

# Mean Daily Temperature Regulates Plant Quality Attributes of Annual Ornamental Plants

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**Abstract.** In protected environments, temperature is often regulated to produce ornamental crops for specific market dates. Temperature primarily controls plant developmental rate and thus production time, but it can also interact with light quantity to affect crop quality attributes such as flower number, branching, and biomass accumulation. We quantified how mean daily temperature (MDT) between 14 and 26 °C influenced quality characteristics of 15 common bedding plant crops. American marigold (*Tagetes erecta*), cup flower (*Nierembergia caerulea*), diascia (*Diascia barberae*), flowering tobacco (*Nicotiana alata*), geranium (*Pelargonium × hortorum*), globe amaranth (*Gomphrena globosa*), heliotrope (*Heliotropium arborescens*), nemesia (*Nemesia foetans*), New Guinea impatiens (*Impatiens hawkeri*), osteospermum (*Osteospermum ecklonis*), pot marigold (*Calendula officinalis*), snapdragon (*Antirrhinum majus*), stock (*Matthiola incana*), and torenia (*Torenia fournieri*) were grown under two mean daily light integrals (9.0 and 18.0 mol·m<sup>-2</sup>·d<sup>-1</sup>) in five environmentally controlled greenhouse compartments with a 16-h photoperiod. As MDT increased from 14 to 26 °C, flower or inflorescence number decreased for nearly all crops. In six crops, flower or inflorescence size decreased as MDT increased, whereas in five crops, there was an initial increase in flower size with an increase in MDT and then a subsequent decrease at MDT greater than 20 °C. In 10 of the crops, shoot weight at flowering decreased linearly or quadratically with an increase in MDT. Branch number was inversely related with MDT in eight crops and was positively correlated with an increase in flower number. We conclude that in a majority of the crops studied, plant quality decreased as the MDT increased, which can at least partially be attributed to earlier flowering at the higher MDTs. Therefore, there is often a tradeoff between faster crop timing and higher plant quality, especially for plants with a low estimated base temperature (T<sub>min</sub>) for development.

Plant quality is subjective and situational with desired attributes largely depending on the customer, plant, and season. For flowering ornamental crops, attributes of plant quality can include absence of insect and disease pests, presence of flowers at a desirable stage (e.g., first flowers have recently opened), height in proportion to the container, adequate lateral branching, sufficiently strong stems to avoid breakage, high flower bud or inflorescence

count, and large flowers with vivid colors. Commercial production of high-quality plants therefore requires vigilant pest management; management of proper irrigation and fertility; a growing environment that includes management of light, temperature, and humidity; and, in many cases, proper use of plant growth regulators. These production inputs can be divided into cultural growing practices (e.g., watering, fertility, pest control) and environmental control regimens to regulate growth and plant development.

MDT and the mean photosynthetic daily light integral (DLI) control growth and development of plants, assuming other growing inputs are not limited (Carvalho et al., 2006; Moccaldi and Runkle, 2007; Niu et al., 2001b). In addition, temperature and DLI influence plant quality characteristics, including flower number and size, branch number, plant height, and plant biomass. Ornamental crops grown in greenhouses are exposed to a wide range of DLIs. Assuming a greenhouse light transmission factor of 50%, crops typically receive 7.5 mol·m<sup>-2</sup>·d<sup>-1</sup> or less in the northern half of the continental United States in January

to 17.5 mol·m<sup>-2</sup>·d<sup>-1</sup> or greater throughout the United States in May (Korczynski et al., 2002). Several studies have reported a decrease in quality with an increase in MDT when plants are grown at the same or similar DLI (Blanchard and Runkle, 2011a, 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001b; Pramuk and Runkle, 2005). Plant quality is important to commercial producers because buyers can reject crops if quality is insufficient or the crops can receive a lower price.

MDT primarily controls the rate of plant development and thus time for a particular event such as development of a leaf or flowering (Blanchard and Runkle, 2011a). Although higher temperatures can decrease time to flower, faster crop timing may not always be desirable because plant quality characteristics such as flower bud number, flower size, branch number, and plant biomass are often inversely related to MDT and rapid plant development rates (Blanchard and Runkle, 2011a, 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001a; Pramuk and Runkle, 2005; Warner and Erwin, 2006). For example, as MDT increased from 15 to 25 °C (under a DLI of 15 mol·m<sup>-2</sup>·d<sup>-1</sup>), plant biomass, inflorescence number, and inflorescence diameter in marigold (*Tagetes patula*) decreased by 35%, 53%, and 31%, respectively (Moccaldi and Runkle, 2007), but crop development rates were accelerated. Similarly, in petunia (*Petunia × hybrida*) ‘Dreams Neon Rose’, each degree increase in MDT decreased the flower and branch number by 0.9 and 0.3, respectively (Mattson and Erwin, 2003), but the plants flowered earlier than those grown with a lower MDT. Therefore, there is often a tradeoff between fast crop timing and high plant quality, especially under light-limiting conditions. The objective of this research was to comprehensively quantify the effect of MDT, at two different mean DLIs, on plant quality attributes of 15 popular ornamental annual crops using linear and nonlinear mathematical models.

## Materials and Methods

Seedlings of 15 common ornamental annuals were chosen for study according to popularity, breeder input, availability, and lack of published information. American marigold (*Tagetes erecta* ‘Inca II Mix’), cup flower (*Nierembergia caerulea* ‘Purple Robe’), diascia (*Diascia barberae* ‘Diamonte Mix’), flowering tobacco (*Nicotiana alata* ‘Perfume Deep Purple’), geranium (*Pelargonium × hortorum* ‘Pinto Red’ and ‘Ringo 2000 Deep Red’), globe amaranth (*Gomphrena globosa* ‘Gnome Purple’), heliotrope (*Heliotropium arborescens* ‘Blue Wonder’), nemesia (*Nemesia foetans* ‘Poetry White’), New Guinea impatiens (*Impatiens hawkeri* ‘Divine Cherry Red’), osteospermum (*Osteospermum ecklonis* ‘Asti Purple’), pot marigold (*Calendula officinalis* ‘Bon Bon Orange’), snapdragon (*Antirrhinum majus* ‘Liberty Classic Cherry’), stock (*Matthiola incana* ‘Hot Cakes Purple’ or ‘Garden Vintage

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Mix'), and torenia (*Torenia fournieri* 'Clown Blue') seedlings were grown in 288-cell (6-mL), 128-cell (12-mL), or 36-cell (42.3-mL) plug trays, depending on species, by a commercial plug producer as reported by Vaid and Runkle (2013).

The experiment was performed twice, once in the spring and again in the fall to record data under different DLI conditions (18.0 and 9.0 mol·m<sup>-2</sup>·d<sup>-1</sup>, respectively). The leaf count of starting plants in the second replication was similar to that in the first replicate, which was conducted by raising seedlings in a controlled environment chamber at a constant temperature set point of 20 °C under a photosynthetic photon flux (PPF) of 180 μmol·m<sup>-2</sup>·s<sup>-1</sup> (DLI ≈10 mol·m<sup>-2</sup>·d<sup>-1</sup>) with a 16-h photoperiod, as described by Vaid and Runkle (2013). The seedlings were then transplanted into 10-cm round containers (480 mL) filled with a peat-based medium (Suremix; Michigan Grower Products, Galesburg, MI). Nemesia and diascia seedlings were flowering on receipt and thus were pinched to three or four nodes and treated with a 500-mg·L<sup>-1</sup> spray of ethephon (Florel; Southern Agricultural Insecticides, Inc., Palmetto, FL) at a volume of 0.2 L·m<sup>-2</sup> before transplant to abort flowers and flower buds. The seedlings were thinned to one plant per cell before transplant, and 10 plants of each species were grown at constant temperature set points of 14, 17, 20, 23, or 26 °C in separate glass-glazed greenhouse compartments. Plants were grown under a 16-h photoperiod (0600 to 2200 HR) created by using the natural photoperiod (lat. 43° N) and day-extension lighting from high-pressure sodium lamps that provided a PPF of 100 to 120 μmol·m<sup>-2</sup>·s<sup>-1</sup>. Air temperature and light intensity were measured and recorded as described by Vaid and Runkle (2013), and the MDT and DLI were calculated for each plant. The mean DIF value (day–night temperature) ranged from 0.5 to 2.0 °C in the spring experiment and 0.4 to 0.9 °C in the fall experiment. Vapor pressure deficit was maintained between ≈0.8 and 1.1 kPa by steam injection. Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing (mg·L<sup>-1</sup>) 125 nitrogen, 12 phosphorus, 100 potassium, 65 calcium, 12 magnesium, 1.0 iron and copper, 0.5 manganese and zinc, 0.3 boron, and 0.1 molybdenum (MSU RO Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

When each plant flowered according to the individual characteristics for each species (Vaid and Runkle, 2013), flower and flower bud or inflorescent number, axillary branch number, and plant height (from medium surface to apex of the tallest branch) or length of the longest lateral were recorded. During the fall experiment, flower or inflorescence diameter at first open flower was also measured, with the exception of globe amaranth and snapdragon. After data collection, plants were cut at the medium surface and the roots were thoroughly washed to remove medium particles. The shoots (for all species) and

roots (for flowering tobacco, geranium 'Ringo', nemesia, pot marigold, snapdragon, stock, and torenia) were separately placed in labeled brown paper bags and dried in a forced-air oven at 79 °C for 3 d or longer and then weighed on an electrical balance. The experiment was set up as a randomized complete block design; five temperature treatments were randomly assigned to the experimental units during the fall and spring replicates (blocks).

SAS 8.0 (SAS Institute, Cary, NC) was used to analyze the experimental data. When linear regression slopes between replications were non-significant ( $P \leq 0.05$ ), data were pooled for statistical analysis. Linear and quadratic regression (REG procedure) analysis was used to generate equations to describe the effect of MDT on plant quality characteristics. To facilitate data interpretation, the temperature treatments with the greatest shoot fresh and dry weight and flower or inflorescence size at flowering were identified for each species, and values in other treatments were calculated relative to those values to yield relative weight or size data. The actual MDTs were calculated for each plant and used in data presentation and regression analysis.

## Results

Flower or inflorescence number decreased with an increase in MDT from 14 to 26 °C for nearly all of the crops studied (Fig. 1). For example, an increase in MDT from 14 to 26 °C decreased the predicted inflorescence number in pot marigold by 57% and flower number in stock by 54%. In globe amaranth, New Guinea impatiens, and torenia, flower number was similar or increased slightly with temperature up to ≈20 °C and then decreased with higher temperatures.

MDT had various effects on branch number among the species studied (Fig. 2). In both cultivars of geranium, pot marigold, flowering tobacco, and snapdragon, branch number at flowering decreased with MDT. Of these, the effect of MDT was greatest on branching of geranium 'Pinto' and snapdragon, in which branching was 41% to 61% less at 26 °C than at 16 °C. There was no consistent effect of temperature on branching between replications of stock, diascia, heliotrope, or cup flower, and there was no significant effect in either replication in American marigold, New Guinea impatiens, or osteospermum (data not shown). In contrast, branch number in torenia increased by 20% as MDT increased from 16 to 26 °C.

There was a strong effect of MDT on shoot dry weight at flowering in all crops studied except for diascia (Fig. 3A–C). In 10 of the crops, shoot weight at flowering decreased with an increase in MDT in a linear or quadratic manner. Of these 10 crops, the reduction in shoot weight at 26 °C compared with 14 °C was, respectively, 40% to 60% in heliotrope and flowering tobacco; 60% to 80% in nemesia, stock, both geranium cultivars, and pot marigold; and greater than 80%

in snapdragon and cupflower. The opposite trend occurred in globe amaranth; shoot weight increased 4-fold as temperature increased from 16 to 26 °C. In American marigold, New Guinea impatiens, and torenia, shoot dry weight first increased with MDT up to ≈20 °C and then decreased. Similar responses were observed among the seven species in which root weight was measured at flowering; the correlation between MDT and root weight was negative in flowering tobacco, geranium 'Ringo', nemesia, pot marigold, snapdragon, and stock (Fig. 3D). In contrast, root weight of torenia increased with temperature until ≈23 °C. There was a positive correlation between shoot and root weight in all seven species measured ( $P < 0.001$ ).

Plant height (stem length) at flowering decreased as temperature increased from 14 to 26 °C in nemesia, osteospermum, stock, both geranium cultivars, flowering tobacco, and snapdragon (Fig. 4; Table 1). In contrast, plant height decreased with a decrease in MDT in globe amaranth, torenia, and American marigold. There was no significant effect of temperature on plant height in diascia. Height at flowering slightly increased and then slightly decreased as temperature increased in New Guinea impatiens, whereas the opposite occurred in cup flower and pot marigold.

There were significant trend effects of temperature on flower or inflorescence size in 11 of the 13 crops measured. In New Guinea impatiens, torenia, osteospermum, diascia, and flowering tobacco, there was an initial increase in flower size with an increase in temperature and then a subsequent decrease at temperatures greater than 20 °C. Flower or inflorescence size decreased as MDT increased in nemesia, cup flower, pot marigold, stock, and both geranium cultivars. Compared with the temperature that produced the largest flowers, flower size at 26 °C was reduced in osteospermum (by 8%), flowering tobacco (by 11%), diascia (by 17%), cup flower (by 18%), geranium 'Ringo' (by 19%), torenia (by 23%), geranium 'Pinto' (by 24%), New Guinea impatiens (by 25%), stock (by 26%), nemesia (by 43%), and pot marigold (by 47%).

## Discussion

The rate of progress toward flowering typically decreases as temperature decreases, and thus plants can harvest light for a longer period before flowering when grown at relatively low temperatures. These cultivars all had a flowering rate (1/d to flower) that was inversely related to temperature (Vaid and Runkle, 2013). The higher plant quality attributes (e.g., greater flower number and shoot biomass accumulation) at the lower temperatures is thus not surprising. However, shoot biomass at flowering was greatest at 20 °C for American marigold, New Guinea impatiens, and torenia and at 26 °C for globe amaranth. Similarly, flower number was greatest at ≈20 °C for New Guinea impatiens, torenia, and globe amaranth. Furthermore,

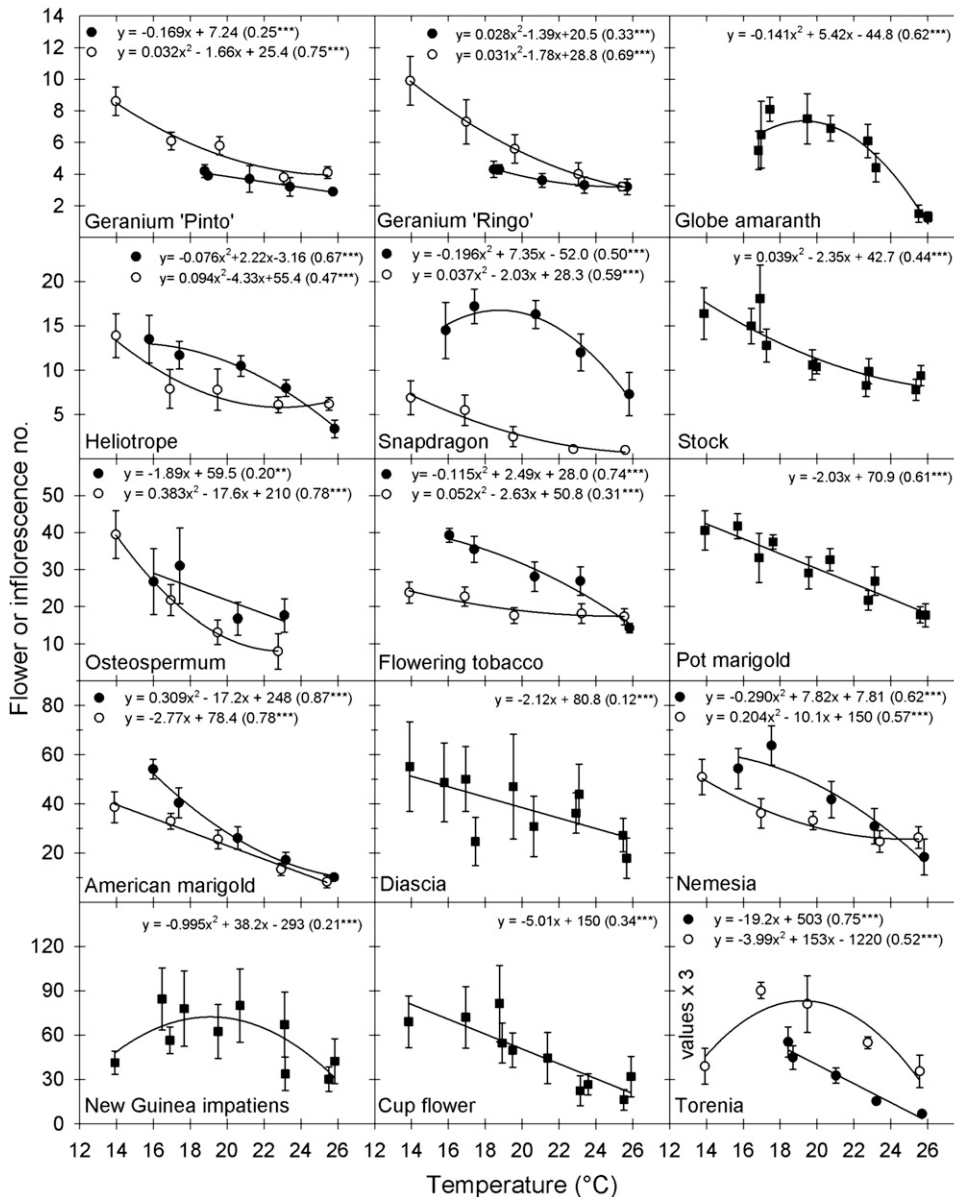


Fig. 1. The effect of mean daily temperature on flower or inflorescence number in 15 ornamental annual crops modeled for the spring (●) and fall replication (○). When regression slopes were nonsignificant between the two replications ( $P \leq 0.05$ ), data were pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. For torenia, the y-axis values are multiplied by three, as noted; regression values are for the original data (not multiplied by three).  $R^2$  values are in parentheses; \*\*, \*\*\* Significant at  $P \leq 0.01$  or 0.001, respectively.

flower size, lateral branching, or both for these four crops was greatest at moderate to high temperatures. We cannot readily explain why these four crops responded differently than the other crops, and their responses are apparently not associated with their estimated  $T_{min}$  values, which ranged from 0.1 °C for American marigold to 13.8 °C for globe amaranth (Vaid and Runkle, 2013).

Flower number and size are two of the factors that influence overall quality of ornamental crops. A high-quality plant would typically have a high inflorescence or flower count and flowers would be large. In many species, MDT influences flower number such that as MDT increases, flower number decreases (Mattson and Erwin, 2003; Moccaldi and Runkle, 2007). In our experiments, flower number of 12 of the 15 crops investigated

decreased in a linear or quadratic manner with an increase in temperature. When data were pooled between replications, flower number at 15 vs. 25 °C was greater in diascia (by 76%), globe amaranth (by 85%), stock (by 95%), pot marigold (by 101%), and cup flower (by 202%). Similar results have been reported for other ornamental crops; for example, an increase in MDT from 16 to 26 °C decreased flower number of tickseed (*Coreopsis grandiflora*) by 80%, Shasta daisy (*Leucanthemum ×superbum*) by 55%, and black-eyed Susan (*Rudbeckia fulgida*) by 75% (Yuan et al., 1998).

Flower development requires carbon import from the source organs (leaves). Sucrose hydrolysis in the sink organs (flowers) is necessary to establish a concentration gradient for carbon transport between the source

and the sink (Dinar and Rudich, 1985). High temperature reduces sucrose hydrolysis and therefore increases its concentration in flowers, which reduces or inhibits uptake of carbon by the developing flower buds (Dinar and Rudich, 1985) and may consequently reduce final flower size. This is further evident from a reduction in the percentage of dry matter that is partitioned to the flowers relative to vegetative structures under high-temperature stress in chrysanthemum (Karlsson and Heins, 1992). High temperature also reduces photosynthetic efficiency because of increased photorespiration (van Iersel, 2003).

Branch number was inversely related to MDT in eight species and cultivars, and an increase in branch number was positively correlated with an increase in flower number in those species. Many researchers have

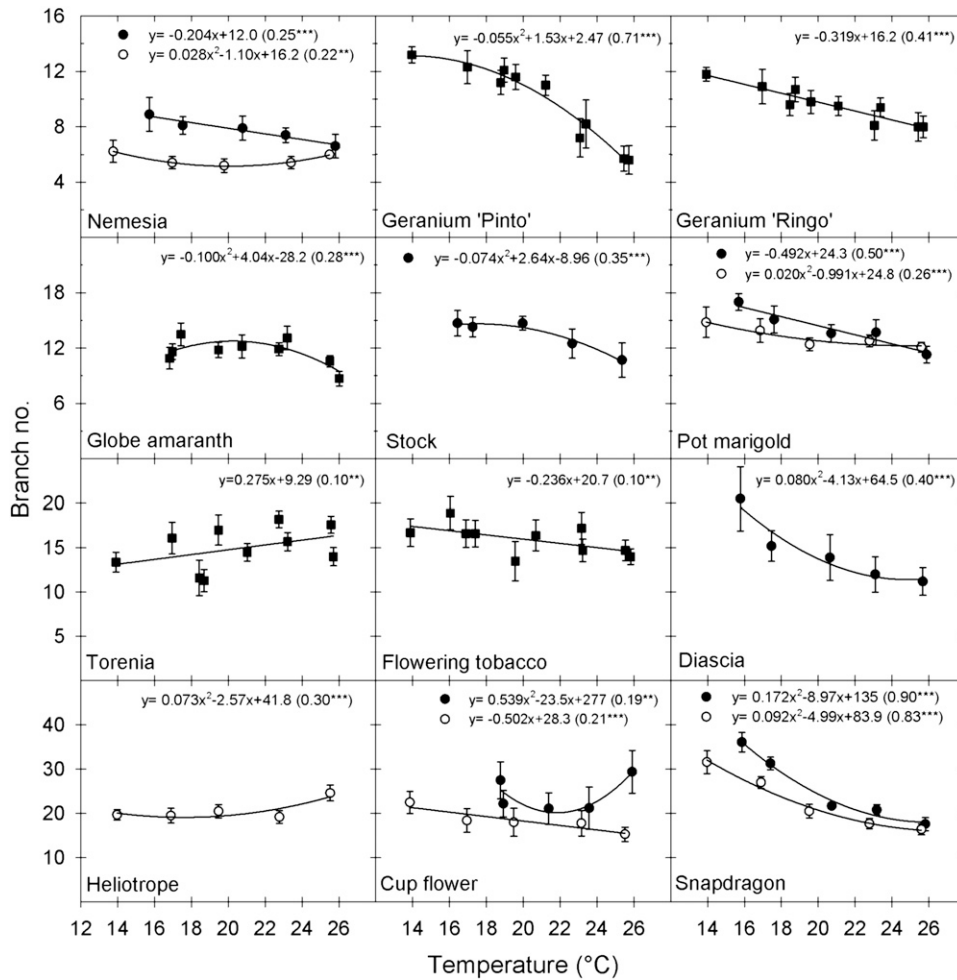


Fig. 2. The effect of mean daily temperature ( $^{\circ}\text{C}$ ) on axillary branch number in 12 ornamental annual crops modeled for the spring ( $\bullet$ ) and fall replication ( $\circ$ ). When regression slopes were nonsignificant between the two replications ( $P \leq 0.05$ ), data were pooled ( $\blacksquare$ ) for statistical analysis. An absence of data indicates response was not significant. Each symbol represents the treatment means, and error bars represent 95% confidence intervals.  $R^2$  values are in parentheses; \*\*, \*\*\* Significant at  $P \leq 0.01$  or  $0.001$ , respectively.

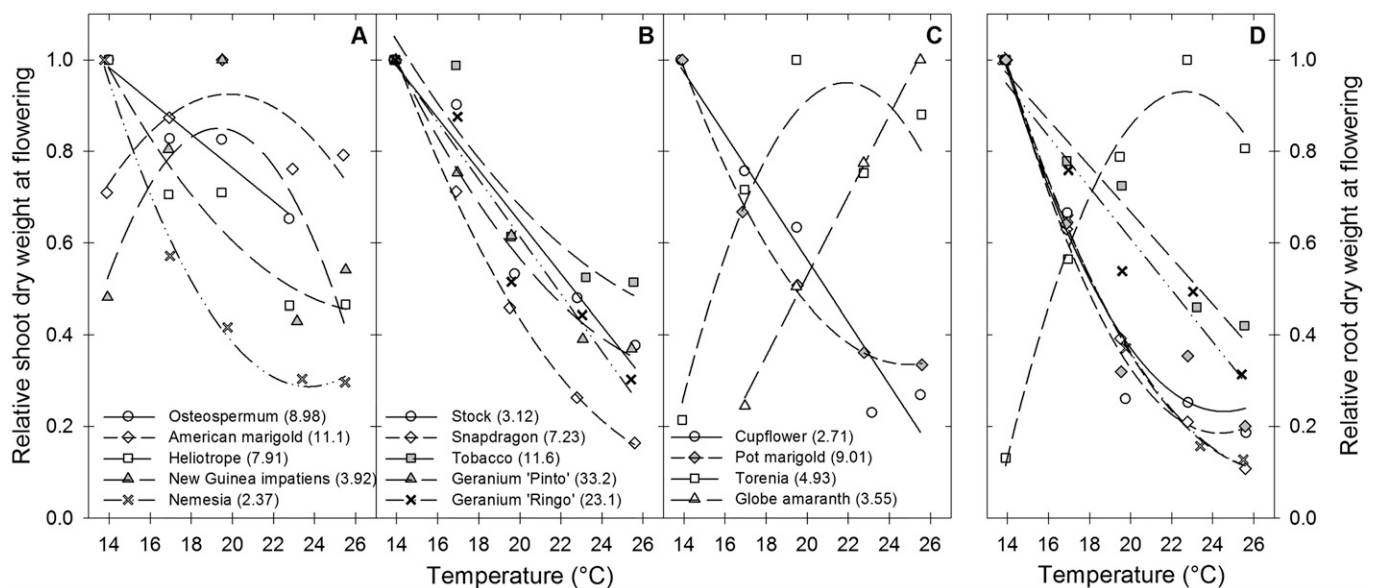


Fig. 3. Relative shoot (A–C) and root (D) dry weights at flowering of 14 and seven ornamental annual crops, respectively. Legend in A–C applies to D and species are listed in increasing order of the estimated base temperature, from  $-0.5^{\circ}\text{C}$  for osteospermum to  $13.8^{\circ}\text{C}$  for globe amaranth (Vaid and Runkle, 2013). In the legend, values in parentheses refer to the greatest shoot dry weight (in milligrams) among the temperature treatments, and other values are relative to that treatment.

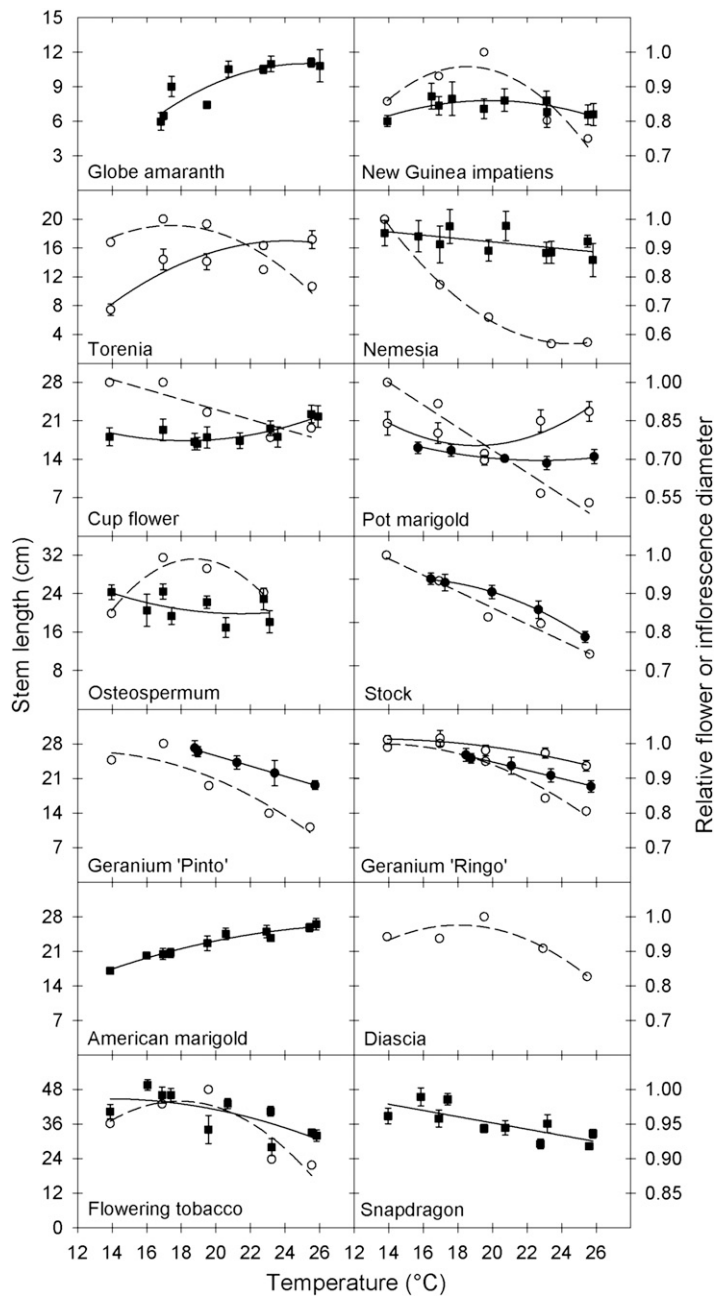


Fig. 4. The effect of mean daily temperature on stem length (solid lines) and relative flower or inflorescence diameter (dashed lines) in ornamental annual crops modeled for the spring replication (●) and fall replication (○). When regression slopes for stem length were nonsignificant between the two replications ( $P \leq 0.05$ ), data were pooled (■) for statistical analysis. An absence of data indicates the response was not significant. Each symbol represents the treatment means, and error bars represent 95% confidence intervals.

reported a decrease in branching with an increase in MDT such as in balloon flower (*Platycodon grandiflorus*; Park et al., 1998), pansy (Mattson and Erwin, 2003; Warner and Erwin, 2006), and petunia (Kaczkowski et al., 1991; Mattson and Erwin, 2003). In some of those cases, a decrease in lateral branch number was correlated with a decrease in flower number (Mattson and Erwin, 2003; Warner and Erwin, 2006). When the DLI is relatively constant, an increasing MDT creates a decreasing photothermal ratio (PTR; ratio of radiant energy to thermal energy). In poinsettia, plant quality attributes including

dry weight, bract size, and stem strength decreased as the PTR decreased (Liu and Heins, 2002). In this study, the inverse relationship between MDT and branching (and other quality attributes) could be related to the PTR. As the rate of development increases with temperature, there is relatively less radiant energy to support growth, leading to less branching.

Plant quality in many of the species in this study was generally higher in the spring than in the fall replication, which was not surprising because the DLI received during spring was double that received during the fall.

Several studies have reported an increase in quality with DLI (Fausey et al., 2005; Moccaldi and Runkle, 2007; Warner and Erwin, 2005). For example, increasing DLI from 10 to 20  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  (MDT of 20 °C) increased flower bud number by 63% in snapdragon, 56% in impatiens, 61% in mimulus, and 15% in wishbone flower (Warner and Erwin, 2005). Similarly, in the herbaceous perennial butterfly gaura (*Gaura lindheimeri*), lateral inflorescence number per plant tripled and flower number per inflorescence nearly doubled as DLI increased from 5.0 to 20.0  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  (Fausey et al., 2005). Those studies did not investigate both DLI and MDT on plant quality, however.

Shoot dry mass at first flowering increased as MDT decreased in 10 of the cultivars studied. Similar responses were observed in balloon flower (Park et al., 1998), pot marigold (Warner and Erwin, 2005), geranium (White and Warrington, 1988), impatiens (Prasuk and Runkle, 2005; Warner and Erwin, 2005), marigold (Moccaldi and Runkle, 2007), mimulus (Warner and Erwin, 2005), pansy (Niu et al., 2000; Warner and Erwin, 2006), salvia (Moccaldi and Runkle, 2007), and snapdragon (Wai and Newman, 1992; Warner and Erwin, 2005). In addition, van Iersel (2003) reported an increase in the net photosynthetic rate ( $P_{\text{net}}$ ) with a decrease in MDT for geranium, marigold, pansy, and petunia. High temperatures decrease  $P_{\text{net}}$  by modifying Rubisco kinetics (Brooks and Farquhar, 1985), increasing  $\text{O}_2\text{:CO}_2$  solubility (Ku and Edwards, 1977), or both.

In contrast, shoot biomass increased with increasing temperature in American marigold, New Guinea impatiens, torenia, and globe amaranth. Similar results were reported in celosia (Prasuk and Runkle, 2005), summer snapdragon (Miller and Armitage, 2002), Texas firebush (*Hamelia patens*; Armitage, 1995), and torenia (Warner and Erwin, 2005). Many of these plants have a high estimated  $T_{\text{min}}$ : for celosia and summer snapdragon, it was 10.2 °C under a DLI of 15  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  (Prasuk and Runkle, 2005) and 9.9 °C (Blanchard and Runkle, 2011b), respectively. We previously identified torenia and globe amaranth as cold-sensitive crops ( $T_{\text{min}}$  greater than 8 °C), although American marigold and New Guinea impatiens were considered cold-tolerant crops ( $T_{\text{min}}$  less than 4 °C; Vaid and Runkle, 2013). Accumulation of root mass in response to MDT followed a trend similar to that observed for shoot mass in our study. However, these results could not be compared with previous work because, to our knowledge, the response of root mass accumulation to MDT has not been published for annual bedding plants.

Among the species studied, there was an inverse relationship between temperature and plant height at flowering in seven crops. Of these, node number at flowering decreased as temperature increased only in the two geranium cultivars and snapdragon (Vaid and Runkle, 2013). In contrast, plant height increased with temperature in three crops, two of which developed fewer nodes before

Table 1. Regression equations for stem length (height) and flower or inflorescence diameter (flower size) of ornamental annual crops grown at different mean daily temperatures in two experimental replicates (spring and fall).<sup>z</sup>

Species	Parameter	Replicate	Equation	R <sup>2</sup>
Globe amaranth	Height	Combined	$y = -0.060x^2 + 3.05x - 27.5$	0.55***
New Guinea impatiens	Height	Combined	$y = -0.041x^2 + 1.61x - 8.09$	0.11**
	Flower size	Fall	$y = -0.029x^2 + 1.07x - 4.16$	0.35***
Torenia	Height	Fall	$y = -0.084x^2 + 4.06x - 31.9$	0.72***
	Flower size	Fall	$y = -0.010x^2 + 0.355x - 0.236$	0.40***
Nemesia	Height	Combined	$y = -0.236x + 21.6$	0.08**
	Flower size	Fall	$y = -0.0069x^2 - 0.339x + 5.20$	0.75***
Cup flower	Height	Combined	$y = 0.075x^2 - 2.75x + 42.5$	0.25***
	Flower size	Fall	$y = -0.064x + 4.18$	0.34***
Pot marigold	Height	Spring	$y = 0.045x^2 - 2.03x + 35.5$	0.37***
		Fall	$y = 0.144x^2 - 5.47x + 66.7$	0.25**
	Flower size	Fall	$y = -0.323x + 11.9$	0.77***
Osteospermum	Height	Combined	$y = 0.069x^2 - 2.99x + 52.3$	0.12*
	Flower size	Fall	$y = -0.031x^2 + 1.16x - 4.99$	0.25*
Stock	Height	Spring	$y = -0.109x^2 + 3.38x - 2.32$	0.79***
	Flower size	Fall	$y = -0.086x + 5.20$	0.43***
Geranium Pinto	Height	Spring	$y = -1.03x + 46.2$	0.57***
	Flower size	Fall	$y = -0.0077x^2 + 0.191x + 4.37$	0.69***
Geranium Ringo	Height	Spring	$y = -0.725x + 35.4$	0.53***
		Fall	$y = -0.030x^2 + 0.792x + 19.6$	0.58***
American marigold	Flower size	Fall	$y = -0.0085x^2 + 0.123x + 4.06$	0.78***
	Height	Combined	$y = -0.039x^2 + 2.29x - 6.88$	0.74***
Diascia	Flower size	Fall	$y = 0.0054x^2 + 0.193x + 0.290$	0.26***
Flowering tobacco	Height	Combined	$y = -0.095x^2 + 2.58x + 27.2$	0.41***
	Flower size	Fall	$y = -0.0095x^2 + 0.337x + 2.34$	0.14*
Snapdragon	Height	Combined	$y = -1.09x + 58.1$	0.43***

<sup>z</sup>Data were pooled for statistical analysis when regression slopes were NS between replications ( $P \leq 0.05$ ). See Figure 4 for graphical presentation of data in absolute or relative terms. \*, \*\*, \*\*\* Significant at  $P \leq 0.05$ , 0.01, or 0.001, respectively.

flowering as temperature decreased (American marigold and torenia). Although the greenhouse temperature set points in these experiments were constant, the day was often warmer than the night in the lower-temperature treatments, especially in the spring replication, because of high ambient temperatures. For many plants, height at flowering decreases as day temperature relative to the night decreases (as the value of DIF decreases) (Erwin and Heins, 1990; Erwin et al., 1991). For example, as DIF increased from -6.0 to +6.0 °C, plant height increased by 39% in fuchsia (Erwin et al., 1991), 19% in geranium (Strefeler, 1995), and 9% in Italian bellflower (*Campanula isophylla*; Moe and Mortensen, 1992). However, because the DIF in our experiment was variable between treatments and was generally small (0.5 to 2.0 °C), the plant height response observed in this study is probably a function of MDT and not DIF.

In a majority of the crops studied, plant quality decreased as the MDT increased, which can at least partially be attributed to the more rapid flowering at the higher temperatures. Therefore, there is often a tradeoff between faster crop timing and higher plant quality, especially for plants with a low  $T_{min}$ . The notable exceptions were 1) New Guinea impatiens and torenia, in which flower number and shoot biomass at flowering were maximal at intermediate temperatures ( $\approx 20$  °C) and decreased at a lower or higher MDT; and 2) globe amaranth, in which flower number appeared to plateau at intermediate temperatures ( $\approx 20$  °C) but shoot biomass continued to increase with temperature. The crop models generated in this study were at temperatures between 14 and 26 °C and may not be valid

outside this temperature range. However, because plants respond to the integrated MDT (de Koning, 1990), the models are applicable to constant or fluctuating temperatures within this temperature range. Finally, DLI can also influence plant quality parameters (Fausey et al., 2005; Moccaldi and Runkle, 2007; Warner and Erwin, 2005), and therefore the linear and quadratic equations describing the relationship between plant quality parameters and MDT may not be applicable under DLI conditions outside the range in this study.

#### Literature Cited

Armitage, A.M. 1995. Photoperiod, irradiance, and temperature influence flowering of *Hamelia patens* (Texas firebush). HortScience 30:255–256.

Blanchard, M. and E. Runkle. 2011a. Temperature, p. 67–81. In: Nau, J. (ed.). Ball redbook. 18th Ed., Vol. 2. Ball Publishing, Chicago, IL.

Blanchard, M.G. and E.S. Runkle. 2011b. Quantifying the thermal flowering rates of eighteen species of annual bedding plants. Sci. Hort. 128:30–37.

Brooks, A. and G.D. Farquhar. 1985. Effect of temperature on the CO<sub>2</sub>/O<sub>2</sub> specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Estimates from gas-exchange measurements on spinach. Planta 165:397–406.

Carvalho, S.M.P., S.E. Wuillai, and E. Heuvelink. 2006. Combined effects of light and temperature on product quality of *Kalanchoe blossfeldiana*. Acta Hort. 711:121–126.

de Koning, A.N.M. 1990. Long-term temperature integration of tomato. Growth and development under alternating temperature regimes. Sci. Hort. 45:117–127.

Dinar, M. and J. Rudich. 1985. Effect of heat stress on assimilate partitioning in tomato. Ann. Bot. (Lond.) 56:239–248.

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.

Fausey, B.A., R.D. Heins, and A.C. Cameron. 2005. Daily light integral affects flowering and quality of greenhouse-grown *Achillea*, *Gaura*, and *Lavandula*. HortScience 40:114–118.

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

Karlsson, M.G. and R.D. Heins. 1992. Chrysanthemum dry matter partitioning patterns along irradiance and temperature gradients. Can. J. Plant Sci. 72:307–316.

Korczynski, P.C., J. Logan, and J.E. Faust. 2002. Mapping monthly distribution of daily light integrals across the contiguous United States. HortTechnology 12:12–16.

Ku, S.B. and G.E. Edwards. 1977. Oxygen inhibition of photosynthesis. 1. Temperature dependence and relation to O<sub>2</sub>/CO<sub>2</sub> solubility ratio. Plant Physiol. 59:986–990.

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

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

Miller, A. and A.M. Armitage. 2002. Temperature, irradiance, photoperiod, and growth retardants influence greenhouse production of *Angelonia angustifolia* Benth. Angel Mist series. HortScience 37:319–321.

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. and L.M. Mortensen. 1992. Thermomorphogenesis in pot plants. Acta Hort. 305:19–25.

Niu, G., R.D. Heins, A. Cameron, and W.H. Carlson. 2001a. Day and night temperatures, daily light integral, and CO<sub>2</sub> enrichment affect growth and flower development of *Campanula carpatica* 'Blue Clips'. Sci. Hort. 87:93–105.

Niu, G., R.D. Heins, A. Cameron, and W. Carlson. 2001b. Temperature and daily light integral influence plant quality and flower development of *Campanula carpatica* 'Blue Clips', 'Deep Blue Clips', and *Campanula* 'Birch Hybrid'. HortScience 36:664–668.

Niu, G., R.D. Heins, A.C. Cameron, and W.H. Carlson. 2000. Day and night temperatures, daily light integral, and CO<sub>2</sub> enrichment affect growth and flower development of pansy (*Viola* × *wittrockiana*). J. Amer. Soc. Hort. Sci. 125:436–441.

Park, B.H., N. Oliveira, and S. Pearson. 1998. Temperature affects growth and flowering of the balloon flower [*Platycodon grandiflorus* (Jacq.) A. DC. cv. Astra Blue]. HortScience 33:233–236.

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.

- Strefeler, M.S. 1995. Growth response of 20 seed geranium cultivars to three day-night temperature regimes. *HortScience* 30:1465–1466.
- Vaid, T.M. and E.S. Runkle. 2013. Developing flowering rate models in response to mean temperature for common annual ornamental crops. *Sci. Hort.* 161:15–23.
- van Iersel, M.W. 2003. Short-term temperature change affects the carbon exchange characteristics and growth of four common bedding plant species. *J. Amer. Soc. Hort. Sci.* 128:100–106.
- Wai, K.S. and S.E. Newman. 1992. Air and root-zone temperatures influence growth and flowering of snapdragons. *HortScience* 27:796–798.
- 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. *Sci. Hort.* 108:295–302.
- 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. Cameron. 1998. Effect of forcing temperature on time to flower for *Coreopsis grandiflora*, *Gaillardia × grandiflora*, *Leucanthemum × superbum*, and *Rudbeckia fulgida*. *HortScience* 33:663–666.