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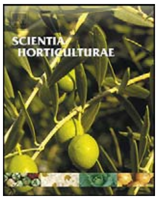

Quantifying the thermal flowering rates of eighteen species of annual bedding plants

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ABSTRACT

The effect of 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 an irradiance of 160–180 μmol m^{-2} s^{-1}, 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} were only observed for 8–10 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.), whereas 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 two to seven 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.

1. 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 that predict crop time or quality under various environmental conditions 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; Liu and Heins, 2002), petunia (*Petunia* × *hybrida* Vilm.-Andr.; Adams et al., 1998), and potted rose (*Rosa* L.; Steininger et al., 2002).

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/days). The rate of plant development in response to MDT increases between the base temperature (T_{min}) and optimum temperature (T_{opt}). T_{min} is the species-specific temperature at or below which the rate of progress toward 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 developmental 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, whereas potted rose had an estimated T_{min} of 8.1–9.5 °C from bud break to open flower (Niu et al., 2001; Steininger et al., 2002).

As MDT increases above T_{min}, developmental rate increases until a maximum rate at the species-specific 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}, developmental rate decreases as MDT increases and the rate becomes zero at the maximum temperature (T_{max}).

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Estimation of T_{min}, T_{opt}, and T_{max} requires the 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, 23.0–25.5 °C, and 30.8 °C, respectively (Faust and Heins, 1993).

Relationships between MDT and plant development rates have been modeled with linear, quadratic, cubic, and exponential functions (Landsberg, 1977; Larsen, 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 an 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; developmental 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) hypothesized 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 whether other species display a similar asymmetrical temperature response around T_{opt} (Summerfield et al., 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 accumulated only at temperatures $>T_{min}$ and $\leq T_{opt}$ (Roberts and Summerfield, 1987; Wang, 1960). Therefore, the determination of T_{min} and T_{opt} is 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 differed ±5.6 °C 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 m^{-2} 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 are 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 patul*a L.), and pansy (Adams et al., 1996, 1998; Armitage et al., 1981; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Pietsch et al., 1995; Pramuk and Runkle, 2005a). The estimation of T_{min} for additional annual species could be useful in the development of crop models that predict flowering rates under different environmental 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 those data, to develop mathematical models that estimate T_{min} and T_{opt} for flowering rates. Bedding plants were selected because they compose the largest segment (49%) of floriculture crop production in the United States, with a reported wholesale value of $1.81 billion in 2009 (U.S. Department of Agriculture, 2010). The 18 species investigated in this study are commonly produced in greenhouses throughout the world.

2. 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). These cultivars were selected by the plug producer based on their commonality and commercial availability. Seven to ten days 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 wattage) of 3.6 and at an intensity of 160–180 μmol m^{-2} 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 L^{-1} $CaCO_3$ and containing 95, 34, and 29 mg L^{-1} Ca, Mg, and S, respectively. At every irrigation, the water was supplemented with a water-soluble fertilizer providing (mg L^{-1}) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, 0.3 Mn, 0.3 Zn, 0.1 B, and 0.1 Mo (MSU Well Water Special; GreenCare Fertilizers, Inc., Kankakee, IL). No plant growth regulating chemicals were applied during the study.

When seedlings were ready for transplant [16–44 d after seed sowing, depending on species (Table 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). Seedlings were subjectively deemed ready for transplant when the plugs were well rooted and leaves formed a dense canopy in the tray. 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 (Walworth and Warner, 2009). Within each growth chamber, species were grouped based on their height, and then plants within each group were randomly placed at a density of 62 plants per m^2.

The experiment was performed twice with each species, and the time from seed sowing to transplant was the same or ±7 d between replications (Table 1). For each species, the mean node number at transplant was determined as an average of the 8 plants in each replication (16 plants; Table 1). Species in which a treat-