45
Dianthus chinensis 'Super Parfait Raspberry'	82	87	0.96	*	NS	45
Gazania rigens 'Daybreak Bronze'	51	67	0.88	NS	NS	45
Lobelia erinus 'Riviera Midnight Blue'	56	76	0.67	NS	NS	45
Osteospermum ecklonis 'Passion Mixed'	–	–	–	–	–	–
Pelargonium ×hortorum 'Florever Violet'	–	–	–	–	–	–
Pentas lanceolata 'Graffiti Lavender'	16	23	0.94	NS	*	44
Petunia ×hybrida 'Dreams Neon Rose'	89	100	0.67	NS	NS	45
Petunia ×hybrida 'Fantasy Blue'	84	98	0.32	*	*	45
Petunia ×hybrida 'Easy Wave Coral Reef'	67	96	0.60	*	*	45
Petunia ×hybrida 'Wave Purple'	98	100	0.93	NS	*	45
Portulaca grandiflora 'Margarita Apricot'	49	60	0.88	NS	NS	45

Table 5.6 (cont'd).

Species	±5 d (%)	±7 d (%)	r^2	Slope= 1	Intercept= 0	N[z]
Rudbeckia hirta 'Becky Cinnamon Bicolor'	57	76	0.51	*	*	45
Salvia farinacea 'Blue Bedder'	71	73	0.86	NS	*	45
Tagetes erecta 'Antigua Primrose'	40	69	0.80	*	*	45
Tagetes erecta 'Moonstruck Orange'	–	–	–	–	–	–
Tagetes patula 'Janie Flame'	91	100	0.60	NS	*	45
Verbena ×hybrida 'Obsession Lilac'	22	31	0.84	*	*	45
Verbena ×hybrida 'Quartz Waterfall Mix'	57	66	0.67	*	*	44
Viola cornuta 'Sorbet Plum Velvet'	96	100	0.84	NS	NS	45
Zinnia elegans 'Dreamland Coral'	100	100	0.94	*	*	45

[z]Number of observations in data set.

[y]Validation experiment not performed.

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

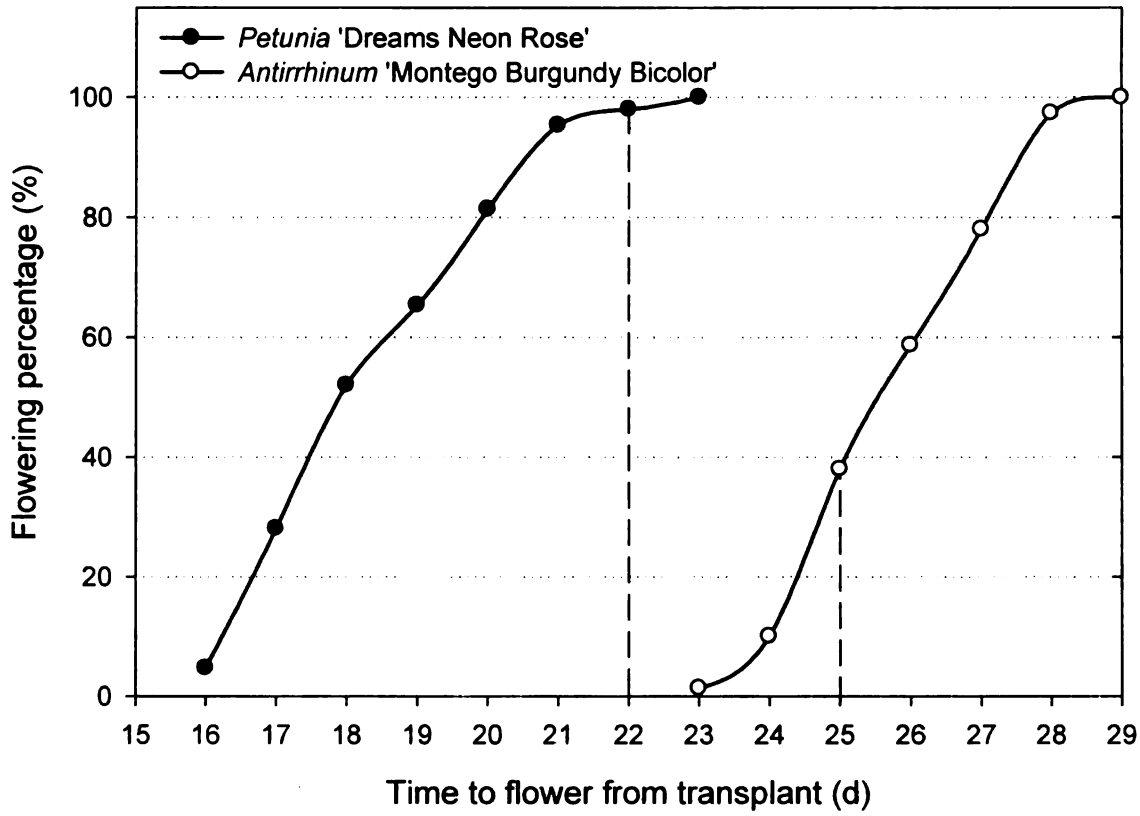


Fig. 5.1. Time to flower from transplant of 150 plants each of *Petunia* ×*hybrida* 'Dreams Neon Rose' and *Antirrhinum majus* 'Montego Burgundy Bicolor' grown under the same environmental conditions. Plants were grown in a glass greenhouse at a mean daily temperature of 21 °C and under a mean daily light integral of 21 $mol \cdot m^{-2} \cdot d^{-1}$ with a 16-h photoperiod. *Petunia* was considered flowering when individual plants had one flower with a fully open corolla. *Antirrhinum majus* was considered flowering when individual plants had 2 flowers open on an inflorescence. Dashed vertical lines indicate the predicted time to flower for each species using the flower development rate models (Table 5.3).

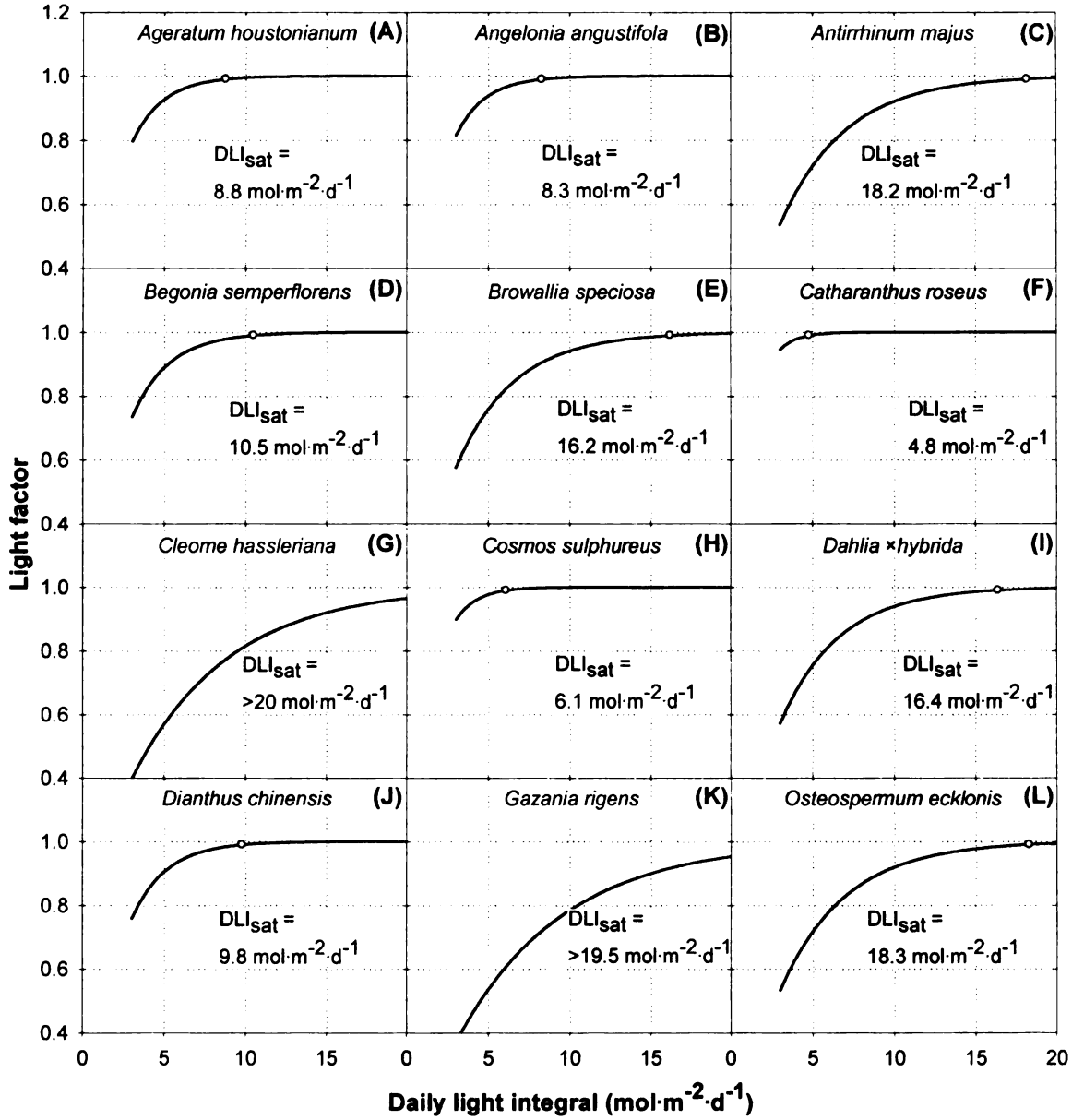


Fig. 5.2. The increase in flower development rate as the daily light integral (DLI) increases in 12 species of bedding plants grown under a 16-h photoperiod. Circles represent the estimated saturation DLI (DLI_{sat}; light factor ≥ 0.99) for the shortest time to flower for each species. Symbols are not presented if DLI_{sat} is predicted to occur above of the DLI range for which the models were developed.

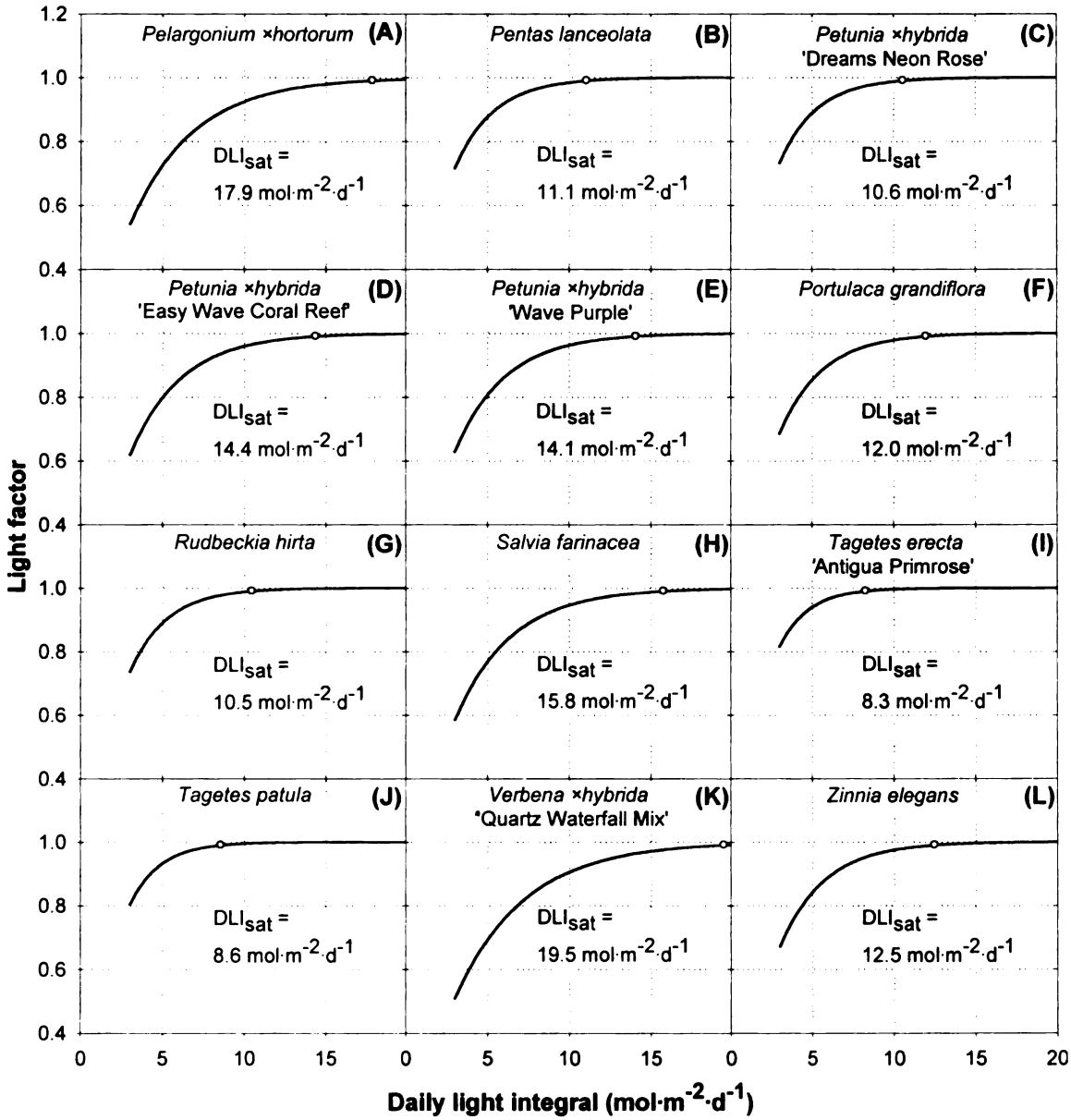


Fig. 5.3. The increase in flower development rate as the daily light integral (DLI) increases in 12 species of bedding plants grown under a 16-h photoperiod. Circles represent the estimated saturation DLI (DLI_{sat}; light factor ≥ 0.99) for the shortest time to flower for each species.

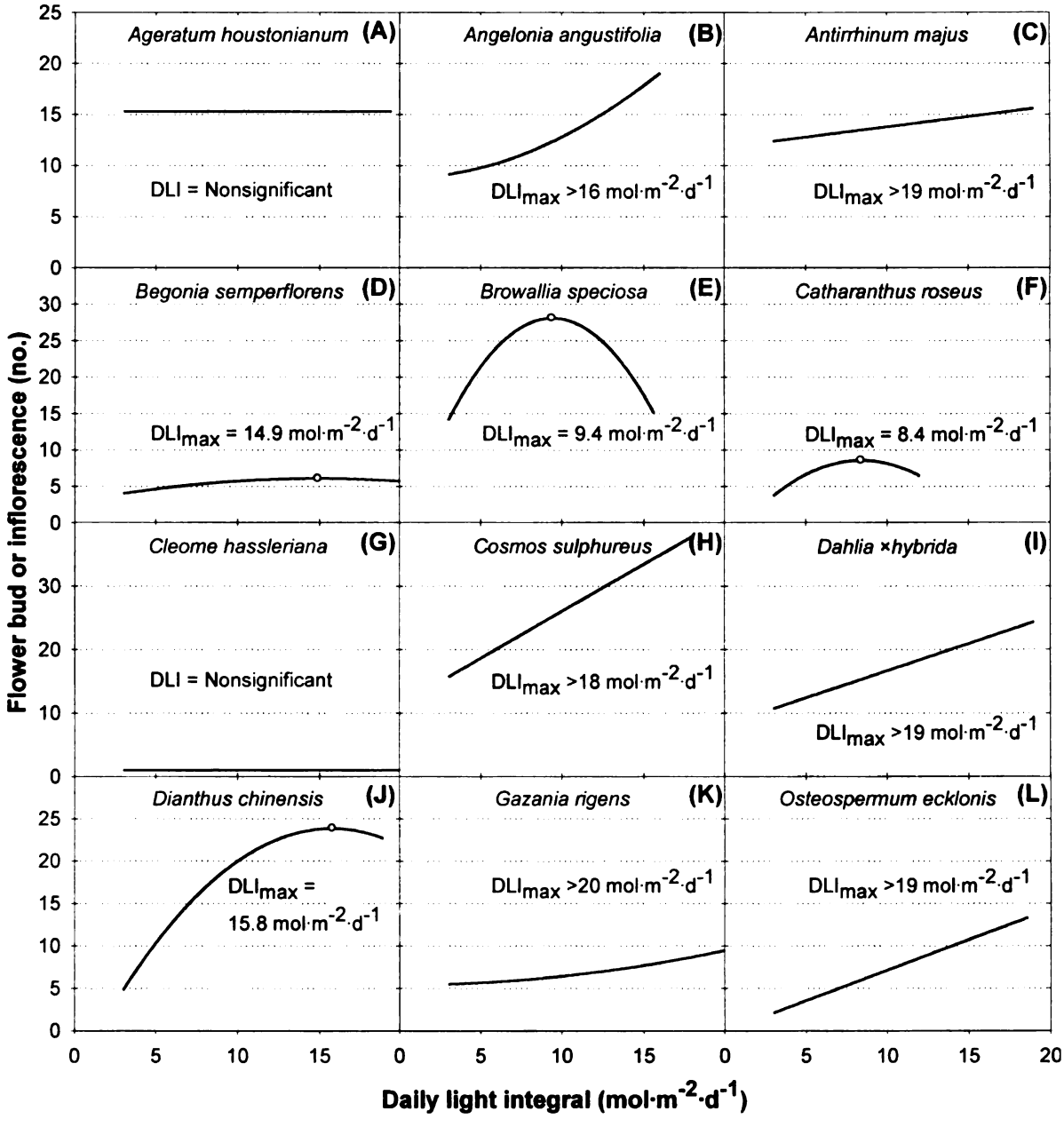


Fig. 5.4. The increase in flower bud or inflorescence number as the daily light integral (DLI) increases in 12 species of bedding plants grown at a constant temperature set point of 20 °C and under a 16-h photoperiod. Predictions were determined using the polynomial response surface equations presented in Table 5.5. Circles represent the estimated maximum DLI (DLI_{max}) for the greatest flower bud or inflorescence number for each species. Circles are not presented if DLI_{max} is predicted to occur above of the DLI range for which the models were developed.

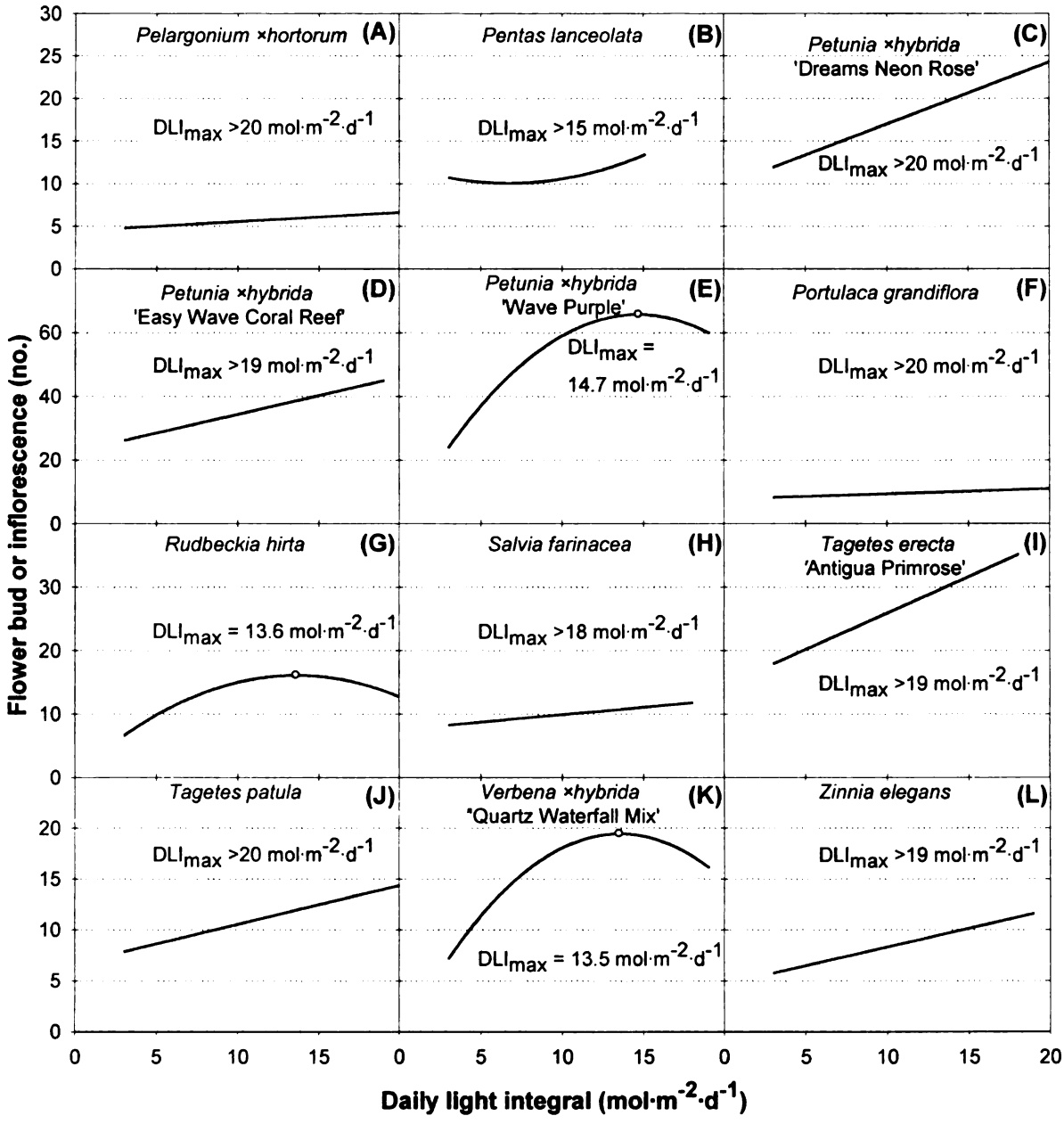


Fig. 5.5. The increase in flower bud or inflorescence number as the daily light integral (DLI) increases in 12 species of bedding plants grown at a constant temperature set point of 20 °C and under a 16-h photoperiod. Predictions were determined using the polynomial response surface equations presented in Table 5.5. Circles represent the estimated maximum DLI (DLI_{max}) for the greatest flower bud or inflorescence number for each species. Circles are not presented if DLI_{max} is predicted to occur above of the DLI range for which the models were developed.

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.

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

Faust, J.E. and R.D. Heins. 1994. Modeling inflorescence development of the African violet (*Saintpaulia ionantha* Wendl.). J. Amer. Soc. Hort. Sci. 119:727–734.

Hidén, C. and R.U. Larsen. 1994. Predicting flower development in greenhouse grown chrysanthemum. Scientia Hort. 58:123–138.

Landsberg, J.J. 1977. Some useful equations for biological studies. Expt. Agr. 13:273–286.

Larsen, R.U. 1989. A prediction model for floral development of *Senecio* × *hybridus* Hyl. 'Molls Stams'. Acta Hort. 248:247–254.

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

Larsen, R.U. and L. Persson. 1999. Modeling flower development in greenhouse chrysanthemum cultivars in relation to temperature and response group. Scientia Hort. 80:73–89.

Moccaldi, L.A. and E.S. Runkle. 2007. Modeling the effects of temperature and photosynthetic daily light integral on growth and flowering of *Salvia splendens* and *Tagetes patula*. J. Amer. Soc. Hort. Sci. 132:283–288.

Pramuk, L.A. and E.S. Runkle. 2005. Modeling growth and development of celosia and impatiens in response to temperature and photosynthetic daily light integral. J. Amer. Soc. Hort. Sci. 130:813–818.

Reed, K.L., E.R. Hamerly, B.E. Dinger, and P.G. Jarvis. 1976. An analytical model for field measurement of photosynthesis. J. Appl. Ecol. 13:925–942.

APPENDIX B

COMPARISON OF DIFFERENT LIGHT SOURCES ON GROWTH AND FLOWERING OF BEDDING PLANTS

Comparison of Different Light Sources on Growth and Flowering of Bedding Plants

Research Objective

To compare the effects of high-pressure sodium (HPS) lamps with sunlight on growth and flowering during the finish stage of three bedding plant species.

Materials and Methods

On 6, 4, and 5 Mar. 2009, seeds of petunia (*Petunia ×hybrida* 'Dreams Neon Rose'), snapdragon (*Antirrhinum majus* L. 'Montego Orange Bicolor'), and verbena (*Verbena ×hybrida* 'Obsession Lilac'), respectively, were sown in plug trays [288-cell size (6-ml volume)] by a commercial greenhouse (C. Raker & Sons, Litchfield, MI). After germination, plugs were received at Michigan State University (MSU) and were grown in a controlled environmental growth chamber (TC-2; Environmental Growth Chambers, Chagrin Falls, OH) at a constant temperature set point of 20 °C. A 16-h photoperiod was provided by 215-W cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and 60-W incandescent lamps (INC; Philips), at a CWF:INC (by W) of 3.6, and at an intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. On 1 April 2009, plugs were transferred to a controlled environmental growth chamber at a constant temperature set point of 10 °C and under a 9-h photoperiod to slow the rate of development.

All plugs were thinned to one seedling per cell. During the plug stage, plants were irrigated as necessary with well water acidified with H_2SO_4 to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$ and containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively.

The water was supplemented with a water-soluble fertilizer providing (in $mg \cdot L^{-1}$) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, Mn, and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

On 9 April 2009, seedlings were transplanted into 10-cm round plastic containers (480-ml volume) filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). Petunia, snapdragon, and verbena had a mean node number at transplant of 12, 7, and 4, respectively. After transplant, plants were randomly assigned to three different photosynthetic daily light integral (DLI) treatments that each delivered 8 $mol \cdot m^{-2} \cdot d^{-1}$. Each treatment contained 15 plants of each species. The DLI treatments consisted of (1) 8 $mol \cdot m^{-2} \cdot d^{-1}$ delivered entirely from 400-W HPS lamps (100% HPS), (2) 4 $mol \cdot m^{-2} \cdot d^{-1}$ each from sunlight and HPS lamps, delivered separately (50% HPS), and (3) 8 $mol \cdot m^{-2} \cdot d^{-1}$ delivered entirely from natural sunlight (0% HPS).

DLI Treatments

1. *100% HPS.* Plants of each species were grown in an environmental growth chamber under HPS lamps delivering 139 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 16 h (8 $mol \cdot m^{-2} \cdot d^{-1}$). The HPS lamps operated continuously from 0600 to 2200 HR. Plants remained in the same growth chamber throughout the study and were not shaken during the experiment.

2. *50% HPS.* Plants of each species were grown under HPS lamps delivering 139 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from 0600 to 0900 HR (1.5 $mol \cdot m^{-2} \cdot d^{-1}$) in a compartment that excluded natural sunlight (CompENS). Each day at 0900 HR, plants were transferred to a greenhouse and were grown under natural sunlight with a maximum photosynthetic

photon flux (*PPF*) of 1080 $\mu mol \cdot m^{-2} \cdot s^{-1}$. After plants received 4 $mol \cdot m^{-2} \cdot d^{-1}$ of sunlight (141 to 447 min, depending on irradiance), they were subsequently transferred back to the CompENS and were grown under HPS lamps delivering 139 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 5 h (2.5 $mol \cdot m^{-2} \cdot d^{-1}$). In the CompENS, the photoperiod was extended to 16 h with 2 to 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps. The time required to transfer plants between environments was ≤5 min.

3. *0% HPS.* Every day at 0900 HR, plants of each species were transferred from an CompENS to a greenhouse and were grown under natural sunlight with a maximum *PPF* of 1080 $\mu mol \cdot m^{-2} \cdot s^{-1}$. After plants received 8 $mol \cdot m^{-2} \cdot d^{-1}$ of sunlight (≥234 min, depending on irradiance), they were subsequently transferred back to the CompENS. In the CompENS, plants were grown under a 16-h photoperiod provided as day-extension lighting from 0600 to 2200 HR from HPS lamps delivering 2 to 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$. On some days during the study, plants did not receive 8 $mol \cdot m^{-2} \cdot d^{-1}$ of sunlight in the greenhouse environment because of cloudy conditions. Therefore, plants were transferred to the CompENS between 1700 to 1900 HR, and on the following day, plants received more than 8 $mol \cdot m^{-2} \cdot d^{-1}$ from sunlight to make up the deficit. The time required to transfer plants between environments was ≤5 min.

Environmental Monitoring and Plant Culture

In each environment, plants were grown at a constant air temperature set point of 22 °C. Air temperature was independently measured in each environment by aspirated, shielded thermocouples (0.13-mm type E; Omega Engineering, Stamford, CT) positioned at plant height. At 10 cm above the bench in each DLI treatment, the *PPF* was measured

by a quantum sensor (LI-190SA; LI-COR, Inc., Lincoln, NE). In the greenhouse environment, the *PPF* was measured by a line quantum sensor containing 10 photodiodes (Apogee Instruments, Inc., Logan, UT). In each treatment, a thermocouple (0.13-mm type E; Omega Engineering) was inserted 0.5 cm below the shoot tip of one plant of each species and the actual plant temperature was recorded. Thermocouples were reinserted daily after plants were transferred between environments. In the growth chamber, thermocouples were repositioned weekly as plants developed.

Environmental measurements were collected every 10 s and hourly means were recorded by data loggers (CR10X; Campbell Scientific, Logan, UT). A vapor-pressure deficit was not maintained during the study. Plants in the growth chamber were irrigated as previously described, but with a water-soluble fertilizer providing ($mg \cdot L^{-1}$) 125 N, 11 P, 126 K, 13 Ca, 1 Fe, 0.5 Cu, Mn, and Zn, 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers, Inc.). Plants in the CompENS and greenhouse were irrigated with reverse osmosis water supplemented with a water-soluble fertilizer providing (in $mg\ L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc.).

Data Collection and Analysis

The date of first open flower per plant was recorded and time to first open flower was calculated for each plant. Petunia were considered flowering when one flower had a fully open corolla. Snapdragon and verbena were considered flowering when plants had 2 and 6 flowers, respectively, open on an inflorescence. When each plant flowered, the following data were recorded: total number of flower buds (petunia) or inflorescences

(snapdragon and verbena), plant height from the soil surface to the base of the open flower or inflorescence, number of nodes on the primary shoot below the first open flower, number of branches, and total shoot dry weight. Data were analyzed using SAS mixed-model procedure (PROC MIXED), and pairwise comparisons between treatments were performed using Tukey's honestly significant difference test at $P \leq 0.05$.

Results

Plants of petunia and snapdragon flowered a mean of 4 to 5 d earlier under 100% HPS compared with 0% HPS (Table 6.1). In verbena, there was no difference in time to flower among treatments. Verbena grown under 100% HPS had a 0.8 to 1.0 g higher shoot dry weight at flower compared to 50% HPS and 0% HPS. Snapdragon and verbena grown under 100% HPS were a mean of 4 to 8 cm taller at flower than other treatments. In all species, there were no differences among treatments in the number of flowers, leaf nodes, or branches. Mean air temperature was within 0.3 °C among treatments, but mean plant temperature was 0.4 to 0.9 °C higher under 100% HPS versus 0% HPS.

Table 6.1. Influence of light source on time to flower, shoot dry weight, height, and on the number of flowers, nodes, and branches at flowering in petunia, snapdragon, and verbena. Plants were grown under a daily light integral (DLI) of 8 $mol \cdot m^{-2} \cdot d^{-1}$ delivered either (1) entirely from high-pressure sodium (HPS) lamps (100% HPS), (2) 4 $mol \cdot m^{-2} \cdot d^{-1}$ each from sunlight and HPS lamps, delivered separately (50% HPS), and (3) entirely from natural sunlight (0% HPS).

	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)		Mean temperature (°C)							
Treatment	HPS	Sunlight	Air	Plant	Time to flower (d)	Flower no.	Height (cm)	Node no.	Branch no.	Shoot dry weight (g)
					Petunia 'Dreams Neon Rose'					
100% HPS	8.0	0.0	22.1	21.4	17.7 b[z]	10.3	5.3	12.9	-[y]	1.3
50% HPS	4.0	4.0	22.3	21.4	20.9 ab	12.2	5.4	13.5	-	1.5
0% HPS	0.0	8.0	22.4	21.0	22.8 a	9.7	4.8	13.5	-	1.5
					Snapdragon 'Montego Orange Bicolor'					
100% HPS	8.0	0.0	22.1	21.5	18.6 b	3.6	14.5 a	9.1	15.3	0.6
50% HPS	4.0	4.0	22.2	21.3	19.9 ab	4.6	10.5 b	9.5	13.5	0.8
0% HPS	0.0	8.0	22.3	20.9	22.3 a	3.1	10.3 b	9.3	14.3	0.6
					Verbena 'Obsession Lilac'					
100% HPS	8.0	0.0	22.1	21.7	29.1	13.3	20.6 a	6.9	13.5	2.4 a
50% HPS	4.0	4.0	22.1	21.2	30.5	12.1	13.4 b	7.2	13.9	1.6 b
0% HPS	0.0	8.0	22.3	20.8	31.3	12.2	11.9 b	6.9	13.1	1.4 b

[z]Mean separation within each species and column by Tukey's honestly significant difference test at $P \leq 0.05$.
[y]Data not collected.