IMPROVING THE SCHEDULING AND PROFITABILITY OF ANNUAL BEDDING PLANT PRODUCTION BY MANIPULATING TEMPERATURE, DAILY LIGHT INTEGRAL, PHOTOPERIOD, AND TRANSPLANT SIZE

By

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ABSTRACT

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Volatile fuel prices, an increased emphasis on sustainable production practices, and declining profit margins have motivated commercial growers of annual bedding plants to reduce energy inputs and improve crop scheduling accuracy. The objectives of this research were to quantify the influence of average daily temperature (ADT), photosynthetic daily light integral (DLI), photoperiod, and transplant size on the flowering characteristics of popular bedding plant crops. Increasing ADT from 14 to 26 ºC decreased flowering time and plant quality in nearly all of the 18 species and varieties evaluated in one experiment. In a separate experiment, similar but variety-specific responses occurred in 16 petunia (*Petunia* ×*hybrida*) cultivars grown at 12 to 23 ºC. Linear and non-linear mathematical models were developed under a range of DLI conditions to predict the influence of ADT on flowering time of these crops, and the base temperatures (T_{min}) at which the flowering rates were zero were estimated. The estimated T_{min} ranged from –3.9 ºC for *Diascia barberae* to 13.8 ºC for *Gomphrena globosa*. An additional study quantified the effects of transplant size and ADT on flowering time and estimated profitability of five species. Flowering time decreased only when the larger transplants contained more mature plants, but transplanting a larger propagule was not necessarily a profitable strategy. Finally, seedling sensitivity and duration of long-day induction, as well as the effects of temperature and photoperiod interaction on flowering, were determined in three petunia varieties.

DEDICATION

I dedicate this thesis to my loving parents, Farida and Fakhrudin Chitalwala who against all odds made sure I received the best education possible.

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SECTION I

LITERATURE REVIEW

Introduction

In the United States, bedding and garden plants are the largest contributors (48%) to the total value of production of all reported floriculture crops, with a 15-state wholesale value of $1.90 billion in 2011 (USDA, 2012). Michigan ranks third among 15 states, with a reported wholesale value of > $260 million for bedding and garden plants (USDA, 2012). Bedding plants are typically grown during some of the coldest months of the year, especially in northern climates, where heating typically accounts for ≥ 10% of the annual greenhouse production costs (Bartok, 2001). Volatile fuel prices, an increased emphasis on sustainable production practices, and declining profit margins have motivated growers to optimize their greenhouse environments and grow crops as energy-efficiently and as profitably as possible. One way of minimizing the input costs is to reduce crop production duration in the greenhouse. This can reduce production cost by minimizing heating and labor costs, fertilizers, water, and other resources needed to maintain the crops in the greenhouse, and can also potentially increase profitability by enabling more production cycles in a season.

Crop production time depends primarily on the species and cultivar (Blanchard, 2009), starting plant size and characteristics (Fisher et al., 2006), desired finish size, average daily temperature (ADT) (Blanchard and Runkle, 2011a), photosynthetic daily light integral (DLI) (Blanchard, 2009; Moccaldi and Runkle 2007; Pramuk and Runkle, 2005b), and photoperiod (Adams et al., 1997; Adams et al., 1998a). Although fast cropping is an appealing concept, it can result in reduced plant quality. Poor plant quality characteristics, such as tall and weak stems, few branches, few and small flowers, and reduced biomass, can lower consumer appeal. Plant quality is mainly determined by the genotype, cultural practices (e.g., root zone management), and aforementioned environmental conditions (Liu and Heins, 1997). In particular, temperature and light are two environmental factors that primarily influence plant growth and development and thus, plant quality attributes.

Plant growth, defined as an irreversible increase in plant size, is a function of biomass production driven by photosynthesis (Heins et al., 2000). Plants use light energy with wavelengths from approximately 400 to 700 nm, and this waveband is termed photosynthetically active radiation (PAR). The integrated PAR received during a 24-h period is called the DLI. The DLI received outdoors depends on the location, time of the year, and regional weather patterns. For example, the average outdoor DLI in December ranges from 5 to 10 $mol \cdot m^{-2} \cdot d^{-1}$ in Michigan to 20 to 25 $mol \cdot m^{-2} \cdot d^{-1}$ in Florida; in June, the average DLI is 40 to 45 $mol \cdot m^{-2} \cdot d^{-1}$ in both states (Korczynski et al., 2002). Actual DLI received by plants inside a greenhouse is reduced substantially (typically by 40 to 60%) by shading from glazing material and obstructions that block light (Hanan, 1998). Therefore, the actual average DLI received inside a commercial Michigan greenhouse usually ranges from <5 $mol \cdot m^{-2} \cdot d^{-1}$ in December to >20 $mol \cdot m^{-2} \cdot d^{-1}$ in May and June. High-density planting can further reduce the DLI available to individual plants due to shading from adjacent plants or ones hanging overhead. Quantum sensors installed at canopy height can be used to measure the PAR (in $\mu mol \cdot m^{-2} \cdot s^{-1}$) and averages can be recorded by a datalogger. The DLI can be determined by integrating those values, or by a light meter specifically designed to measure and calculate the DLI.

Plant development, defined as the process of maturation of plant organs, is a function of temperature-dependent metabolic processes (Heins et al., 2000). The developmental rate in plants is mainly controlled by the ADT. ADT can be calculated by measuring the temperature on a frequent basis (e.g., every 10 s) with a shielded and aspirated thermocouple and then calculating the daily mean. The rate of plant development is controlled by the plant shoot-tip temperature (Harris and Scott, 1969), which is a function of air temperature, glazing material temperature, solar radiation, and vapor-pressure deficit during the day (Faust and Heins, 1998; Shimizu et al., 2004). Faust and Heins (1998) showed that vinca (*Catharanthus roseus* L.) shoot-tip temperature was always below air temperature at night, whereas during the day, it was ±2 °C of air temperature when grown at <25 °C and was 4 to 6 °C lower when grown at >25 °C. In commercial greenhouses, nearly all environmental control systems measure the air temperature, and it is extremely uncommon for shoot-tip temperature to be measured.

The present downturn in the economy has led consumers to critically evaluate product features and prices before they make a purchase (Hall, 2011). This has led to increased market specifications in terms of plant quality and delivery date, while prices have to be maintained competitive. Days to flower (DTF) generally decreases as ADT and DLI increase (Blanchard, 2009; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). At the same time, plant quality of shade-avoiding crops typically improves as ADT decreases and DLI increases (Blanchard, 2009; Pramuk and Runkle, 2005b; Moccaldi and Runkle, 2007). Thus, it is important to quantify the effects of temperature and DLI on plant growth, development, and quality parameters so that growers can balance crop timing with quality.

Temperature Effects on Plant Development

Plant developmental rate depends on the rate of biochemical reactions in meristematic tissues. As temperature increases, activation energy of the reaction molecules driving these biochemical reactions increases and consequently, the number of ‘active’ molecules increases according to the Boltzman energy distribution (Jones, 1983). The rate of a biochemical reaction increases with an increase in the number of molecules with an activation energy equal to or higher than the minimum activation energy required for that particular reaction (Jones, 1983). Therefore, as the rate of biochemical reactions increase with temperature, plants mature at a faster rate, at least up to some species-specific maximum temperature. Plant development rate is mainly controlled by ADT, while plant morphology is influenced by ADT, the difference between day and night temperatures (DIF), and other environmental factors such as light quality.

Average daily temperature regulates plant development by influencing different events in a plant's life cycle such as germination, leaf unfolding, and flowering. The time taken to reach a particular developmental event as a function of temperature can be expressed as the number of days to reach that event (n) or as a developmental rate by taking the reciprocal of that number of days (1/n). Different functions have been used to describe the relationship between the rate of plant development and ADT. For many floriculture crops, the relationship between the rate of plant development and ADT has been described by a simple linear function when the ADT is above the species-specific base temperature (T_b) and at or below the optimum temperature (T_{opt}) (Adams et al., 1997; Clough et al, 2001; Karlsson et al., 1988; Larsen and Hiden, 1995; Niu et al., 2001; Park et al, 1998; Whitman et al., 1997; Yuan et al., 1998). For example, the rate of progress to flowering increased linearly with temperature in the range of 15.2 to 29.8 °C for sundrop (*Oenothera fruticosa* L.) (Clough et al, 2001), 14.0 to 29.0 °C for balloon flower [*Platycodon gradiflorus* (Jaq.)] cv. Astra Blue (Park et al, 1998), 15.0 to 27.0 °C for tussock bellflower (*Campanula carpatica* Jacq). cv. Blue Clips (Niu et al., 2001; Whitman et al., 1997) and 15.0 to 26.0 °C for largeflower tickseed (*Coreopsis grandiflora* Hogg ex Sweet), blanketflower (*Gaillardia ×grandiflora* Van Houtte), Shasta daisy [*Leucanthemum ×superbum* (Bergmans ex J.W. Ingram)] and black-eyed Susan (*Rudbeckia fulgida* Aiton) (Yuan et al., 1998). Similarly, Karlsson et al. (1988) reported a linear increase in leaf unfolding rate with temperature between 14.0 and 30.0 °C in ‘Nellie White’ Easter lily (*Lilium longiflorum* Thunb.).

Within a species-specific temperature range, each degree rise in temperature increases the rate of plant development by the same incremental amount. This linear relationship between temperature and plant development rate can be useful in estimating the T_b and the thermal time (θ) required for a particular developmental event (Roberts and Summerfield, 1987). The base temperature is the minimum temperature below which no development occurs, and thermal time is the summation of all degree days above T_b required for a particular developmental event to occur. A linear relationship is mathematically expressed by the following equation:

$$1/d = a + bT \qquad (1)$$

where 1/d is rate of development of a particular event, a = slope, b = intercept, and T = ADT above T_b and below T_{opt}. Given that the developmental rate at T_b is zero, equation (1) can be used to calculate T_b:

$$T_b = -a / b \qquad (2)$$

The thermal time required for a particular developmental event can be calculated from equation (1) as:

$$\theta = 1 / b \qquad (3)$$

When ADT exceeds the T_{opt}, non-linear functions such as polynomial and exponential functions have been used for some floricultural species. Karlsson et al. (1991) and Karlsson and Werner (2001) expressed leaf unfolding rate in hibiscus (*Hibiscus rosa-sinensis* L.) and cyclamen (*Cyclamen persicum* Mill.) as a polynomial-cubic function of temperature. In contrast, an exponential model was proposed by Larsen (1988) to describe the rate of germination and rate of vegetative and floral development in cineraria (*Senecio* ×*hybridus* Hyl.) as a function of temperature.

Plant developmental rate increases linearly from T_b to T_{opt}, which are specific to each species. For any species, when temperature is below T_b or exceeds a maximum temperature (T_{max}), the developmental rate becomes zero. Above T_b, plant developmental rate increases to a maximum value at T_{opt}. Beyond T_{opt}, the rate decreases and ultimately development ceases at T_{max}. Plant injury and death can occur with prolonged exposure to temperatures below T_b or above T_{max} from irreversible damage to the photosynthetic apparatus and cell membranes (Lie and Huang, 2000; Raison et al., 1980).

The species-specific T_b, T_{opt}, and T_{max} are usually determined by the natural origin and distribution of the species. T_b has been estimated for many floriculture crops and has varied from ≤0.0 °C to ≥10.0 °C (Blanchard, 2009; Clough et al., 2001; Park et al., 1998; Whitman et al., 1997; Yuan et al., 1998). For example, tussock bellflower, native to the Carpathian mountains of Eastern Europe, had an estimated T_b for flowering of 0.0 °C (Whitman et al., 1997). In contrast, for browalia (*Browalia speciosa* Hook.) and summer snapdragon (*Angelonia augustifolia* Benth.), both of tropical origin, the estimated T_b was 9.0 and 10.0 °C, respectively (Blanchard, 2009). Breeding efforts over the years have introduced desirable traits such as early flowering, frost tolerance, and heat tolerance. Therefore, depending on the breeding objective, cultivars of the same species may differ in their base and optimum temperatures, as well as thermal time for a particular event such as flowering. For example, the T_b calculated for petunia (*Petunia* × *hybrida* Vilm.-Andr.) 'Dreams Neon Rose' was 2.7 °C lower than that of 'Wave Purple' (Blanchard, 2009). Base and optimum temperatures within a species can also vary with the developmental process (Clough et al., 2001; Pearson et al., 1995; Yuan et al., 1998; Whitman et al., 1997), physiological process (Van Iersel, 2003) and environmental conditions such as photoperiod (Adams et al., 1997; 1998a; 1998b) and DLI (Adams et al., 1997; Faust and Heins, 1993; Pramuk and Runkle, 2005b). Blanchard (2009) reported a greater delay in flowering at lower temperatures for species with a higher T_b as compared to species with lower T_b values (Table 1). Estimation of T_b and T_{opt} allows one to categorize crops according to their temperature sensitivity and improve greenhouse crop energy efficiency (Blanchard, 2009). In the sections below, the effects of temperature on vegetative growth, flowering, and plant quality characteristics are discussed.

Leaf Unfolding Rate (LUR)

Plant growth can be divided into two developmental phases: vegetative and reproductive. Flower initiation marks the transition from the vegetative phase to the flowering phase. In some plants like Easter lily and chrysanthemum, flower initiation terminates leaf production so that a specific number of leaves (depending on when flower initiation occurs) are formed before flowering. Plant development can be quantified by the number of leaves formed prior to flower initiation and the subsequent rate of leaf unfolding (Faust and Heins, 1993). In some indeterminate plants like begonia (*Begonia ×hiemulis* Fotsch), flower initiation occurs at a particular plant size (leaf number) when grown under short days. The ADT affects the leaf unfolding rate (LUR) such that, as temperature increases, leaves unfold at a faster rate up to T_{opt}, and thereafter the rate starts to decline (Brøndum and Heins, 1993; Faust and Heins, 1993; Karlsson and Werner, 2001; Karlsson, 1992; Karlsson et al., 1991; Larsen and Hiden, 1995). Therefore, knowledge of the leaf number required to unfold prior to flowering in determinate plants (Easter lily and chrysanthemum) or the minimum leaf count for flower initiation to occur (begonia) and the LUR at different temperatures allow for precise scheduling of these plants.

The effect of ADT on leaf development has been studied for many floriculture crops including African violet (*Saintpaulia ionantha* Wendl.) (Faust and Heins, 1993), begonia (Karlsson, 1992), chrysanthemum (Cockshull et al., 1981; Karlsson et al., 1989b; Larsen and Hiden, 1995), cyclamen (Karlsson and Werner, 2001), dahlia (*Dahlia pinnata* Cav.) (Brøndum and Heins, 1993), Easter lily (Karlsson et al., 1988; Roberts et al., 1983; Wang and Roberts, 1983), hibiscus (Karlsson et al., 1991), pansy (*Viola* × *wittrockiana* Gams.) (Adams et al., 1997), poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch.) (Berghage et al., 1990b) and vinca (Pietsch et al., 1995). Although LUR response has been frequently described as a function of average daily air temperature (Adams et al., 1997; Karlsson et al., 1988; Karlsson et al., 1989b; Karlsson, 1992; Karlsson and Werner, 2001; Larsen and Hiden, 1995; Pietsch et al., 1995), average hourly air temperatures (Karlsson et al., 1991) and average plant temperatures (Faust and Heins, 1993) have been used in some studies. In greenhouses where diurnal temperature fluctuations fall outside the linear range of a plant's thermal development response, average hourly temperature predicts LUR more accurately than ADT (Karlsson et al., 1991). Faust and Heins (1993) reported a greater accuracy (63%) in predicting LUR when average plant temperatures were used as opposed to average hourly or daily air temperatures. Individual effects of day and night temperatures on the LUR of Easter lily (Karlsson et al., 1988) and poinsettia (Berghage et al., 1990b) have also been investigated. However, LUR was a function of ADT and not only day or night temperature. Wang and Roberts (1983) reported that high soil temperature (≥24 °C) promoted leaf unfolding in Easter lily when air temperature was lower. This promotive effect of higher soil temperature on the LUR was probably from an indirect increase in plant temperature, air temperature surrounding the plant, or both, since the LUR increased with an increase in air temperature even for unheated soil.

Researchers have used different functions, such as linear (Adams et al., 1997; Karlsson et al., 1988; Karlsson et al., 1989b), quadratic (Karlsson, 1992) or cubic (Karlsson et al., 1991; Karlsson and Werner, 2001), to quantify the relationship between LUR and temperature. LUR increased linearly as ADT increased from 0.2 leaves$\cdot$d^{-1} at 10.0 °C to 0.5 leaves$\cdot$d^{-1}at 30.0 °C in chrysanthemum, and 1.2 leaves$\cdot$d^{-1} at 14.0 °C to 2.7 leaves$\cdot$d^{-1} at 30.0 °C in Easter lily (Karlsson et al., 1988; Karlsson et al., 1989b). Karlsson (1992) reported a quadratic increase in the LUR with temperature between 13.0 and 28.0 °C in begonia under long days prior to flower initiation, with T_{opt} at 21.0 °C. Similarly, a cubic-polynomial function was found to best describe the LUR as a function of temperature between 10.0 and 35.0 °C in hibiscus (Karlsson et al., 1991) and between 8.0 and 24.0 °C in cyclamen (Karlsson and Werner, 2001). The cubic-polynomial model predicted a maximum rate of 0.23 leaves$\cdot$d^{-1} at 32.0 °C for hibiscus (Karlsson et al., 1991) and 0.33 leaves$\cdot$d^{-1} at 19.1 °C for cyclamen (Karlsson and Werner, 2001), beyond which the LUR began to decrease. When temperatures above T_{opt} are included in the experimental range, the temperature response curve follows an asymmetric peak shape, such that the absolute value of LUR decreases more rapidly at temperatures greater than T_{opt} as compared to increase in LUR from T_b to T_{opt} (Brøndum and Heins, 1993; Faust and Heins, 1993; Karlsson and Werner, 2001; Larsen and Hiden, 1995).

At any given temperature, the LUR varies widely among floriculture crops. For example, plants at an ADT of 18.0 °C unfolded 0.08 leaves$\cdot$d^{-1} in vinca under supplemental lighting (Pietsch et al., 1995), 0.11 leaves$\cdot$d^{-1} in begonia (Karlsson, 1992), 0.18 leaves$\cdot$d^{-1} in poinsettia (Berghage et al., 1990b), 0.21 leaves$\cdot$d^{-1} in African violet under 10.0 mol$\cdot$m$^{-2}\cdot$d^{-1} of light (Faust and Heins, 1993), 0.23 leaves$\cdot$d^{-1} in hibiscus (Karlsson et al., 1991), 0.33 leaves$\cdot$d^{-1} in cyclamen (Karlsson and Werner, 2001), 0.34 leaves$\cdot$d^{-1} in chrysanthemum (Karlsson et al., 1989b) and 1.5 leaves·d^{-1} in Easter lily (Karlsson et al., 1988). Although differences in the LUR among these species are largely due to genetic variations in temperature response, to some extent, differences in experimental conditions such as DLI and the use of air versus plant temperature to describe the LUR response (Faust and Heins, 1993) probably also influenced these inter-specific rates. Similarly, T_b for LUR ranged from 1.6 °C for chrysanthemum (Karlsson et al., 1989b) to 9.8 °C for hibiscus (Karlsson et al., 1991) and T_{opt} ranged from 19.1 °C for cyclamen (Karlsson and Werner, 2001) to 32.0 °C for hibiscus (Karlsson et al., 1991). In begonia (Karlsson, 1992), cyclamen (Karlsson and Werner, 2001) and hibiscus (Karlsson et al, 1991), the LUR of different cultivars within a species was found to be similar. However, cultivars or species that have a similar LUR may not flower at the same time due to differences in the number of leaves formed prior to flower initiation (Karlsson et al., 1991).

Flowering

Temperature influences flowering time by affecting flower initiation, development, or both. Many studies have quantified the influence of temperature on flowering time, and reported a decrease in DTF with an increase in ADT, within a species-specific range (Adams et al., 1999; 1998b; 1998c; Blanchard and Runkle, 2011a; Clough et al., 2001; Kanellos and Pearson, 2000; Miller and Armitage, 2002; Moccaldi and Runkle, 2007; Niu et al., 2001; 2000; Pramuk and Runkle, 2005b; White and Warrington, 1988). A decrease in DTF with an increase in ADT may be due to earlier flower initiation, which can be observed by repeated apical dissections or reduced leaf number below the first open flower (Adams et al., 1998b; 1998c; Mattson and Erwin, 2003), or from faster flower development rate (Brøndum and Heins, 1993; Faust and Heins, 1994; Karlsson and Werner, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). When plants are subjected to ADT above T_{opt}, the flower development rate (reciprocal of DTF) begins to decline (Blanchard and Runkle, 2011a; Brøndum and Heins, 1993; Faust and Heins, 1994; Semeniuk, 1975). Exposure to high temperatures caused a developmental delay in flowering (greater node number prior to flowering) in calendula, chrysanthemum, impatiens, pansy, snapdragon and torenia (Warner and Erwin, 2005; 2006; Whealy et al., 1987). A decrease in flowering rate at temperatures > T_{opt} is known as heat delay, and may be due to a delay in flower induction, initiation and/or development (Warner and Erwin, 2006). Biochemically, inhibition of flowering at higher temperatures may be due to peroxidation of membrane unsaturated fatty acids that causes cell damage (Gutteridge and Halliwell, 1990).

In many plants, a linear function has been used to describe the relationship between flowering rate and ADT, when ADT is between T_b and T_{opt} (Clough et al., 2001; Niu et al., 2001; 2000; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). In other crops, a quadratic function best described the effect of ADT on DTF, since the decrease in DTF with an increase in ADT was not linear between T_b and T_{opt} (Armitage et al., 1981; Clough et al., 2001; Niu et al., 2001; 2000; Park et al., 1998; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). For example, a greater decrease in flowering time was observed when ADT increased from 15 to 20 °C compared to when ADT increased from 20 to 25 °C. Although linear and quadratic equations can be used to simply describe these responses, they lack biological significance because their constants do not have physiological meaning (Landsberg, 1977).

Several studies have quantified the effect of ADT on flowering time using mathematical models that contain parameters of biological significance (T_{max}, T_{opt} and/or T_b) (Blanchard and Runkle, 2011a; Blanchard et al., 2011a; Brondum and Heins, 1993; Hiden and Larsen, 1994; Larsen, 1988; 1989; Larsen and Persson, 1999). T_b and T_{opt} for flower development have been estimated for numerous species and vary among species and in some cases also with the phase of development. For example, T_b for flower development varied from 0.0 °C in tussock bellflower (Whitman et al., 1997) to 9.9 °C in summer snapdragon (Blanchard and Runkle, 2011a), and T_{opt} varied from 19.1 °C in dahlia to 28.0 °C in blue salvia (*Salvia farinacea* Benth.) (Blanchard and Runkle, 2011a). Similarly, a few studies have also reported different T_b and T_{opt} for different phases of flower development in blanketflower, chrysanthemum, Shasta daisy, sundrop, and tussock bellflower (Clough et al., 2001; Karlsson et al., 1989a; Whitman et al., 1997; Yuan et al., 1998).

The effect of DIF on flowering development has been evaluated in many plants. When DT and NT were within the species-specific linear range, flowering time was a function of ADT and did not vary between DT or NT (Blanchard and Runkle, 2011b; Brøndum and Heins, 1993; Cockshull et al., 1981; Erwin and Heins, 1990; Lepage et al., 1984; Moe, 1990; Mortensen and Moe, 1992; Niu et al., 2001; 2000; Pietsch et al., 1995). Since ADT and not DIF controls flowering time in plants, a +DIF can be used to potentially lower heating costs, since most greenhouse heating occurs at night (Blanchard and Runkle, 2011b). However, PGR application or other height control strategies may be required when plants are grown at a +DIF.

A few studies have evaluated the influence of root-zone temperature on flowering time of a few species (Vogelezang, 1990; 1992; Wai and Newman, 1992). A warmer root zone radiates heat to the surrounding cool air, which is evident from the increase in air temperature as root-zone temperature increased (Vogelezang, 1990; 1992). Therefore, the promotive effect of higher root-zone temperature on flowering time can be attributed to an increase in air and thus, shoot-tip temperature.

Although flowering time response to ADT has been extensively studied, the exact mechanism that induces this response is still not known. However, genetic and molecular research over the last decade has proposed that an independent thermal induction pathway (thermosensory) may regulate flowering by affecting the expression of the *FT* (floral integrator) gene (Blazquez et al., 2003; Sureshkumar et al., 2006). Blazquez et al. (2003) reported a reduction in flowering time and a simultaneous increase in *FT* expression in mouse-ear cress [*Arabidopsis thaliana* (L.) Heynh] at 23.0 °C compared to 16.0 °C. Similarly, Sureshkumar et al. (2006) observed a 10-fold increase in mRNA levels of *FT* in mouse-ear cress at 27 °C compared to 23 °C. In addition, changes in ambient temperature had little or no effect on DTF and leaf number below first open flower in mouse-ear cress plants overexpressing *FT* (Blazquez et al., 2003).

Several genes that play an important role in this pathway have already been identified in mouse-ear cress: *FCA* and *FVE* which sense ambient temperature and regulate the flowering time response (Blazquez et al., 2003), and *SVP* (short vegetative phase) and *FLM* (flowering locus M) which act as negative regulators of *FT* expression (Lee et al., 2007; Scortecci et al., 2003). *FCA* and *FVE* act separately through an *FLC*-independent pathway to regulate flowering time in response to ambient temperature (Blazquez et al., 2003). *SVP* negatively regulates *FT* expression by directly binding to the CArG motifs in the *FT* gene (Lee et al., 2007). In addition, *svp* mutants flowered earlier especially at cooler temperatures (16.0 °C), while plants overexpressing *SVP* flowered later especially at warmer temperatures (23.0 °C) (Lee et al., 2007). Recently, Lee et al. (2010) demonstrated the involvement of miR172, regulated by *SVP*, in the thermosensory pathway. Although several components of this pathway have been identified, the sequence of these components, their exact function and how they interact to influence temperature-dependent flowering in plants requires further research.

Effect of Temperature on Plant Quality

In addition to plant development, temperature (and other factors) influences plant quality parameters including flower number and size, branch number, plant height, and plant biomass. Several studies have quantified the influence of temperature on plant quality, and have reported a decrease in plant quality with an increase in ADT when grown at the same or similar DLI (Blanchard et al., 2011a; 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2001; 2000; Pramuk and Runkle, 2005b). Plant quality is important to growers since buyers purchase plants that are of the highest quality. The influence of temperature on flower number and size, branch number, plant height, and plant biomass is discussed in detail below.

Effect of Temperature on Flower Number and Quality

Flower number and size are two of the factors that influence overall plant quality. A high quality plant would typically have a relatively large number of big flowers and flower buds. In many shade-avoiding species, ADT influences flower number such that as ADT increases, flower number decreases (Blanchard et al., 2011a; 2011b; Brøndum and Hein, 1993; Clough et al., 2001; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2001; 2000; Pramuk and Runkle, 2005b; Whitman et al., 1997; Yuan et al., 1998). The magnitude of decrease in flower number with increase in temperature varies widely among species and cultivars. For example, an increase in ADT from 16.0 to 26.0 °C decreased the flower number of tussock bellflower by 181% (under 10.8 $mol \cdot m^{-2} \cdot d^{-1}$ and at 400 $umol \cdot mol^{-1}$ CO_2; Niu et al., 2001), largeflower tickseed by 80% (Yuan et al, 1998), Shasta daisy by 55% (Yuan et al, 1998), sundrop by 167% (Clough et al., 2001), *Petunia axillaris* (Lam.) Britton, et al. by 96% (Warner, 2001), black-eyed Susan by 75% (Yuan et al, 1998) and pansy by 84% (under 10.6 $mol{\cdot}m^{-2}{\cdot}d^{-1}$) (Niu et al., 2000). Similarly, in 'Avalanche Pink', 'Dreams Rose' and 'Wave Purple' petunia cultivars, an increase in temperature from 14.0 to 24.0 °C decreased the flower bud number by 67%, 340% and 28%, respectively (Mattson and Erwin, 2003). Increased flower number at lower temperatures is sometimes correlated with an increase in leaf number (Mattson and Erwin, 2003) or branch number (Mattson and Erwin, 2003; Warner and Erwin, 2006).

However, flower bud number increased as temperature increased in some species such as Chinese lantern lily (*Sandersonia aurantiaca* Hook.) (Davies et al., 2002), chrysanthemum (Carvalho et al., 2005), cyclamen (Karlsson and Werner, 2001), and orchid pansy (*Achimenes* Pers.; Vlahos et al., 1992). For these crops, increased flower number at higher temperatures was correlated with an increase in leaf number (Carvalho et al., 2005; Karlsson and Werner, 2001; Vlahos et al., 1992) or with a reduction in aborted flowers (Davies et al., 2002).

Flower quality is often determined by its size (diameter, area or dry weight) and color intensity. For many crops, ADT and flower size are inversely related (Brøndum and Heins, 1993; Carvalho et al., 2005; Clough et al., 2001; Niu et al., 2001; 2000; Moccaldi and Runkle, 2007; Pearson et al., 1995; Whitman et al., 1997; Yuan et al., 1998). Each degree rise in ADT decreased flower diameter or area by 0.97 mm in tussock bellflower 'Blue Chips' (under 10.8 $mol{\cdot}m^{-2}{\cdot}d^{-1}$) (Niu et al., 2001), 1.42 cm in dahlia 'Royal Dahlietta Yellow' (Brøndum and Heins, 1993), 0.19 cm in sundrops 'Youngii-lapsley' (Clough et al., 2001) and 1.05 cm^2 in pansy 'Universal Violet' (Pearson et al., 1995). Flower bud development requires carbon import from the source organs (leaves). Sucrose hydrolysis in the sink organs (flower buds) is necessary to establish a concentration gradient for carbon transport between the source and the sink (Dinar and Rudich, 1985). High temperatures reduce sucrose hydrolysis and therefore increase its concentration in flower buds, 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).

Flower color is determined by the spectral properties of light reflected by certain pigments in petals. The intensity of flower color in some plants, particularly those that are red, blue, or purple, is greatly influenced by the ADT. A reduction in flower color intensity at higher temperatures was observed in carnation (*Dianthus caryophyllus* L.) (Maekawa and Nakamura, 1977), chrysanthemum (Carvalho et al., 2005), rose (Dela et al., 2003) and petunia (Shvarts et al., 1997). Anthocyanins are plant pigments that impart a red, blue or purple color to leaves and flowers, and their concentrations are correlated with flower color intensity at different temperatures. For example, at higher temperatures, a reduction in floral anthocyanin content was correlated with a reduction in the color intensity (Nozaki et al., 2006; Stiles et al., 2007). Temperature influences anthocyanin content by regulating its biosynthetic pathway (Shvarts et al., 1997; Stiles et al., 2007). This may be an adaptive thermoregulatory response in plants; as temperature increases, anthocyanin pigmentation decreases and the flower color is lighter and thus more reflective (Stiles et al., 2007). Therefore, more reflection of radiation reduces flower temperature and thus protects the floral organs from heat damage (Stiles et al., 2007). In addition, a greater availability of sugars at lower temperatures may also increase the anthocyanin content by up-regulating the anthocyanin biosynthetic pathway (Solfanelli et al., 2006).

Effect of Temperature on Branch Number

Lateral branch number is another parameter of plant quality, since an increase in branch number is often correlated with an increase in flower number (Mattson and Erwin, 2003; Warner and Erwin, 2006). Branch number decreased with an increase in ADT in fuchsia (*Fuchsia* × *hybrida* hort. ex Siebold & Voss) (Erwin et al., 1991), pansy (Warner and Erwin, 2006) and petunia (Kaczperski et al., 1991; Mattson and Erwin, 2003). In some cases, at higher temperatures, a decrease in branch number was correlated with a decrease in leaf number below the first open flower (Mattson and Erwin, 2003).

Effect of Temperature on Plant Biomass

Temperature affects photosynthetic enzyme activity, and consequently it interacts with other factors (especially light) to influence accumulated plant biomass. For many plants, shoot dry mass at first flowering increases as ADT decreases, including balloon flower (Park et al., 1998), calendula (*Calendula officinalis* L.) (Warner and Erwin, 2005), geranium (*Pelargonium* × *hortorum* Bailey) (White and Warrington, 1988), impatiens (*Impatiens walleriana* Hook. f.) (Pramuk and Runkle, 2005b; Warner and Erwin, 2005), marigold (*Tagetes patula* L.) (Moccaldi and Runkle, 2007), mimulus (*Mimulus hybridus* Hort. Ex Siebert & Voss) (Warner and Erwin, 2005), pansy (Niu et al., 2000; Warner and Erwin, 2006), salvia (*Salvia splendens* F. Sello ex Roem & Schult.) (Moccaldi and Runkle, 2007) snapdragon (*Antirrhinum majus* L.) (Wai and Newman, 1992; Warner and Erwin, 2005), and Texas firebush (*Hamelia patens* Jacq.) (Armitage, 1995). These results are not surprising since plants grown at lower temperatures take longer to flower (and thus can photosynthesize for a longer time) and are also of higher quality (increased branch number and flower number and size) compared to plants grown at warmer temperatures. In addition, van Iersel (2003) reported an increase in the net photosynthetic rate (P_{net}) with a decrease in ADT for geranium, marigold, pansy and petunia. This increase in P_{net} at lower temperatures was mainly attributed to a decrease in the dark respiration rate (R_{dark}), since gross photosynthesis (P_{net} + R_{dark}) was not greatly influenced by ADT. High temperatures decrease P_{net} by modifying Rubisco kinetics (Brooks and Farquhar, 1985), increasing O_2:CO_2 solubility (Ku and Edwards, 1977), or both.

A few exceptions to these plant biomass responses to ADT have been reported in celosia (*Celosia argentea* L.) (Pramuk and Runkle, 2005b), summer snapdragon (Miller and Armitage, 2002), Texas firebush (Armitage, 1995), and wishbone flower (*Torenia fournieri* Linden ex E. Fourn) (Warner and Erwin, 2005), in which plant biomass increased with an increase in ADT. These plants have a high estimated T_b and therefore develop slowly and accumulate less biomass at lower temperatures. For example, the estimated T_b for celosia, summer snapdragon and wishbone flower was 10.2 °C (under a DLI of 15.0 mol·m^{-2}·d^{-1}) (Pramuk and Runkle, 2005b), 9.9 °C (Blanchard, 2009) and 9.4 °C (under a DLI of 18.0 mol·m^{-2}·d^{-1}) (Vaid, unpublished data), respectively.

The effect of DIF has also been evaluated on dry matter partitioning patterns in some floriculture species. Although the effect of DIF on whole plant biomass is variable, many studies have reported an increase in stem and leaf dry weight as DIF increases (Hwang et al., 2005; Karlsson and Heins, 1992; Miller et al., 1993; Myster et al., 1997). In many plants, a +DIF promotes stem elongation, whereas a –DIF suppresses it. This strategy is commonly employed in greenhouses to control plant height (Erwin and Heins, 1995).Stem length and dry weight of Easter lily at anthesis was 79 and 80% greater, respectively when grown under a +8.0 °C DIF than a –8.0 °C DIF (Miller et al., 1993). In addition, a reduction in photosynthesis due to a decrease in chlorophyll content (Berghage et. al., 1990a) and/or an increase in R_{dark} (due to a higher NT) at a –DIF may also contribute to a reduction in stem dry weight. In Easter lily plants grown under a –DIF, Miller et al. (1993) reported a reduction in leaf and stem total soluble carbohydrate content by 39 to 46% at visible bud (VB) and anthesis.

Effect of Temperature on Plant Height

Growers and consumers generally prefer short, compact plants since shipping costs can be lower and the aesthetic value of plants can be increased. Plant growth regulators (PGRs) that inhibit gibberellin biosynthesis are commonly applied in the bedding plant industry to inhibit extension growth. However, due to the cost of chemicals and labor, several non-chemical approaches to suppress plant height have been evaluated. For many plants, height at flowering decreases as day temperature relative to the night temperature decreases (as the value of DIF decreases) (Cockshull, 1981; Erwin et. al., 1991; Erwin and Heins, 1990; Grindal and Moe, 1994; Jensen et al., 1996; Karlsson et al., 1989b; Lepage et al., 1984; Moe, 1990; Moe and Heins, 1990; Myster et al., 1997; Myster and Moe, 1995; Neily et al., 1997; Niu et al., 2001; 2000). For example, as DIF increased from –6.0 to +6.0 °C, plant height increased by 32% in Chinese lantern lily (Davies et al., 2002), 40% in Easter lily (Erwin and Heins, 1990), 39% in fuchsia (Erwin et al., 1991), 19% in geranium (Strefeler, 1995), and 9% in Italian bellflower (*Campanula isophylla* Moretti; Moe and Mortensen, 1992b). An increase in stem length caused by a +DIF is primarily from greater cell elongation and not cell division (Erwin et al., 1994). Elongation of stem parenchyma and epidermal cells increases linearly as DIF increases from –15 to +15 °C, but cell width or number per internode was similar (Erwin et al., 1994). Stem extension occurs more rapidly when DIF increases from zero to a positive value as compared to when DIF increases from a negative value to zero (Erwin and Heins, 1990). For example, as DIF increased from –15.0 to 0.0 °C and 0.0 to +15.0 °C, plant height increased by 29 and 61%, respectively. Although DIF can be used to control plant height, more energy inputs may be required to maintain a –DIF, especially during the winter (Blanchard and Runkle, 2011b). An alternative height control strategy using temperature, but with potentially reduced energy consumption, is a decrease in temperature for 2.0 to 4.0 h towards the end of the night or beginning of the day (DROP), which is when stem extension is sometimes greatest. This technique has been effective in controlling plant height in begonia, Easter lily and poinsettia (Erwin, 1991; Grindal and Moe, 1994; Moe et. al., 1992).

Several studies have investigated the physiological mechanism of DIF. Evidence from these studies suggests that gibberellins (GA) are involved in the thermoperiodic control of plant height. Easter lily bulbs soaked in GA_3 prior to planting and grown in a –DIF environment were 15% taller than those not treated with GA_3 (Zieslin and Tsujita, 1988). In contrast, height suppression by ancymidol, a GA biosynthesis inhibitor, increased as DIF increased (Erwin et al., 1989). Grindal et al. (1998) reported a 60% decrease in endogenous GA content of stems in wild type (WT) garden pea (*Pisum sativum* L.) plants grown under a –DIF as compared to those grown under a +DIF. Using a GA-insensitive slender mutant, these authors reported 8% less stem inhibition in the mutant than in the WT (40 to 50%) when grown under a –DIF. Involvement of GA in thermoperiodic control of stem elongation is not unexpected, since the role of GA in promoting cell elongation has long been established.

In addition to DIF, ADT can also influence plant height by affecting the number of nodes formed prior to flowering. Since increase in ADT developmentally decreases flowering time in many species, an increase in ADT would typically reduce plant height due to fewer nodes formed prior to flowering. However, several studies have reported an increase in plant height with an increase in ADT, although plants flowered earlier at higher temperatures (Armitage et al., 2000; Blanchard et al., 2011a; Kanellos and Pearson, 2000; Miller and Armitage, 2002; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). Since the number of nodes in these studies was either variable or not reported, and the actual DIF values were also not provided, the promotive effect of higher temperatures on plant height can not be clearly understood.

Daily Light Integral (DLI)

Light is electromagnetic radiation and has three characteristics: quantity, quality, and duration. The spectral distribution of light is referred to as light quality, which acts as a signal for plant morphogenesis. Blue light and the ratio of red to far-red light (R:FR) are the primary wavebands that regulate stem extension, and in some cases flower initiation and development (Runkle and Heins, 2001; Runkle et al., 2001). Duration of light or photoperiod regulates flowering in many floriculture species (Mattson and Erwin, 2005). Light intensity refers to the number of photons delivered on either an instantaneous or cumulative basis. As light intensity within the photosynthetically active waveband (PAR; generally defined as 400 to 700 nm) increases, the rate of photosynthesis increases until a species-specific saturation point.

The integrated PAR received during a 24-h period is called the DLI. The natural DLI varies considerably depending on the location, time of year, cloud cover, etc., and this seasonal variation increases with distance from the equator. DLI received inside a greenhouse depends upon glazing material, overhead structures, presence of hanging baskets, plant spacing, and strategies to alleviate heat stress (e.g., shade curtains and whitewash). In regions where annual DLI varies significantly (e.g., >40 °N lat.) growers use supplemental lighting to increase DLI.

Metal halide and high-pressure sodium (HPS) lamps are commonly employed in greenhouses to provide the supplemental lighting. These lamps differ in their spectral outputs, and therefore species irradiated with different lamps may vary in growth and morphology, even if light intensities and photoperiods are similar.

Effect of Daily Light Integral on Plant Development

Under light-limiting conditions, greenhouse growers commonly use supplemental lighting to increase the total DLI at canopy height. Supplemental lighting can modify the development rate of LD plants (i.e., decrease flowering time) when it truncates the night length. In this case, an acceleration of flowering typically causes plants to flower at a lower leaf number. Supplemental lighting can also accelerate flowering by increasing plant temperature from the heat radiated by the lamps. Faust and Heins (1998) and Mattson and Erwin (2005) reported an increase of 1 to 2 °C in plant temperature under supplemental HPS lighting.

Plants can be categorized based on their flowering response to supplemental irradiance: those with a facultative irradiance (FI) response flower at a lower node number with an increase in irradiance, whereas those that flower at a similar node number at different DLIs have an irradiance indifferent (II) response (Erwin and Warner, 2002; Mattson and Erwin, 2005). For example, increasing DLI from 8.3 to 25.5 $mol \cdot m^{-2} \cdot d^{-1}$ decreased leaf number at flowering from 26 to 18 (FI response) in rosa del río (*Hibiscus cisplatinus* St.-Hil.), whereas node number of monarch rosemallow (*H. radiatus* Cav.) was unaffected (II response) by DLI under SD (Warner and Erwin, 2003). DLI and photoperiod interact to influence FI and II responses in some species. Leaf number at flowering of swamp rosemallow (*H. moscheutos* L.) decreased as DLI increased under SD, but was not influenced by DLI when grown under LD (Warner and Erwin, 2003).

Several studies have reported a negative correlation between DTF and DLI during the finish stage for many annual bedding plants (Blanchard et al., 2011a; 2011b; Carvalho et al., 2006; Currey and Erwin, 2011; Warner and Erwin, 2005; Faust et al., 2005; Oh et al., 2009; Pietsch et al., 1995). For example, an increase in DLI from 10.5 to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ (ADT of 20 °C) reduced DTF from transplant by 21 d in snapdragon, 16 d in calendula, 3 d in impatiens, 4 d in mimulus, and 12 d in wishbone flower (Warner and Erwin, 2005). Providing supplemental lighting in greenhouses is most effective when the natural DLI is low, since flowering response to increasing DLI follows a diminishing returns relationship (Blanchard et al., 2011a; Karlsson et al., 1989b; Pramuk and Runkle, 2005b). For example, increasing DLI by 4.0 $mol \cdot m^{-2} \cdot d^{-1}$ when the natural DLI was 4.0 $mol \cdot m^{-2} \cdot d^{-1}$ accelerated flowering in petunia by 10 d, but only by 2 d when the natural DLI was 8.0 $mol \cdot m^{-2} \cdot d^{-1}$ (Blanchard et al., 2011a). Similarly, Gagnon and Dansereau (1990) observed that supplemental lighting treatments were more effective during fall-winter experiments when the natural DLIs were lower compared to winter-spring experiments.

An increase in the DLI during the young plant (liner or plug) stage can reduce flowering time during the finish stage, mainly due to earlier flower initiation (Pramuk and Runkle, 2005a; Oh et al., 2010). In addition, supplemental lighting of petunia and marigold during the later, rather than the early, stage of seedling growth was more effective in reducing DTF, likely because of the greater leaf area available for light interception (Oh et al., 2010). Increasing DLI during the seedling stage can be a cost-effective strategy to reduce production time for finish plants, since lighting costs per transplant are relatively low for young plants, since they are commercially grown at a high density.

Plants have a critical DLI (DLI_{crit}) below which flowering will not occur and a saturating DLI (DLI_{sat}) above which the time to flowering response is not further hastened. White and Warrington (1988) reported a DLI_{crit} of 3.3 $mol \cdot m^{-2} \cdot d^{-1}$ for geranium 'Red Elite'. For many species, DLI_{crit} is <5 $mol \cdot m^{-2} \cdot d^{-1}$, which is the minimum light level tested in most studies (Fausey et al., 2005; Faust et al., 2005; Moccaldi and Runkle, 2007). In some plants, the critical DLI required for flowering varies with each phase of the flowering process (Warner and Erwin, 2003). For example, swamp rosemallow under SD required 10 to 12 $mol \cdot m^{-2} \cdot d^{-1}$ for flower initiation, but at least 14 $mol \cdot m^{-2} \cdot d^{-1}$ for successful flower development (Warner and Erwin, 2003). If these plants were grown at a DLI <12 $mol \cdot m^{-2} \cdot d^{-1}$, they remained vegetative, and if they were grown at a DLI >12 $mol \cdot m^{-2} \cdot d^{-1}$ but <14 $mol \cdot m^{-2} \cdot d^{-1}$, flower buds aborted soon after they formed (Warner and Erwin, 2003).

DLI_{sat} has also been estimated for many crops, and can vary from <5 to >20 $mol \cdot m^{-2} \cdot d^{-1}$ depending on the species, cultivar, temperature, carbon dioxide concentration, etc. (Blanchard, 2009; Hiden and Larsen, 1994; Oh et al., 2009; White and Warrington, 1988). For example, DLI_{sat} for shade-tolerant plants like vinca and sun-loving plants like spider flower (*Cleome hassleriana* Chod.) and treasure flower (*Gazania rigens* L.) was 4.8 and >20.0 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Blanchard, 2009). Similarly, DLI_{sat} for petunia cultivars 'Dreams Neon Rose', 'Wave Purple' and 'Easy Wave Coral Reef' was estimated at 10.6, 14.1 and 14.4 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Blanchard, 2009). Exposing plants to light intensities in excess of their saturation limit can damage photosystem II, which is the light reaction center for photosynthesis. This decreases photosynthetic activity, referred to as photoinhibition, which can considerably reduce plant growth and development under high light intensities. For example, flower development rate decreased when the DLI was at least 12.0 $mol \cdot m^{-2} \cdot d^{-1}$ for begonia and vinca, which are both shade-tolerant species with estimated DLI_{sat} of 10.5 and 4.8 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Blanchard, 2009; Faust et al., 2005).

Several studies in photoperiodic (Corbesier et al., 1998; Roldan et al., 1999) and day-neutral plants (Dielen et al., 2004) have demonstrated that sucrose, a major product of light-driven photosynthesis, plays an important role in flowering. For example, an increase in leaf carbohydrate export or apical sucrose concentration during floral induction has been reported in many plants (Corbesier et al., 1998; Dielen et al., 2001; Lejeune et al., 1993). Since these changes were detected prior to any morphological signs of flower initiation, these authors suggested a signaling role for sucrose. In addition, exogenous sucrose could overcome flowering repression by *FLC* (Flowering locus C), but could not correct the late-flowering phenotypes of *ft* or *fwa* arabidopsis mutants (Roldan et al., 1999). This suggests that sucrose promotes flowering by regulating expression of *FLC* in steps that occur upstream of *FT* and *FWA* (Roldan et al., 1999). Recently, Henry et al. (2011) reported a positive correlation between accumulation of *RhSUC2* (sucrose transporter) and light-induced bud burst in *Rosa* sp. It is possible that under higher light levels, increased sucrose production and mobilization represses *FLC*, thereby turning on a cascade of genes that ultimately lead to *FT* expression, and therefore earlier flowering. However, more research is required to characterize light-induced flowering in plants and the possible role of sucrose in this pathway.

Effect of Daily light integral on Plant Quality

In addition to ADT, DLI also influences plant quality parameters. Several studies have quantified the influence of DLI on plant quality characteristics in many plants, and reported an increase in quality with DLI (Fausey et al., 2005). The effect of DLI on plant quality parameters such as number of flowers and lateral branches, flower size and color, height, and plant biomass are discussed in detail.

<u>Effect of DLI on Flower Number and Quality</u>

There is a positive correlation between DLI and flower bud number in many species (Blanchard et al., 2011a; 2011b; Currey and Erwin, 2011; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). For example, increasing DLI from 10.0 to 20.0 $mol \cdot m^{-2} \cdot d^{-1}$ (ADT 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* Engelm. and Gray), lateral inflorescence number per plant tripled and flower number per inflorescence nearly doubled as DLI increased from 5.0 to 20.0 $mol \cdot m^{-2} \cdot d^{-1}$ (Fausey et al., 2005). In addition, a small increase in DLI from 17.8 to 21.0 $mol \cdot m^{-2} \cdot d^{-1}$ reduced the number of blind shoots by almost 50% in several cultivars of cut roses (*Rosa hybrida* L.) (Bredmose, 1997). However, seedlings of bedding plants grown under a higher DLI during the plug stage and then transferred to a common DLI had a lower flower number at first flowering compared to plugs grown under a lower DLI (Pramuk and Runkle, 2005a; Oh et al., 2010). This could be attributed to the more rapid flowering that occurred with the higher plug DLI, so that plants had a shorter period to intercept light before flowering. The high plug DLI also reduced the leaf number below first open flower which may have contributed to the reduction in axillary inflorescences.

Several studies have reported an increase in flower size with DLI (Karlsson et al., 1989; Moccaldi and Runkle, 2007; Niu et al., 2000; Pietsch et al., 1995; Warner and Erwin, 2005). Warner and Erwin (2005) described a linear relationship between DLI and flower size, such that each unit ($mol{\cdot}m^{-2}{\cdot}d^{-1}$) increase in DLI increased the flower size by 0.09 mm in calendula, 0.59 mm in impatiens, 0.15 mm in mimulus, and 0.25 mm in wishbone flower. Flower bud development after initiation involves active cell division and elongation, which requires sugar import to the developing buds from the leaves. Sugar import depends upon sugar mobilization in the developing buds, and a constant supply of sugars from the leaves. Girault et al. (2010) reported an increase in *RhVI* gene transcription under higher light levels in rose, and consequently an increase in *RhVI* vacuolar acid invertase activity, an enzyme that participates in sucrose breakdown in developing rose buds. Similarly, Henry et al. (2011) demonstrated a correlation between up-regulation of sucrose transporters (*RhSUC2*) and light-induced bud-burst in roses. Therefore, under higher light levels, accumulation of sugars due to increased photosynthesis (Nemali and van Iersel, 2004), stimulation of sugar metabolism in flower buds (Girault et al., 2010), and up-regulation of sucrose transporters (Henry et al., 2011) may all work together to promote flower development and expansion.

Anthocyanins are plant pigments that impart a red, blue, or purple pigmentation to leaves and flowers in many species. Light intensity influences flower pigmentation in plants mainly by regulating the anthocyanin concentration in flower petals. For example, anthocyanin in flowers was positively correlated with light intensity in carnation (Maekawa, 1974), lisanthus [(*Eustoma grandiflorum* (Raf.) Shinners; Meir et al., 2009)], Oriental hybrid lily (*Lilium aurantum* Lindl.; Kawabata et al., 2002), rose (Maekawa et al., 1980), and stock [*Matthiola incana* (L.) W.T. Aiton; Kawabata et al., 2002)]. Meir et al. (2009) reported a reduction in anthocyanin biosynthesis gene expression under light-limiting conditions. These authors suggested that light intensity influences certain transcription factors that act as master regulators for a number of anthocyanin biosynthesis genes. In addition, sucrose availability up-regulates the anthocyanin biosynthetic pathway (Solfanelli et al., 2006). Higher light levels increase the synthesis, mobilization and transport of sugars to the developing flower buds, which may promote anthocyanin biosynthesis in the flower petals. Therefore, plants grown under higher light have a brighter and more intense flower color than those grown under low light conditions.

Effect of DLI on Branch Number and Biomass

A few studies have reported an increase in lateral branch number with an increase in DLI (Carvalho et al., 2006; Faust et al., 2005; Welander, 1983). For example, an increase in DLI from 4.0 to 43.0 $mol \cdot m^{-2} \cdot d^{-1}$ increased the number of lateral shoots by 7 in ageratum (*Ageratum houstonianum* L.) and petunia (Faust et al., 2005). Increased availability of photosynthates at higher light intensities may promote initiation and development of lateral shoots.

Dry matter accumulation in plants primarily depends upon light, carbon dioxide, and water for photosynthesis. Many studies have reported an increase in plant biomass in greenhouse-grown crops with an increase in DLI (Faust et al., 2005; Fausey et al., 2005; Moccaldi and Runkle, 2007; Warner and Erwin, 2005). For example, as DLI increased from 4.0 to 14.0 $mol \cdot m^{-2} \cdot d^{-1}$ during the finish stage, shoot dry weight at anthesis increased by 162%, 187%, and 108% in common yarrow (*Achillea millefolium* L.), butterfly gaura, and lavender (*Lavandula augustifolia* Mill.), respectively (Fausey et al., 2005). A similar increase in DLI during seedling growth linearly increased seedling dry weight by 64% in celosia, 47% in impatiens, 64% in marigold, and 68% in pansy (Pramuk and Runkle, 2005a).

In addition, some studies have investigated the influence of DLI on root and flower dry mass (Faust et al., 2005; Torres and Lopez, 2011). When ambient light levels are low, increasing DLI during propagation increases dry matter accumulation of root and shoot tissues (Lopez and

Runkle, 2008; Torres and Lopez, 2011). A denser root mass increases the surface area for nutrient absorption, and possibly contributes to faster plant growth. Similarly, Faust et al. (2005) reported an increase in flower dry mass with DLI. Interestingly, under higher light levels, these authors observed a greater percentage of dry matter partitioned to flowers in plants in the Asteraceae family compared to others.

When plants are grown under the same DLI, the duration of light interception mainly influences dry matter accumulation. For example, celosia seedlings grown under 4.0 and 14.0 $mol \cdot m^{-2} \cdot d^{-1}$ during the plug stage, and then transferred to a common DLI during the finish stage, flowered in 43 and 33 d, and accumulated 4.5 and 2.9 g of biomass at first flower, respectively (Pramuk and Runkle, 2005a). The DLI required for maximum dry matter accumulation is higher than their DLI_{sat} for flowering. For example, the flowering response in vinca saturated at 4.8 $mol \cdot m^{-2} \cdot d^{-1}$ (Blanchard, 2009), but it required 21 $mol \cdot m^{-2} \cdot d^{-1}$ to attain 50% of the maximum total dry mass (Faust et al., 2005). In addition to DLI, light quality also affects dry matter accumulation. For example, photosynthetic rate (and therefore dry mass accumulation) is generally highest under blue and especially red light. Therefore, plants grown under the same DLI but irradiated with lamps having different spectral outputs would probably vary in dry mass.

Effect of DLI on Plant Height

Under shaded conditions, shade-avoiding plants elongate to increase light interception. Accordingly, some studies have reported a negative correlation between plant height and DLI (Armitage, 1995; Blanchard et al., 2011a; Fausey et al., 2005; Miller and Armitage, 2002). However, the shade-avoidance response in plants is mainly a function of the R: FR (Erwin et al., 2006). In most experiments, higher light levels were created by supplementing ambient daylight with light from HPS lamps (Blanchard et al., 2011a; Fausey et al., 2005) or metal halide lamps (Miller and Armitage, 2002) lamps. Since the R: FR ratio of these lamps is greater than that of sunlight, a reduction in height under higher DLI conditions may be an effect of light quality and not quantity. However, higher light levels may also contribute to height reduction by reducing leaf number below first open flower. For example, for most seedlings grown under a higher DLI (R: FR ratio ≈ 3.6 for all treatments), and then transferred to a common DLI during the finish stage, a reduction in plant height was accompanied by a lower leaf number below first open flower (Pramuk and Runkle, 2005a).

Many studies have observed no consistent relationship between plant height and DLI (Currey and Erwin, 2011; Faust et al., 2005; Moccaldi and Runkle, 2007). In these studies, plant height responses to DLI varied by species. For example, among the six species of *Kalanchoe* studied, plant height decreased, increased, or was unaffected by DLI (similar R: FR ratio across all treatments) in one, two, or three species, respectively (Currey and Erwin, 2011). This variability is not unexpected, since in addition to light quality and quantity, many factors in a greenhouse such as DIF, water and nutrient uptake, and plant spacing can also affect plant height. Plants grown under a higher DLI develop faster and, if plant density does not change as plants grow, they may shade each other. Similarly, due to a greater thermal load and faster plant development under higher light intensities, water and nutrient uptake is generally higher. Therefore, plant height responses to DLI can sometimes be at least partially attributed to other variables that influence stem elongation.

Interaction between Temperature and DLI

Temperature and DLI are the two primary environmental factors that influence plant growth, development and quality. In regions where the natural temperature and DLI vary seasonally, growers commonly use environmental control systems to manipulate ADT and DLI to ensure precise crop timing and better plant quality. The rate of plant development is mainly a function of ADT, while DLI primarily controls dry matter accumulation via photosynthesis. However, these factors interact to influence growth attributes and plant development rates.

Several studies have investigated the interaction of ADT and DLI, and sometimes DIF, on plant timing and quality parameters (Blanchard et al., 2011a; Moccaldi and Runkle, 2007; Niu et al., 2000; Pietsch et al., 1995; Pramuk and Runkle, 2005b). Liu and Heins (2002) applied the concept of photothermal ratio [(PTR); ratio of radiant energy ($mol \cdot m^{-2} \cdot d^{-1}$) to thermal energy (degree days)] to integrate the effects of ADT and DLI on plant timing and quality in poinsettia. A high PTR is created with a high DLI and low temperature, while a low PTR is created by a low DLI and high temperature.

Temperature and DLI Interaction on Plant Development

In many species, flowering time decreases as ADT and DLI increase within species-specific ranges (Blanchard et al., 2011a, 2011b; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). Studies have developed mathematical models to predict the interactive effects of ADT and DLI on flower development rate in celosia, chrysanthemum, cineraria, impatiens, pansy, petunia, marigold, and salvia (Blanchard et al., 2011a, 2011b; Larsen, 1989; Larsen and Persson, 1999; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). Increasing DLI has a greater effect on plant development rate at lower temperatures (Blanchard et al., 2011a;

Kaczperski et al., 1991; Pietsch et al., 1995). For example, an increase in DLI from 9.0 to 30.0 $mol \cdot m^{-2} \cdot d^{-1}$ accelerated flowering time in vinca 'Grape Cooler' by 11 d at 20.0 °C, but only by 4 d at 35.0 °C (Pietsch et al., 1995). Similarly, in petunia 'Wave Purple', a DLI increase from 4.0 to 14.0 $mol \cdot m^{-2} \cdot d^{-1}$ hastened flowering by 22 d at 14.0 °C but by only 9 d at 26.0 °C (Blanchard et al., 2011a). The supplemental lighting treatments may have increased plant temperature more when plants were grown at lower air temperatures. Also, it is possible that an increase in ADT and DLI turn on pathways that overlap to induce accumulation of the *FT* protein (Blazquez et al., 2003; Roldan et al., 1999). On the other hand, suppression of *FT* at lower temperatures may be offset by induction of *FT* expression by higher irradiance.

Some studies have reported a shift in T_b and T_{opt} with increasing DLI (Adams et al., 1997; Faust and Heins, 1993; Pramuk and Runkle, 2005b). Increase in DLI from 5.0 to 15.0 $mol \cdot m^{-2} \cdot d^{-1}$ decreased the estimated T_b of celosia and impatiens by 1.5 and 3.2 °C, respectively (Pramuk and Runkle, 2005b). Since T_b for celosia and impatiens was estimated using ADT and not plant temperature, these authors suggested that a decrease in T_b at higher DLI was probably because of an increase in plant temperature from the higher irradiances. In contrast, Adams et al. (1997) reported a linear increase in T_{opt} as DLI decreased from 6.0 $mol \cdot m^{-2} \cdot d^{-1}$. Similarly, in African violet, T_{opt} for LUR decreased from 25.0 to 23.0 °C as DLI decreased from 10.0 to 1.0 $mol \cdot m^{-2} \cdot d^{-1}$ (Faust and Heins, 1993). This may be due to a limited supply of photoassimilates at lower light levels, since a similar shift in T_{opt} for photosynthesis has been demonstrated in carnation (Enoch and Hurd, 1977). In addition, Karlsson (2002) reported a decrease in DLI_{sat} for flower initiation with an increase in ADT in native primrose [*Primula vulgaris* syn. *P. acaulis* (L.) Hill]. This may not be entirely surprising, since the promotive effect of increasing DLI is generally lower at higher temperatures.

Temperature and DLI Interaction on Plant Quality

Temperature and DLI interact to influence plant quality characteristics such as number of flowers, plant height, flower size and biomass. Since plant quality generally improves as ADT decreases and DLI increases, a higher plant quality is generally obtained when ADT is relatively low and DLI is high. For example, marigold plants grown at 15.0 °C and a DLI of 25.0 $mol \cdot m^{-2} \cdot d^{-1}$ accumulated 144% more dry mass, had 112% more inflorescences, and 49% greater inflorescence diameters than plants grown at 25.0 °C and a DLI of 5.0 $mol \cdot m^{-2} \cdot d^{-1}$ (Pramuk and Runkle, 2005b). Similarly, as PTR increased, flower number, dry weight and, inflorescence diameter increased for several floriculture crops (Blanchard et al., 2011a; Liu and Heins, 2002; Niu et al., 2000). For example, increase in PTR from 0.2 to 1.9 $mol \cdot m^{-2}$ per degree day increased flower number by 197% in petunia 'Easy Wave Coral Reef' (Blanchard et al., 2011a). Similarly, Liu and Heins (2002) reported a linear increase in plant dry weight and size of bracts and cyathia with PTR in poinsettia 'Freedom'.

The influence of PTR on plant height is variable. For example, Blanchard et al. (2011a) reported a negative correlation between PTR and plant height in petunia 'Wave Purple' and 'Easy Wave Coral Reef'. In contrast, Liu and Heins (2002) reported that plant height in poinsettia 'Freedom' was unaffected by PTR. Plant height often decreases as DLI, and sometimes ADT, increases, since both factors influence leaf number below first open flower, and thus plant height. Since a higher PTR is created by high DLI and lower temperatures, the effects of DLI and ADT on leaf number below first open flower (and therefore plant height) may counteract each other at a given PTR. This may result in variability in plant height between different PTR treatments, and therefore no consistent relationship between PTR and plant height.

Some studies suggest an interaction between DIF and DLI to influence stem elongation (Erwin and Heins, 1995; Niu et al., 2000). Niu et al. (2000) observed a greater stem elongation response to DIF under lower than higher DLI. In contrast, Erwin and Heins (1995) reported an increase in stem elongation response with irradiance. These differences in stem elongation response to DIF could be attributed to differences in light quality, and not DLI. For example, Niu et al. (2000) used HPS lamps to provide supplemental lighting in the medium and high DLI treatments. Since light from HPS lamps has a greater R: FR ratio than sunlight, plants grown under the higher DLI treatments may have been shorter because of the light quality in treatments and less by DIF.

In general, flowering time is hastened as ADT and DLI increases, while plant quality of shade-avoiding plants decreases as ADT increases and DLI decreases. Therefore, if plants are grown at a warmer ADT to accelerate flowering, a reduction in plant quality can be offset by increasing the DLI (Blanchard et al., 2011a). For example, in marigold plants grown at 25.0 °C, increasing the DLI from 5.0 to 25.0 $mol \cdot m^{-2} \cdot d^{-1}$ increased inflorescence number, inflorescence diameter, and plant dry weight by 47%, 16%, and 93%, respectively.

Conclusions

Temperature and light are the two environmental factors that strongly influence crop timing and plant quality. Greenhouse growers, especially in temperate regions, manipulate the ADT and DLI to precisely schedule crops and regulate plant quality. Although the physiological mechanisms underlying plant responses to ADT and DLI are well understood, a greater understanding of the molecular mechanisms is desirable. In addition, several other environmental and cultural factors in a greenhouse influence plant timing and morphology such as DIF, light quality, plant nutrition, carbon dioxide concentration, plant spacing, and watering. Therefore, when investigating plant responses to ADT and DLI, it is important to consider the possible influence of these factors on the parameters studied, and when possible, control and monitor them.

Table 1.1. Temperature response categories for popular bedding plant species based on their estimated T_b and the corresponding percentage delay in flowering time when grown at 15 versus 20 °C.

Species and Cultivar	**T_b (°C)**	**Delay in flowering time**	**Reference**
		Cold tolerant (T_b <4 °C)	
Campanula carpatica 'Blue Chips'	0.0	29%	Whitman et al., 1997
Gaillardia ×grandiflora 'Goblin'	3.3	31%	Yuan et al., 1998
Leucanthemum ×superbum 'Snowcap'	−3.4	25%	Yuan et al., 1999
Petunia ×hybrida 'Dreams Neon Rose'	2.8	28%	Blanchard and Runkle, 2011a
Platycodon grandiflorus 'Astra Blue'	2.9	38%	Park et al., 1998
		Cold intermediate (4 °C< T_b <7 °C)	
Coreopsis grandiflora 'Sunray'	6.8	44%	Yuan et al., 1998
Oenothera fruticosa 'Youngii Lapsley'	4.4	50%	Clough et al., 2001
Petunia ×hybrida 'Wave Purple'	5.5	45%	Blanchard and Runkle, 2011a
Rudbeckia hirta 'Toto Rustic'	4.6	43%	Blanchard and Runkle, 2011a
Tagetes erecta 'Antigua Primrose'	4.4	33%	Blanchard and Runkle, 2011a
		Cold sensitive (T_b >7 °C)	
Angelonia augustifolia 'Serena Purple'	9.9	81%	
Browallia speciosa 'Bells Marine'	8.9	57%	
Pentas lanceolata 'Graffiti Lavender'	9.3	53%	Blanchard and Runkle, 2011a
Salvia farnacea 'Victoria Blue'	9.4	62%	
Zinnia elegans 'Dreamland Coral'	7.8	50%	

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SECTION II

EFFECT OF AVERAGE DAILY TEMPERATURE ON FLOWERING TIME AND PLANT QUALITY OF EIGHTEEN SPECIES AND CULTIVARS OF ANNUAL BEDDING PLANTS

Effect of Average Daily Temperature on Flowering Time and Plant Quality of Eighteen Species and Cultivars of Annual Bedding Plants

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Abstract

The effect of average daily air temperature on the flowering time and plant quality was quantified for 18 cultivars of 16 common bedding plant species. *Antirrhinum*, *Calendula*, *Diascia*, *Gerbera*, *Gomphrena*, *Heliotropium*, *Impatiens*, *Matthiola*, *Nemesia*, *Nicotiana*, *Nierembergia*, *Osteospermum*, *Pelargonium*, *Petunia*, *Tagetes*, and *Torenia* were grown in five glass greenhouse compartments maintained at constant temperature setpoints of 14, 17, 20, 23 or 26 °C. The 16-h photoperiod consisted of the natural photoperiod with supplemental high-pressure sodium lighting from 0600 to 2200 HR. The mean photosynthetic daily light integral during the two replications of this experiment varied from 9 to 18 $mol \cdot m^{-2} \cdot d^{-1}$. Days to flower from transplant (DTF), flower or inflorescence number (FN), flower or inflorescence diameter (FD), branch number (BN), number of nodes below the first open flower (NN), dry shoot mass (SM), dry root mass (RM), and plant height or length of the longest lateral branch (PH) were measured when the first flower opened on each plant. As temperature increased from 14 to 26 °C, DTF decreased for all crops except *Impatiens walleriana* Hook. Plant quality parameters (FN, FD, BN, SM, RM, and PH) increased as temperature decreased for 14, 9, 8, 14, 7, and 10 crops, respectively. Linear or non-linear regression analysis was performed on the flowering rate (reciprocal of days to flower) data to estimate the base temperature (T_{min}) for each species, which is the temperature at which the flowering rate is zero. T_{min} ranged from –3.9 ºC for *Diascia barberae* Hook.f. to 13.8 ºC for *Gomphrena globosa* L. A positive correlation was observed between the estimated T_{min} and the percentage delay in flowering time when grown at 17 versus 23 ºC. This information can be used by growers to predict plant timing and crop quality at different temperatures, and to grow crops with a similar temperature response together for energy-efficient greenhouse production.

Introduction

Bedding plants are typically grown during some of the coldest months of the year, especially in northern climates, where heating typically accounts for ≥ 10% of the annual greenhouse production costs (Bartok, 2001). Some growers lower their greenhouse temperatures in winter in an attempt to save on heating costs. However, potential fuel savings at lower temperatures are generally offset by an increase in the crop production period (Blanchard et al., 2011b). Volatile fuel prices, an increased emphasis on sustainable production practices, and declining profit margins have motivated growers to optimize their greenhouse environments and grow crops as energy-efficiently yet profitably as possible. Energy-efficient production in temperate climates requires species-specific information on how average daily temperature (ADT) influences flowering time and plant quality.

Average daily temperature regulates plant development by influencing different events in a plant's life cycle such as germination, leaf unfolding, and flowering. The time taken to reach a particular developmental event as a function of temperature can be expressed as the number of days to reach that event (n) or as a developmental rate by taking the reciprocal of that number of days (1/n). Temperature influences flowering time of crops such that as ADT increases within a species-specific range, days to flower (DTF) decreases (Adams et al., 1999, 1998b, 1998c; Blanchard and Runkle, 2011a; Clough et al., 2001; Kanellos and Pearson, 2000; Miller and Armitage, 2002; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001; Pramuk and Runkle, 2005b; White and Warrington, 1988). A decrease in DTF with an increase in ADT can be due to earlier flower initiation, which can be observed by repeated apical dissections or reduced leaf number below the first open flower (Adams et al., 1998b, 1998c; Mattson and Erwin, 2003), or from a faster development rate (Brøndum and Heins, 1993; Faust and Heins, 1994; Karlsson and

Werner, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). When plants are grown at an ADT above the optimum temperature (T_{opt}), the flower development rate (reciprocal of DTF) begins to decline (Blanchard and Runkle, 2011a; Brøndum and Heins, 1993; Faust and Heins, 1994; Semeniuk, 1975). A decrease in flowering rate at temperatures > T_{opt} is known as heat delay, and may be due to a delay in flower induction, initiation and/or development (Warner and Erwin, 2006).

In many plants, a linear function has been frequently used to describe the relationship between flowering rate and ADT, when ADT is between T_{min} and T_{opt} (Clough et al., 2001; Niu et al., 2000, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). With a linear function, plant development rate increases by the same incremental amount with each degree rise in temperature, and this relationship can be useful in estimating the T_{min} and the thermal time (θ) required for a particular developmental event (Roberts and Summerfield, 1987). The base temperature is the minimum temperature below which no development occurs, and thermal time is the summation of all degree days above T_{min} required for a particular developmental event to occur. A quadratic function was found to best describe the effect of ADT on DTF of some crops, since the decrease in DTF with an increase in ADT was not linear between T_{min} and T_{opt} (Armitage et al., 1981; Clough et al., 2001; Niu et al., 2000, 2001; Park et al., 1998; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). For example, a greater decrease in flowering time was observed when ADT increased from 15 to 20 °C compared to when ADT increased from 20 to 25 °C. Although linear and quadratic equations can be used to simply describe these responses, they lack biological significance because their constants do not have physiological meaning (Landsberg, 1977).

Several studies have quantified the effect of ADT on flowering time using mathematical models that contain parameters of biological significance (T_{max}, T_{opt} and/or T_{min}) when temperatures beyond the species-specific linear limit are included in the experimental range (Blanchard and Runkle, 2011a; Brøndum and Heins, 1993; Faust and Heins, 1993; Hiden and Larsen, 1994; Larsen, 1988, 1989; Larsen and Persson, 1999). The species-specific T_{min}, T_{opt}, or T_{max} are usually determined by the natural origin and distribution of a particular species. For example, tussock bellflower (*Campanula carpatica* Jacq.), native to the Carpathian Mountains of Eastern Europe, had an estimated T_{min} for flowering of 0.0 °C (Whitman et al., 1997). In contrast, for browalia (*Browalia speciosa* Hook.) and angelonia (*Angelonia augustifolia* Benth.), both of tropical origin, the estimated T_{min} was 8.9 and 9.9 °C, respectively (Blanchard, 2009). Breeding efforts have introduced desirable traits such as early flowering, frost tolerance, and heat tolerance. Therefore, depending on the breeding objective, cultivars of the same species may differ in their base and optimum temperatures, as well as thermal time for a particular event such as flowering. For example, the T_{min} calculated for petunia (*Petunia ×hybrida* Vilm.-Andr.) 'Dreams Neon Rose' was 2.7 °C lower than that of 'Wave Purple' (Blanchard, 2009).

Base and optimum temperatures within a species can also vary with the developmental process (Clough et al., 2001; Karlsson et al., 1989a; Pearson et al., 1995; Yuan et al., 1998; Whitman et al., 1997), physiological process (van Iersel, 2003) and environmental conditions such as photoperiod (Adams et al., 1997, 1998a, 1998b) and DLI (Adams et al., 1997; Faust and Heins, 1993; Pramuk and Runkle, 2005b). For example, T_{opt} estimated for four different phases of growth and development in chrysanthemum (*Chrysanthemum ×morifolium* Ramat.) varied from 19.2 to 23.1 °C (Karlsson et al., 1989a). Similarly, Adams et al. (1998a) reported a linear increase in T_{opt} for flower development rate in petunia with an increase in photoperiod, from 20.7 °C under an 8-h photoperiod to 24.3 °C under a 14.4-h photoperiod.

Estimation of T_{min} is useful in calculating the thermal time for a particular event and categorizing plants based on their thermal tolerance (Blanchard, 2009). Blanchard (2009) reported a greater delay in flowering at lower temperatures for species with a higher T_{min} as compared to species with lower T_{min} values. For example, flowering time of petunia 'Dreams Neon Rose' (T_{min} = 2.8 ºC) and summer snapdragon (T_{min} = 9.9 ºC) was delayed by 28% and 81% when grown at 15 ºC versus 20 ºC, respectively (Blanchard, 2009). Therefore, estimations of T_{min} and T_{opt} allow growers to quickly categorize crops according to their temperature sensitivity and grow them together for energy-efficient production (Blanchard, 2009).

Although higher temperatures can decrease flowering time, faster crop timing may not always be desirable, since plant quality parameters like flower bud number, flower size, branch number, and plant biomass are often inversely related with ADT (Blanchard et al., 2011a, 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001; Pramuk and Runkle, 2005b; Warner and Erwin, 2006). For example, as ADT increased from 15 to 25 ºC (under 15 $mol \cdot m^{-2} \cdot d^{-1}$), plant biomass, inflorescence number, and inflorescence diameter in marigold (*Tagetes patula* L.) decreased by 35, 53, and 31%, respectively (Moccaldi and Runkle, 2007). Similarly, in petunia 'Dreams Neon Rose', each degree rise in ADT decreased the flower and branch number by 0.9 and 0.3, respectively (Mattson and Erwin, 2003). Therefore, there is often a trade-off between fast crop timing and high plant quality, especially under light-limiting conditions.

For many annual bedding plant species, the flowering time response to ADT has been quantified, but the nature of that response varies widely among species and cultivars (Adams et al., 1998; Armitage et al., 1981; Blanchard and Runkle, 2011a; Moccaldi and Runkle, 2007; Mattson and Erwin, 2003; Pietsch et al., 1995; Pramuk and Runkle, 2005a). Therefore, research-based information that describes the effect of ADT on flowering time and plant quality is needed for crops in which data has not been published. The objective of this research was to quantify the effect of ADT on flowering time and plant quality of 18 species and cultivars of popular bedding plants using linear and non-linear mathematical models, and to estimate T_{min} for each of the species and cultivars studied.

Materials and Methods

Plant material: Experimental protocol, data collection and analysis was similar to that reported by Blanchard and Runkle (2011) and Pramuk and Runkle (2005a). Seedlings of American marigold (*Tagetes erecta* L. 'Inca II Mix'), cup flower (*Nierembergia caerulea* (Miers) Millán 'Purple Robe'], diascia (*Diascia barberae* Hook.f. 'Diamonte Mix'), flowering tobacco (*Nicotiana alata* Link and Otto 'Perfume Deep Purple'), geranium (*Pelargonium* × *hortorum* L.H.Bailey 'Pinto Red' and 'Ringo 2000 Deep Red'), gerbera (*Gerbera jamesonii* Bolus ex Hook. f. 'Jaguar Deep Orange'), globe amaranth (*Gomphrena globosa* L. 'Gnome Purple'), heliotrope (*Heliotropium arborescens* L. 'Blue Wonder'), impatiens (*Impatiens walleriana* Hook. f. 'Blitz 3000 Deep Orange'), nemesia (*Nemesia foetans* Vent. 'Poetry White'), New Guinea impatiens (*Impatiens hawkeri* W. Bull 'Divine Cherry Red'), osteospermum [*Osteospermum ecklonis* (D.C.) Norl. 'Asti Purple'], petunia 'Bravo Blue', pot marigold (*Calendula officinalis* L. 'Bon Bon Orange'), snapdragon (*Antirrhinum majus* L. 'Liberty Classic Cherry'), stock [*Matthiola incana* (L.) W.T. Aiton 'Hot Cakes Purple'], and torenia (*Torenia fournieri* Linden ex E. Fourn. 'Clown Blue') were grown in 288-cell (6-mL), 128-cell (12-mL) or 36-cell (42.3-mL) plug trays depending on species (Table 2.1) by a commercial greenhouse (C. Raker & Sons, Litchfield, MI) and received at Michigan State University (MSU) on 30 March 2010 and 13 April 2010. Gerbera 'Jaguar Deep Orange,' petunia 'Bravo Blue' and stock 'Hot Cakes Purple' grown during the spring experiment were replaced with 'Jaguar Deep Rose,' 'Single Frost Blue' and 'Garden Vintage Mix' for the fall experiment, respectively, due to availability.

The experiment was repeated in fall 2010 to record data under different DLI conditions using the protocol described below. Seedlings were received at MSU on 26 October 2010 and grown in the controlled environment chambers until the leaf number for each species was similar to that of the plugs grown in spring 2010. Once the desired leaf count was achieved, the seedlings were transplanted and grown in greenhouses maintained the five different temperature set points. Time between seed sow and transplant was within 12 d between replications in time (Table 2.1).

Growth Chamber Treatments and Environment: Seedlings that were not ready for transplant on receipt were grown in controlled environment chambers at a constant temperature setpoint of 20 ºC under a *PPF* of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (DLI ≈ 10 $mol \cdot m^{-2} \cdot d^{-1}$) provided by a combination of cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and incandescent lamps (INC, Philips, Somerset, NJ) with a 16-h photoperiod. The seedlings were subjectively deemed ready for transplant ≈ 3–5 weeks after seed sow and were accordingly transplanted. The mean leaf number at transplant was recorded for each species (Table 2.1). The light intensity in the environment chambers was checked periodically with an instantaneous quantum sensor (Apogee Instruments Inc., Logan, UT) at canopy height and adjustments were made by replacing and/or lowering the lamps when required. Plugs were irrigated by hand as necessary with acidified well water (140 mg·L^{-1} titratable alkalinity of $CaCO_3$) containing (mg·L^{-1}) 95, 34, and 29 Ca, Mg, and S, and supplemented with a water-soluble fertilizer providing (mg·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 Treatments and Environment: Plants that were deemed ready for transplant were 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 3 to 4 nodes and treated with a 500 mg·L^{-1} spray of ethephon at a volume of 0.2 L·m^{-2} (Florel; Bayer CropScience LP, NC) prior to transplant. The seedlings were thinned to one plant per cell prior to 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 (HPS) lamps that provided a *PPF* of 100 to 120 µmol·m^{-2}·s^{-1}. In each greenhouse compartment, a shielded and aspirated 0.13 mm type E thermocouple (Omega Engineering, Stamford, CT) recorded the air temperature and a line quantum sensor containing 10 photodiodes (Apogee Instruments) placed at canopy height (22 cm above bench height) recorded the light intensity. A CR10 datalogger (Campbell Scientific, Logan, UT) collected the environmental data every 10 s and hourly averages were recorded. Actual average air temperatures during the spring and fall experiments were 18.4, 18.9, 21.4, 23.6, or 26.0 ºC and 14.0, 17.0, 19.6, 23.1, or 25.6 ºC, respectively. Mean DLI during the spring and fall experiments were 18.0 and 9.0 mol·m^{-2}·d^{-1}, respectively. Average DIF values (day – night temperature) ranged from 0.5 to 2.0 ºC, and 0.4 to 0.9 ºC in the spring and fall experiments, respectively.

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 ($mg \cdot L^{-1}$) 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 Special; GreenCare Fertilizers, Inc.).

Data collection and analysis: When each plant flowered according to the individual characteristics for each species (Table 2.1), the date of flowering was recorded and DTF from transplant was calculated for each species. Flowering rate was then calculated by taking the reciprocal of DTF. Flower and flower bud number, axillary branch number, number of nodes below first open flower on the primary stem, and plant height or length of longest lateral were also recorded at first open flower. Branch number was not recorded in gerbera. 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 media surface and the roots were thoroughly washed to remove media particles. The shoots (for all species) and roots (for 9 species) were separately placed in labeled brown paper bags and dried in a forced-air oven (Model 630; Precision and Napco, Winchester, VA) at 79 °C for ≥ 3 d 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, N.C.) was used to analyze the experimental data. When linear regression slopes between replications were non-significant ($P \leq 0.05$), data was pooled for statistical analysis. Linear and quadratic regression (REG procedure) analysis was used to generate equations to describe the effect of ADT on plant quality parameters. Data for leaf number below first open flower was compared among treatments using Tukey's honestly significant difference test at $P \leq 0.05$. Linear regression analysis was performed on the flowering rate data, and the slope and intercept values generated from the equations were used to calculate the base temperatures for each species (Roberts and Summerfield, 1987). Many researchers have estimated the T_{min}, and described the flowering time response as a function of ADT using linear regression when $T_{min} < ADT < T_{opt}$ (Clough et al., 2001; Niu et al., 2000, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998):

$$1/\text{d to flower} = b_0 + b_1 \times ADT \qquad (1)$$

where 1/d to flower = the rate of progress towards flowering, b_1 = slope, b_0 = intercept, and ADT = average daily temperature (°C) above T_{min} and below T_{opt}. Given that the developmental rate at T_{min} is zero, equation (1) can be used to calculate T_{min}:

$$T_{min} = -\, b_0 / b_1 \qquad (2)$$

where T_{min} = temperature at or below which the flower development rate is zero.

In gerbera, globe amaranth, and pot marigold, an exponential function was used to describe the flowering rate response as a function of temperature:

$$1/\text{d to flower} = R_{max} \times (1 - \exp(-C \times (ADT - T_{min}))) \qquad (3)$$

where R_{max} = maximum flower development rate, and C is a constant that defines the curve of the function. This exponential function incorporates parameters of biological significance (T_{min}, R_{max}), and has been used to quantify the effect of ADT on flower development and leaf unfolding rate in several potted and annual bedding plant species (Blanchard and Runkle, 2011a; Hidén and Larsen, 1994; Larsen 1988, 1989; Larsen and Hidén, 1995; Larsen and Persson, 1999).

In impatiens, T_{opt} was observed, and therefore a non-linear model was used to describe the relationship between flower development rate and ADT (Landsberg, 1977; Reed et al., 1976):

$$1/\text{d to flower} = A \times (ADT - T_{min}) \times (T_{max} - ADT)^{B} \quad (4)$$

$$\text{where } A = R_{max} / ((T_{opt} - T_{min}) \times (T_{max} - T_{opt})^{B}) \quad (5)$$

$$\text{and } B = (T_{max} - T_{opt}) / (T_{opt} - T_{min}) \quad (6)$$

where T_{opt} is the optimum temperature above which the flower development rate starts to decrease until it reaches zero at T_{max}, and B describes the curve of the function. This non-linear model includes constants that have biological meaning (T_{min}, T_{opt}, T_{max}, and R_{max}), and have been previously used to model an asymmetrical temperature response curve in African violet (*Saintpaulia ionantha* Wendl.; Faust and Heins, 1993), dahlia (*Dahlia pinnata* Cav.; Brøndum and Heins, 1993), and several annual bedding plant species (Blanchard and Runkle, 2011a). Flowering rate data for impatiens in the first replicate did not show a significant trend, and could not be fit with a linear or non-linear model (Eqns. [1], [3], and [4]). Since we had only 50 observations from the second replicate, T_{max} was fixed at 35 ºC (Blanchard and Runkle, 2011a) and T_{opt} was fixed at 25.1 (estimated from quadratic equations generated from the observed data) to allow for precise estimates of T_{min} and R_{max}.

Non-linear regression (NLIN procedure) of SAS was used to generate non-linear models and estimate the values for T_{min}, R_{max}, and *C* for eqns. [3] and [4] using 50 to 100 observations. Initial parameter estimates for T_{min} and R_{max} were obtained from eqn. [2] and observed data, respectively. Eqn. [3] was solved using initial estimates for T_{min} and R_{max} and a specific value of temperature to estimate an initial value for *C*. R^2 values for non-linear regression were generated by linearly regressing predicted values on the observed data (Blanchard and Runkle, 2011a).

Results

Flower development rate increased with an increase in ADT from 14 to 26 ºC for all the species studied except impatiens, but the magnitude of this response varied widely among species and cultivars (Figures 2.1 and 2.2). For example, the increase in rate of progress towards flowering with each degree increase in temperature from 14 to 26 ºC ranged from 0.00092 in diascia to 0.0027 in torenia (Table 2.2). The relationship between flowering rate and ADT was best described using a linear function in 14 of the 18 species studied, whereas a non-linear function was used for globe amaranth, gerbera, impatiens, and pot marigold (Figures 2.1 and 2.2). In American marigold, diascia, flowering tobacco, geranium 'Pinto Red', impatiens, petunia, and torenia, the flowering rate response to ADT varied between the spring (replication 1) and fall (replication 2) experiments, and separate functions were used to describe the response for each replicate. Differences in flowering time response between replications in petunia can most likely be attributed to cultivar differences, since the petunia cultivar 'Bravo Blue' grown during the spring was replaced with 'Single Frost Blue' in the fall replication. The coefficients of determination generated for linear (r^2) and non-linear models (R^2) ranged from 0.33 to 0.94 (Table 2.2). The variability in flowering time response differed between replications of diascia and cultivars of petunia, which considerably influenced the r^2 values. For example, the r^2 values of diascia were 0.65 in replication 2 and 0.33 in replication 1 (Table 2.2).

The estimated T_{min} for flower development rate varied among species and cultivars, and in some cases between replications for the same species (Figures 2.1 and 2.2). For example, T_{min} range from –3.9 ºC for diascia to 13.8 ºC for globe amaranth (Figures 2.1 and 2.2). When T_{min} varied between replications or cultivars within a species, it was generally < 2 ºC. Species and cultivars in which the estimated T_{min} was ≤ 4 ºC were American marigold, diascia, heliotrope, nemesia, New Guinea impatiens, osteospermum, petunia ‘Bravo Blue’, snapdragon, and stock. Those with an estimated T_{min} between 4 to 8 ºC were cupflower, flowering tobacco, geranium (both cultivars), gerbera, impatiens, petunia ‘Single Frost Blue’, and pot marigold. The only two crops studied with a $T_{min} > 8$ ºC were globe amaranth and torenia. All of globe amaranth and 20% of torenia plants died when grown at 14 ºC. Although 80% of torenia plants flowered at 14 ºC, they were of poor quality and likely not commercially marketable. There was a positive correlation ($P < 0.0001$) between the estimated T_{min} and delay in flowering time when plants were grown at 17 versus 23 ºC. For example, the delay in flowering time when plants were grown at 17 ºC compared to 23 ºC was 105, 53, and 34% in globe amaranth (T_{min} = 13.8 ºC), geranium ‘Ringo 2000 Deep Red’ (T_{min} = 5.7 ºC), and osteospermum (T_{min} = –0.5 ºC), respectively.

Flower or inflorescence number increased with an increase in ADT from 14 to 26 ºC for 14 of the 18 species studied (Figures 2.3-2.9, 2.11-2.13, 2.15, 2.17-2.19, panel A). For example, an increase in ADT from 14 to 26 ºC increased the predicted inflorescence number in pot marigold by 24. In globe amaranth, New Guinea impatiens, petunia ‘Single Frost Blue’, and torenia, flower number increased with temperature up to 20 ºC and then decreased (Figures 2.12, 2.14, 2.16, 2.20, panel B). The response of flower bud number to ADT differed between replications for impatiens and petunia (Figures 2.12, 2.16). For example, in replication 1, impatiens flower number showed a quadratic response with an increase in temperature. In contrast, in replication 2, flower bud number linearly increased with a decrease in temperature.

Average daily temperature had various effects on branch number among the species studied (Figures 2.3-2.20, panel B). In diascia, flowering tobacco, geranium ‘Pinto Red’ and ‘Ringo 2000 Deep Red’, nemesia, pot marigold, snapdragon, and stock, branch number increased with ADT. There was a positive correlation between flower or inflorescence number and branch number in these species and cultivars ($P < 0.0001$). There was no such relationship between replications in cupflower, diascia, heliotrope, impatiens, petunia, and stock. For example, in stock, branch number increased as ADT decreased from 26 to 14 ºC in the first replication, but a significant temperature response was not observed in the second replication. In general, number of flowers and branches were higher during the spring (when the DLI was higher) compared to the fall experiment.

A decreasing temperature caused a developmental delay in flowering in cupflower, geranium 'Pinto Red' and 'Ringo 2000 Deep Red', gerbera, petunia, and snapdragon; leaf number below the first flower decreased linearly or quadratically with an increase in ADT (Table 2.3). In contrast, leaf number decreased with a decrease in ADT in American marigold, heliotrope, impatiens, and torenia. Temperature did not significantly affect leaf number below first open flower in diascia, flowering tobacco, globe amaranth, nemesia, New Guinea impatiens, osteospermum, pot marigold, and stock.

As temperature increased from 14 to 26 ºC, plant height decreased in cupflower, flowering tobacco, geranium 'Pinto Red' and 'Ringo 2000 Deep Red', gerbera, nemesia, osteospermum, pot marigold, snapdragon, and stock (Figures 2.4, 2.6-2.9, 2.13, 2.15, 2.17-2.19, panel C). However, among these species and cultivars, a decrease in leaf number with an increase in ADT only occurred in cupflower, geranium 'Pinto Red' and 'Ringo 2000 Deep Red', gerbera, and snapdragon. On the other hand, plant height decreased with a decrease in ADT in African marigold, heliotrope, impatiens, and torenia. Leaf number also decreased with ADT in these species. Heliotrope and impatiens height first increased and then decreased with ADT, while there was no significant effect of temperature on plant height in diascia, flowering tobacco, globe amaranth, nemesia, New Guinea impatiens, pot marigold, and stock.

Shoot dry mass was inversely related with ADT in cupflower, flowering tobacco, geranium ‘Pinto Red’ and ‘Ringo 2000 Deep Red’, heliotrope, nemesia, osteospermum, petunia, pot marigold, snapdragon, and stock (Figures 2.3-2.20, panel D). The opposite trend was observed in globe amaranth. In American marigold, New Guinea impatiens, and torenia shoot dry weight first increased with decrease in ADT up to an optimum temperature, and then decreased. There was no significant relationship between shoot dry mass and ADT in diascia, gerbera, and impatiens. Among the nine species in which root mass was measured, the correlation between ADT and root mass was negative in flowering tobacco, geranium ‘Ringo 2000 Deep Red’, nemesia, petunia, pot marigold, snapdragon, and stock; positive in torenia; and not significant in impatiens (Figures 2.6, 2.8, 2.12-2.13, 2.16-2.20, panel E). For example, as ADT increased from 14 to 26 ºC, root mass decreased in flowering tobacco, but increased in torenia. There was a positive correlation between shoot and root mass in all nine species measured ($P < 0.0001$). Flower or inflorescence diameter increased with ADT from 14 to 26 ºC in only nine of the 18 species studied (Figures 2.3-2.20, panel F). Optimum temperature for flower or inflorescence diameter was observed in diascia, flowering tobacco, impatiens, New Guinea impatiens, osteospermum, and torenia in the temperature range included in this study.

Discussion

Linear models adequately described the effect of temperature on flowering rate in 14 of the 18 species studied, since the temperature range (14 to 26 ºC) included in this experiment was between T_{min} and T_{opt} for these species. This temperature range was selected because it encompasses temperatures in which most bedding plants are commercially grown in greenhouses. Non-linear models were evaluated to describe the flowering rate as a function of ADT for all the species, but they either failed to converge or did not precisely estimate the model parameters. Several studies have used a linear function to describe the relationship between flowering rate and ADT, when ADT is between T_{min} and T_{opt} (Clough et al., 2001; Niu et al., 2000, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998). Although linear models lack constants with biological meaning, they are simple and, within clearly defined limits, can adequately describe a biological response (Landsberg, 1977). Many researchers have quantified the effect of ADT on flowering time using mathematical models that contain parameters of biological significance (T_{min}, T_{max}, and T_{opt}) (Blanchard and Runkle, 2011a; Blanchard et al., 2011a; Brøndum and Heins, 1993; Faust and Heins, 1993; Hidén and Larsen, 1994; Larsen, 1988, 1989; Larsen and Persson, 1999). However, these researchers studied plant responses over a wider temperature range than the one used in this study, and either observed or approached T_{min}, T_{opt}, or both. In our experiments, non-linear models were used in gerbera, globe amaranth, impatiens, and pot marigold. Although T_{min} or T_{opt} was observed only in globe amaranth and impatiens, non-linear models had a relatively high coefficient of determination, parameter estimates with an acceptable standard error, and improved predictions, especially at lower temperatures in gerbera and pot marigold.

The flowering rate response to ADT varied between replications in American marigold, geranium ‘Pinto Red’, flowering tobacco, petunia, and torenia. Except for flowering tobacco and petunia, a greater flowering rate and a lower leaf number was observed in the spring (when the DLI was higher) compared to the fall experiment. Although flowering tobacco and petunia plants flowered earlier at higher temperatures in fall than in the spring experiment, the difference between replications was ≤ 4 d. Several studies have reported a negative correlation between DTF and DLI during the finish stage for many annual bedding plants (Blanchard et al., 2011a, 2011b; Carvalho et al., 2006; Currey and Erwin, 2011; Warner and Erwin, 2005; Faust et al., 2005; Oh et al., 2009; Pietsch et al., 1995). For example, an increase in DLI from 10.5 to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ (ADT of 20 °C) reduced DTF from transplant by 21 d in snapdragon, 16 d in pot marigold, 3 d in impatiens, 4 d in mimulus (*Mimulus hybridus* Hort. Ex Siebert & Voss), and 12 d in torenia (Warner and Erwin, 2005). A higher DLI can reduce flowering time by initiating flowering at a lower node, by accelerating the flower development rate due to an increase in plant temperature, or both. Faust and Heins (1998) and Mattson and Erwin (2005) reported an increase of 1 to 2 °C in plant temperature under supplemental HPS lighting.

In this experiment, the estimated T_{min} ranged from –3.9 to 13.8 °C, which indicates the range of thermal sensitivity among the different species and cultivars studied. Blanchard and Runkle (2011a) observed a similar variability in cold tolerance among 18 species of annual bedding plants. Our previous research on T_{min} estimates for the same species (Vaid and Runkle, 2011) has been revised in the current study using observations from two replications performed under different DLI conditions. The estimated T_{min} values here are generally ± 2 °C of those estimated in previous studies for the same species, but at times different cultivars. For example, our T_{min} estimated for snapdragon and geranium was 2.0 and 0.7 to 1.5 °C higher, respectively, than that estimated by Blanchard (2009). Pramuk and Runkle (2005b) and Moccaldi and Runkle (2007) estimated T_{min} for impatiens and marigold at 7.5 and –3.0 °C, which was 0.3 higher and 1.7 °C lower than our estimates of 7.2 and –1.3 °C, respectively.

When the flowering rate response varied between replications, T_{min} estimated under the high DLI (spring) was 0.7 to 2.8 °C higher than that estimated under the low DLI (fall), except in flowering tobacco and petunia. Several studies have evaluated the effect of DLI on the estimated T_{min} or T_{opt} for flower development rate, but the results have not been consistent (Adams et al., 1997; Faust and Heins, 1993; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). For example, an increase in DLI from 5 to 15 $mol \cdot m^{-2} \cdot d^{-1}$ decreased the estimated T_{min} of celosia (*Celosia argentea* L.) and impatiens by 1.5 and 3.2 °C, respectively (Pramuk and Runkle, 2005b), but did not influence the T_{min} in marigold and salvia (*Salvia splendens* F. Sello ex Roem & Schult.) (Moccaldi and Runkle, 2007). In contrast, Adams et al. (1997), Faust and Heins (1993), and Pietsch et al. (1995) reported a decrease in T_{opt} or T_{min} with a decrease in DLI.

Based on the estimated T_{min}, species can be subjectively categorized as cold-tolerant when $T_{min} \leq 4$ °C; cold-intermediate when 4 °C < T_{min} < 8 °C; and cold-sensitive when $T_{min} \geq$ 8 °C. When cold-sensitive species torenia and globe amaranth were grown at 17 versus 23 °C, the percentage delay in flowering time was 79 to 106. In contrast, in cold-tolerant species, the delay in flowering time varied from 29 to 41%. Estimations of T_{min} enables categorization of species according to their thermal sensitivity, and therefore can help facilitate energy-efficient crop production.

As ADT increased from 14 to 26 °C, flower number, branch number, plant height, shoot mass, and flower diameter decreased in 14, 8, 10, 14, and 9 of the 18 crops studied, respectively. In addition, root mass decreased as ADT increased in 7 of the 9 crops measured. Plant quality parameter responses to temperature were consistent with previous studies (Blanchard et al., 2011a; Blanchard et al., 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2001; 2000; Pramuk and Runkle, 2005b). For example, an increase in ADT from 16 to 26 °C decreased the flower number of tickseed (*Coreopsis grandiflora* Hogg ex Sweet) by 80%, Shasta daisy [*Leucanthemum* ×*superbum* (Bergmans ex J.W. Ingram)] by 55%, and black-eyed Susan

(*Rudbeckia fulgida* Aiton) by 75% (Yuan et al, 1998). Similarly, each degree rise in ADT decreased flower diameter or area by 0.97 mm in tussock bellflower 'Blue Clips' (under 10.8 $mol \cdot m^{-2} \cdot d^{-1}$; Niu et al., 2001), 1.42 cm in dahlia 'Royal Dahlietta Yellow' (Brøndum and Heins, 1993), 0.19 cm in sundrops (*Oenothera fruticosa* L.) 'Youngii-lapsley' (Clough et al., 2001) and 1.05 cm^2 in pansy (*Viola* × *wittrockiana* Gams.) 'Universal Violet' (Pearson et al., 1995). Flower bud development requires carbon import from the source organs (leaves). Sucrose hydrolysis in the sink organs (flower buds) is necessary to establish a concentration gradient for carbon transport between the source and the sink (Dinar and Rudich, 1985). High temperatures reduce sucrose hydrolysis and therefore increase its concentration in flower buds, 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).

Branch number was inversely related with ADT in 8 species and cultivars, and an increase in branch number was positively correlated with an increase in flower number in those species. Many researchers have reported a decrease in branching with an increase in ADT, such as in balloon flower [*Platycodon grandiflorus* (Jacq.) A. DC. 'Astra Blue'; Park et al., 1998], fuchsia (*Fuchsia* × *hybrida* hort. ex Siebold & Voss; Erwin et al., 1991), pansy (Mattson and Erwin, 2003; Warner and Erwin, 2006) and petunia (Kaczperski et al., 1991; Mattson and Erwin, 2003). In some of those cases, an increase in lateral branch number was positively correlated with an increase in flower number (Mattson and Erwin, 2003; Warner and Erwin, 2006). Plant quality in many of the species in this study was generally higher in the spring than in the fall replication, which was not unexpected, since the DLI received during spring was almost 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 10.0 to 20.0 $mol \cdot m^{-2} \cdot d^{-1}$ (ADT 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* Engelm. and Gray), lateral inflorescence number per plant tripled and flower number per inflorescence nearly doubled as DLI increased from 5.0 to 20.0 $mol \cdot m^{-2} \cdot d^{-1}$ (Fausey et al., 2005).

Shoot dry mass at first flowering increased as ADT decreased in 11 of the species and 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 (Pramuk and Runkle, 2005b; 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). These results are not surprising since plants grown at lower temperatures take longer to flower (and thus can photosynthesize for a longer time before flowering) and are also of higher quality (increased branch number and flower number and size) compared to plants grown at higher temperatures. In addition, van Iersel (2003) reported an increase in the net photosynthetic rate (P_{net}) with a decrease in ADT for geranium, marigold, pansy and petunia. High temperatures decrease P_{net} by modifying Rubisco kinetics (Brooks and Farquhar, 1985), increasing O_2:CO_2 solubility (Ku and Edwards, 1977), or both.

In contrast, shoot biomass increased with increasing temperature in American marigold, globe amaranth, New Guinea impatiens, and torenia. Similar results were reported in celosia (Pramuk and Runkle, 2005b), summer snapdragon (Miller and Armitage, 2002), Texas firebush

(*Hamelia patens* Jacq.; Armitage, 1995), and torenia (Warner and Erwin, 2005). Many of these plants have a high estimated T_{min}; for celosia and summer snapdragon, it was 10.2 °C under a DLI of 15 $mol \cdot m^{-2} \cdot d^{-1}$ (Pramuk and Runkle, 2005b) and 9.9 °C (Blanchard, 2009), respectively. In our study, torenia and globe amaranth were identified as both cold-sensitive crops (T_{min} > 8 °C). Accumulation of root mass in response to ADT followed a trend similar to that observed for shoot mass in our study. However, these results could not be compared to previous work since, to our knowledge, the response of root mass accumulation to ADT has not been investigated in annual bedding plants.

Among the 18 species studied, plant height decreased in 10 species, but increased in 4 species, with an increase in temperature. Although the greenhouse temperature setpoints in these experiments were constant, the day was often higher 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 et. al., 1991; Erwin and Heins, 1990). For example, as DIF increased from –6.0 to +6.0 °C, plant height increased by 40% in Easter lily (Erwin and Heins, 1990), 39% in fuchsia (Erwin et al., 1991), 19% in geranium (Strefeler, 1995), and 9% in Italian bellflower (*Campanula isophylla* Moretti; Moe and Mortensen, 1992). However, since 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 ADT and not DIF. A high ADT can also decrease plant height by reducing the number of nodes formed prior to flowering (Clough et al., 2001; Yuan et al., 1998). In contrast, several studies have reported an increase in plant height with an increase in ADT (Armitage et al., 2000; Blanchard et al., 2011a; Kanellos and Pearson, 2000; Miller and Armitage, 2002; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b). Since the number of nodes in these studies was either variable or not reported, and the actual DIF values were also not provided, the promotive effect of higher temperatures on plant height can not be clearly understood.

Conclusion

In general, flowering time and plant quality decrease as the ADT increases, especially under light-limiting conditions. The nature of these responses varies widely among species and in some cases, also with cultivars. Therefore, there is often a trade-off between faster crop timing and higher plant quality. Growers can use the temperature response categories and crop models generated in this study to estimate the consequences of changing the greenhouse temperature on flowering time and plant quality parameters. In addition to temperature, environmental conditions such as DLI and photoperiod can also affect the flower development rate (Erwin and Warner, 2002). Our models assume a 16-h photoperiod and a DLI of $\geq 9\ \mathrm{mol \cdot m^{-2} \cdot d^{-1}}$, and may not be valid under a lower DLI or if plants with a facultative photoperiodic response are grown under a shorter photoperiod. In addition, the crop models generated in this study were at temperatures between 14 and 26 °C, and may not be accurate outside this temperature range. Finally, DLI greatly influences different 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 ADT may not be applicable under DLI conditions other than those reported in this study.

Table 2.1. Days from seed sow to transplant (TP), plug size and mean node no. at TP, and characteristics used to determine flowering date for 18 varieties of 16 bedding plant species in two experimental replicates.

Species	Days from seed sow to TP	Plug size (mean leaf no.) at TP	Flowering characteristics
African marigold 'Inca II Mix'	21 or 27	288 (6)	1 inflorescence with ≥50% of the petals reflexed
Cupflower 'Purple Robe'	34 or 40	288 (10)	1 flower open
Diascia 'Diamonte Mix'	50 or 62	128 (8)	2 flowers open on an inflorescence
Flowering tobacco 'Perfume Deep Purple'	32 or 34	288 (7)	2 flowers open on an inflorescence
Geranium 'Pinto Red'	22 or 26	288 (3)	5 flowers open on an inflorescence
Geranium 'Ringo 2000 Deep Red'	22 or 26	288 (3)	5 flowers open on an inflorescence
Gerbera 'Jaguar Deep Orange' or 'Jaguar Deep Rose'	52 or 63	128 (7)	1 inflorescence with all of the petals reflexed
Gerbera 'Revolution Neon Rose'	27	288 (2)	1 inflorescence with all of the petals reflexed
Globe amaranth 'Gnome Purple'	37 or 42	128 (8)	1 inflorescence with outer 2 whorls of petals reflexed
Heliotrope 'Blue Wonder'	44 or 49	128 (10)	2 flowers open on an inflorescence
Impatiens 'Blitz 3000 Deep Orange'	27 or 33	288 (6)	1 flower open
Nemesia 'Poetry White'	61 or 73	128 (7)	2 flowers open on an inflorescence
New Guinea impatiens 'Divine Cherry Red'	47 or 55	128 (10)	1 flower open
Osteospermum 'Asti Purple'	24 or 39	36 (15 or 18)	1 flower open
Petunia 'Bravo Blue' or 'Single Frost Blue'	34	288 (6)	1 flower open
Pot marigold 'Bon Bon Orange'	23 or 35	288 (8)	1 inflorescence with ≥50% of the petals reflexed
Snapdragon 'Liberty Classic Cherry'	38 or 48	288 (12)	2 flowers open on an inflorescence
Stock 'Hot Cakes Purple' or 'Garden Vintage Mix'	23 or 30	128 (6)	2 flowers open on an inflorescence
Torenia 'Clown Blue'	29 or 31	288 (7)	1 flower open

Table 2.2. Parameter estimates for linear and non-linear models (Eqns. [1], [3], and [4]) describing the flowering rate response to average daily temperature in 18 bedding plant species and cultivars. T_{min} and T_{max} are the species-specific base and maximum temperatures (ºC), respectively at which the flower development rate is zero. T_{opt} is the optimum temperature (ºC) at which the flower development rate reaches a maximum value (R_{max}), and *C* defines the curvature of the function. CI = confidence interval.

Eq.	Parameter	Estimate	95% CI (±)	No.[z]	R^{2y} or r^{2x}
		African marigold 'Inca II Mix'			
[1]	$Intercept_1$[w]	–0.0019	0.0021	50	0.93
	$Slope_1$	0.0013	0.00010		
	$Intercept_2$[w]	0.0014	0.0024	50	0.87
	$Slope_2$	0.0011	0.00012		
		Cupflower 'Purple Robe'			
[1]	Intercept	–0.011	0.0031	100	0.86
	Slope	0.0018	0.00015		
		Diascia 'Diamonte Mix'			
[1]	$Intercept_1$	0.012	0.0038	50	0.33
	$Slope_1$	0.00088	0.00018		
	$Intercept_2$	0.0035	0.0019	50	0.65
	$Slope_2$	0.00092	0.00010		
		Flowering tobacco 'Perfume Deep Purple'			
[1]	$Intercept_1$	–0.0097	0.0030	50	0.93
	$Slope_1$	0.0018	0.00014		
	$Intercept_2$	–0.014	0.0032	50	0.94
	$Slope_2$	0.0022	0.00016		
		Geranium 'Pinto Red'			
[1]	$Intercept_1$	–0.0081	0.0033	50	0.85
	$Slope_1$	0.0012	0.00015		
	$Intercept_2$	–0.0049	0.0015	50	0.94
	$Slope_2$	0.0010	0.000076		
		Geranium 'Ringo 2000 Deep Red'			
[1]	Intercept	–0.0071	0.0016	100	0.91
	Slope	0.0012	0.000077		

Table 2.2. (cont'd).

Eq.	Parameter	Estimate	95% CI (±)	No.[z]	R^{2y} or r^{2x}
	Gerbera 'Jaguar Deep Orange' or 'Jaguar Deep Rose'				
[3]	T_{min}	7.6	3.67	100	0.85[y]
	R_{max}	0.039	0.023		
	C	0.055	0.064		
	Globe amaranth 'Gnome Purple'				
[3]	T_{min}	13.9	0.45	100	0.86[y]
	R_{max}	0.048	0.0080		
	C	0.13	0.046		
	Heliotrope 'Blue Wonder'				
[1]	Intercept	–0.0021	0.0027	100	0.84
	Slope	0.0014	0.00013		
	Impatiens 'Blitz 3000 Deep Orange'[v]				
[4]	T_{min}	7.2	2.76	50	0.54[y]
	R_{max}	0.038	0.0026		
	Nemesia 'Poetry White'				
[1]	Intercept	–0.0048	0.0040	100	0.81
	Slope	0.0019	0.00019		
	New Guinea impatiens 'Divine Cherry Red'				
[1]	Intercept	–0.0034	0.0069	97	0.43
	Slope	0.0014	0.00033		
	Osteospermum 'Asti Purple'				
[1]	Intercept	0.00053	0.003	64	0.78
	Slope	0.0011	0.00016		
	Petunia 'Bravo Blue' or 'Single Frost Blue'				
[1]	$Intercept_1$	–0.0050	0.0035	50	0.92
	$Slope_1$	0.0019	0.00016		
	$Intercept_2$	–0.014	0.013	50	0.58
	$Slope_2$	0.0026	0.00064		
	Pot marigold 'Bon Bon Orange'				
[3]	T_{min}	6.5	2.53	100	0.92[y]
	R_{max}	0.053	0.014		
	C	0.066	0.040		
	Snapdragon 'Liberty Classic Cherry'				
[1]	Intercept	–0.0070	0.0028	100	0.87
	Slope	0.0017	0.00014		

Table 2.2. (cont'd).

Eq.	Parameter	Estimate	95% CI (±)	No.[z]	R^{2y} or r^{2x}
	Stock 'Hot Cakes Purple' or 'Garden Vintage Mix'				
[1]	Intercept	–0.0069	0.0076	100	0.59
	Slope	0.0022	0.00037		
	Torenia 'Clown Blue'				
[1]	$Intercept_1$	–0.025	0.0050	50	0.92
	$Slope_1$	0.0027	0.00023		
	$Intercept_2$	–0.019	0.0045	50	0.89
	$Slope_2$	0.0021	0.00022		

[z]Number of observations in data set.
[y]Generated by linearly regressing predicted values on the observed data.
[x]Generated from linear flowering rate models.
[w]$_{1,2}$Parameter estimates for replicate 1 (spring) and 2 (fall), respectively.
[v]T_{max} was fixed at 35 ºC and T_{opt} was fixed at 25.1 ºC. Only data from the second replicate was included in estimating the model parameters.

Table 2.3. The effect of temperature on the number of nodes below first open flower in 18 species and cultivars of bedding plants. Plants were grown in glass-glazed greenhouse compartments at five constant temperature setpoints under a 16-h photoperiod and a DLI of 18 $mol \cdot m^{-2} \cdot d^{-1}$ (spring) or 9 $mol \cdot m^{-2} \cdot d^{-1}$ (fall). When regression slopes were non-significant ($P \leq 0.05$) between the two replications (rep), data was pooled for statistical analysis. During the fall replication, five or ten randomly selected plants of each species were microscopically examined for floral initiation (FI) at transplant.

		Temperature set point (ºC)					
Species	Rep	14	17	20	23	26	Trend[z]
African marigold 'Inca II Mix'	1	14.2b[y]	13.6b	15.1b	15.3b	17.9a	$L_1^{x***} Q_2^{x***}$
	2	15.9a	16.4a	16.6a	16.9a	17.4a	$L_1^{**} Q_2^{*}$
Cupflower 'Purple Robe'		78.1a	74.6a	74.7a	72.7a	76.2a	$L^{NS} Q^{*}$
Diascia 'Diamonte Mix'		16.0	16.9	16.0	17.1	17.0	NS
Flowering tobacco 'Perfume Deep Purple'		11.0	10.3	9.9	10.3	9.9	NS
Geranium 'Pinto Red'	1	9.6a	9.9a	9.9a	9.5a	7.5b	$L_1^{***} Q_2^{***}$
	2	10.9ab	11.0ab	11.3ab	11.7a	9.5b	$L_1^{NS} Q_2^{NS}$
Geranium 'Ringo 2000 Deep Red'		9.5a	9.2ab	8.9abc	8.1bc	7.7c	$L^{***} Q^{***}$
Gerbera 'Jagura Deep Orange' or 'Jaguar Deep Rose'		37.6a	38.7a	34.7a	30.5a	25.1a	$L^{***} Q^{***}$
Globe amaranth 'Gnome Purple'		–[v]	5.1	4.9	5.3	5.0	NS
Heliotrope 'Blue Wonder'	1	12.4	12.3	13.0	13.8	12.4	NS_1
	2	10.4b	10.8b	12.2b	11.6b	16.3a	$L_2^{***} Q_2^{***}$
Impatiens 'Blitz 3000 Deep Orange'	1	5.7c	6.9bc	7.2abc	8.8a	8ab	$L_1^{***} Q_1^{***}$
	2	7.4	8.8	7.7	8.2	8.1	NS_2
Nemesia 'Poetry White'		12.2	12.0	12.2	12.4	11.8	NS
New Guinea impatiens 'Divine Cherry Red'		10.0	9.6	10.1	9.2	10.0	NS
Osteospermum 'Asti Purple'		18.9	18.9	19.6	20.1	–[u]	NS
Petunia 'Bravo Blue' or 'Single Frost Blue'	1	13.7ab	15.2a	12.3bc	11.2bc	10.0c	$L_1^{***} Q_1^{***}$
	2	17.3	17.6	18.7	18.7	16.4	NS_2

Table 2.3. (cont'd).

Species	Rep	Temperature set point (ºC) 14	17	20	23	26	Trend[z]
Pot marigold 'Bon Bon Orange'		15.2	15.5	16.2	15.4	15.9	NS
Snapdragon 'Liberty Classic Cherry'		13.5a	12.2ab	11.3b	10.6b	11.4b	$L^{**}Q^{*}$
Stock 'Hot Cakes Purple' or 'Garden Vintage Mix'		16.7	17.2	17.1	17.3	18.4	NS
Torenia 'Clown Blue'		6.2a	6.5a	5.8a	6.3a	6.8a	$L^{NS}Q^{**}$

[z]Linear and quadratic trends describing the leaf number response to ADT

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

[x]$_{1,2}$Linear and quadratic trends in replicate 1 (spring) and 2 (fall), respectively.

[w]Plants within the column not examined for floral initiation.

[v]Treatment not included in analysis because 100% of plants died.

[u]Treatment not included in the experiment.

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

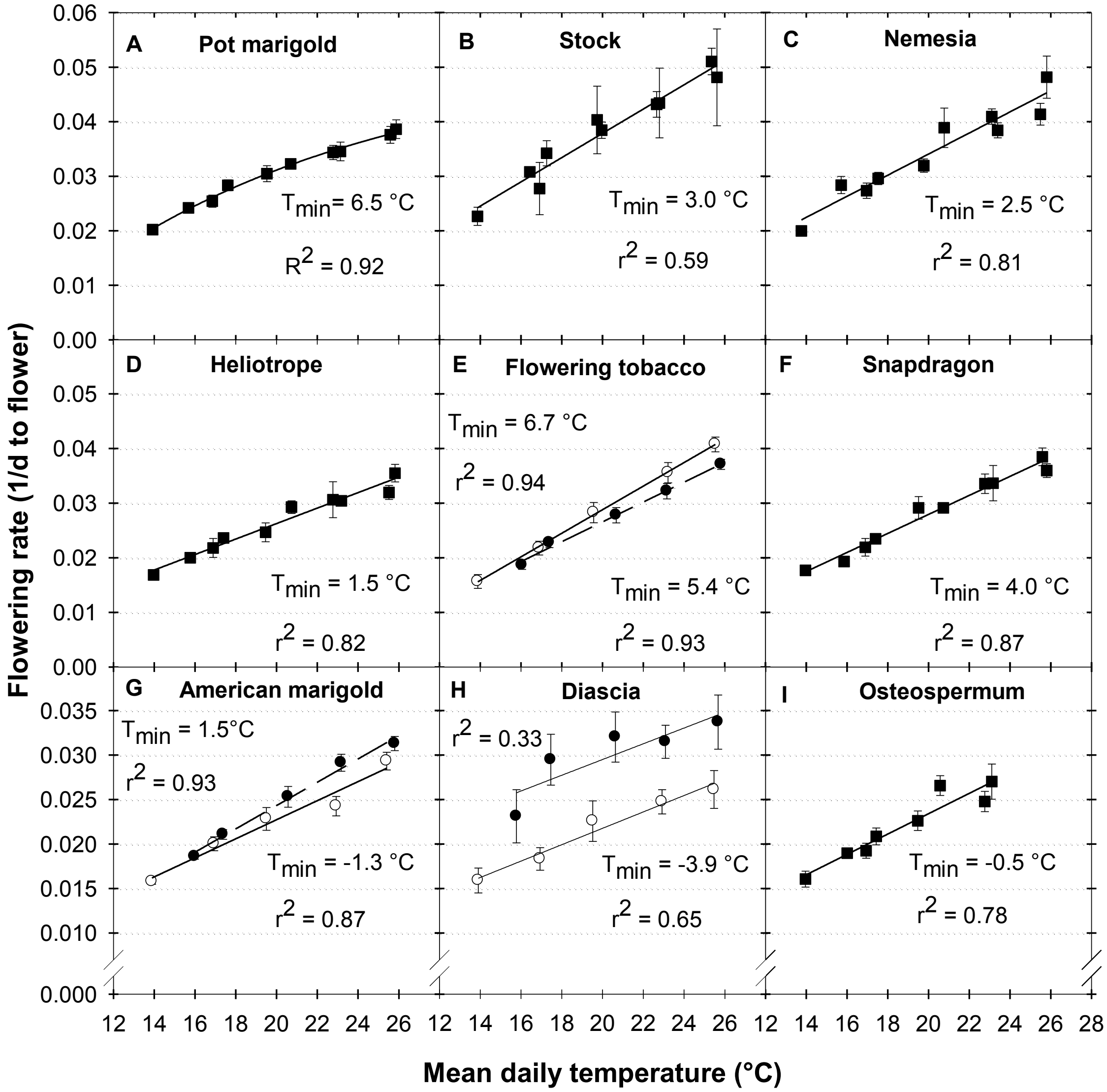

Figure 2.1. The effect of mean daily temperature (°C) on the flowering rate in 9 species of bedding plants modeled using Eq. [1] (panel B-I) and Eq. [3] (panel A) and parameter estimates from Table 2.2. for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Flowering rate was calculated by taking the reciprocal of the number of days to flower. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. T_{min} (base temperature) is the estimated minimum temperature at or below which the rate of progress towards flowering is zero. r^2 or R^2 is the coefficient of determination generated for linear and non-linear crop models, respectively.

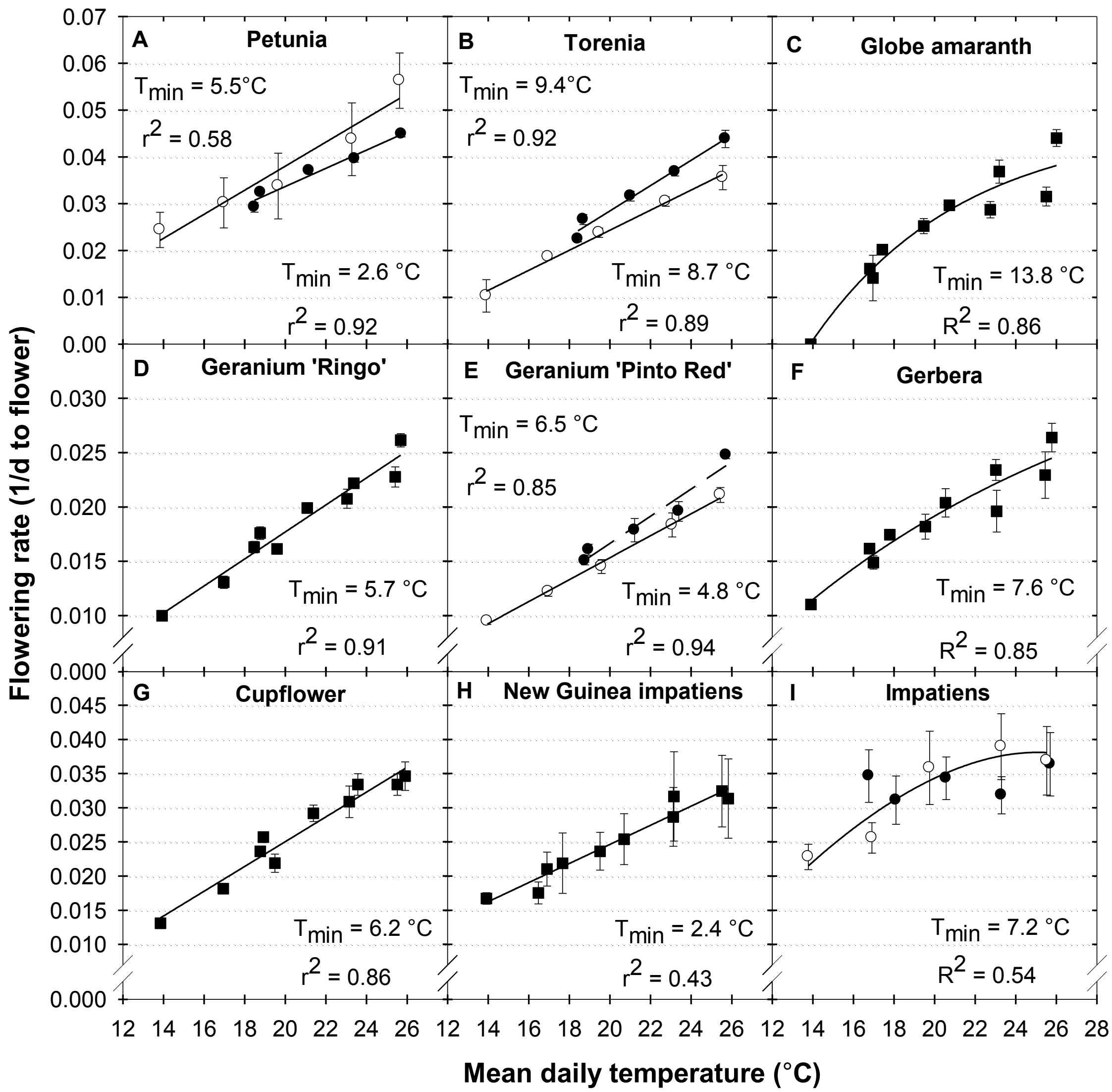

Figure 2.2. The effect of mean daily temperature (°C) on the flowering rate in 9 species of bedding plants modeled using Eq. [1] (panel A, B, D, E, G, H), Eq. [3] (panel C, F), and Eq. [4] (panel I), and parameter estimates from Table 2.2. for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications (*P* ≤ 0.05), data was pooled (■) for statistical analysis. Flowering rate was calculated by taking a reciprocal of the number of days to flower. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. T_{min} (base temperature) is the estimated minimum temperature at or below which the rate of progress towards flowering is zero. r^2 or R^2 is the coefficient of determination generated for linear and non-linear crop models, respectively. In panel A, the petunia cultivar 'Bravo Blue' grown during replication 1 (●) was substituted by 'Single Frost Blue in replication 2 (○). Flowering time data from the first replicate did not show a significant trend (*P* ≤ 0.05) in impatiens and could not be used for statistical analysis. T_{max} and T_{opt} in panel R was fixed at 35 ºC and 25.1 ºC respectively to allow for precise estimation of the other model parameters using 50 observations from the second replicate.

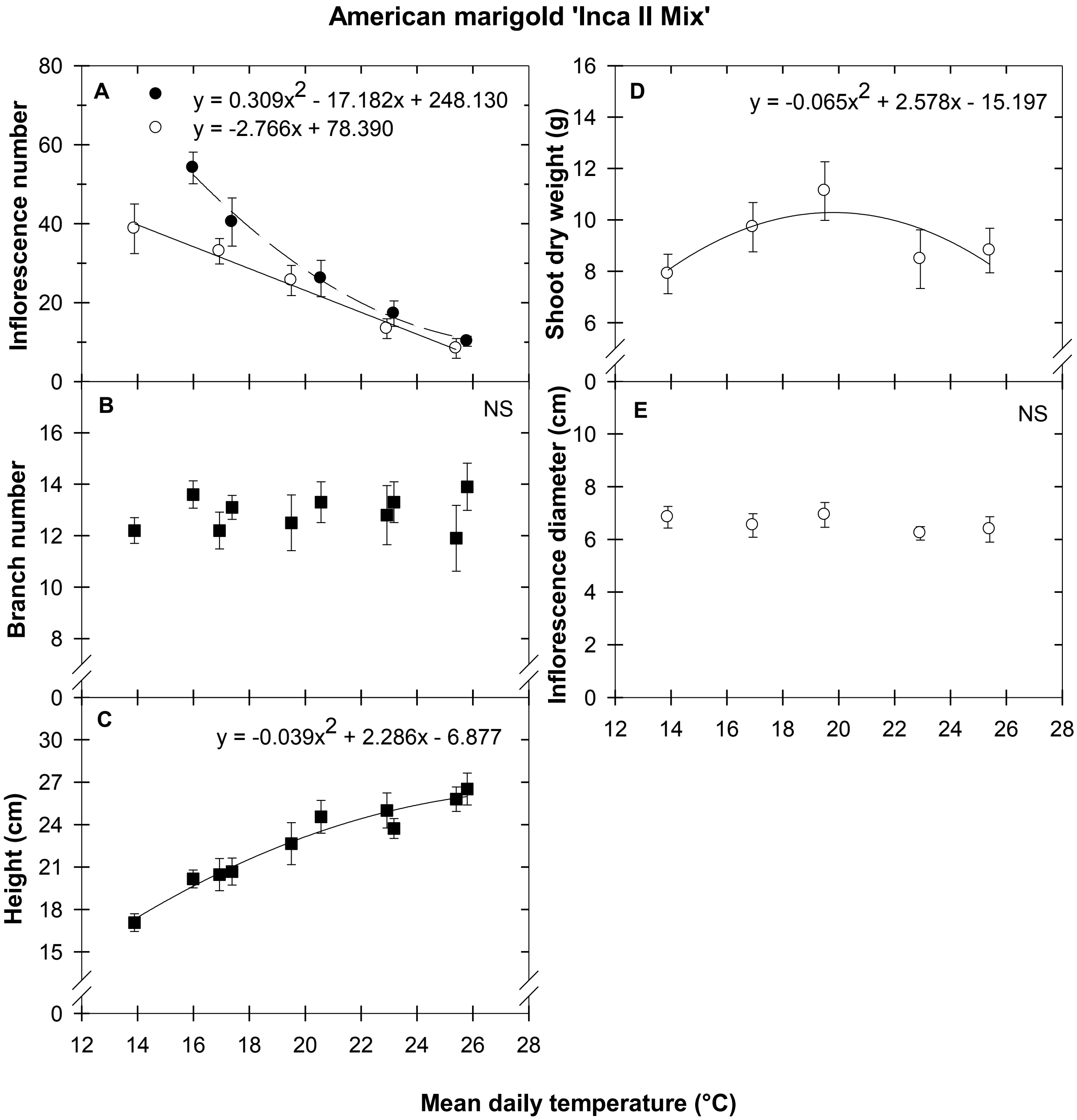

Figure 2.3. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot dry weight (D), and inflorescence diameter (E) in American marigold 'Inca II Mix' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. NS = nonsignificant at $P \leq 0.05$. Dashed and solid lines in panel A represent regression equations for replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

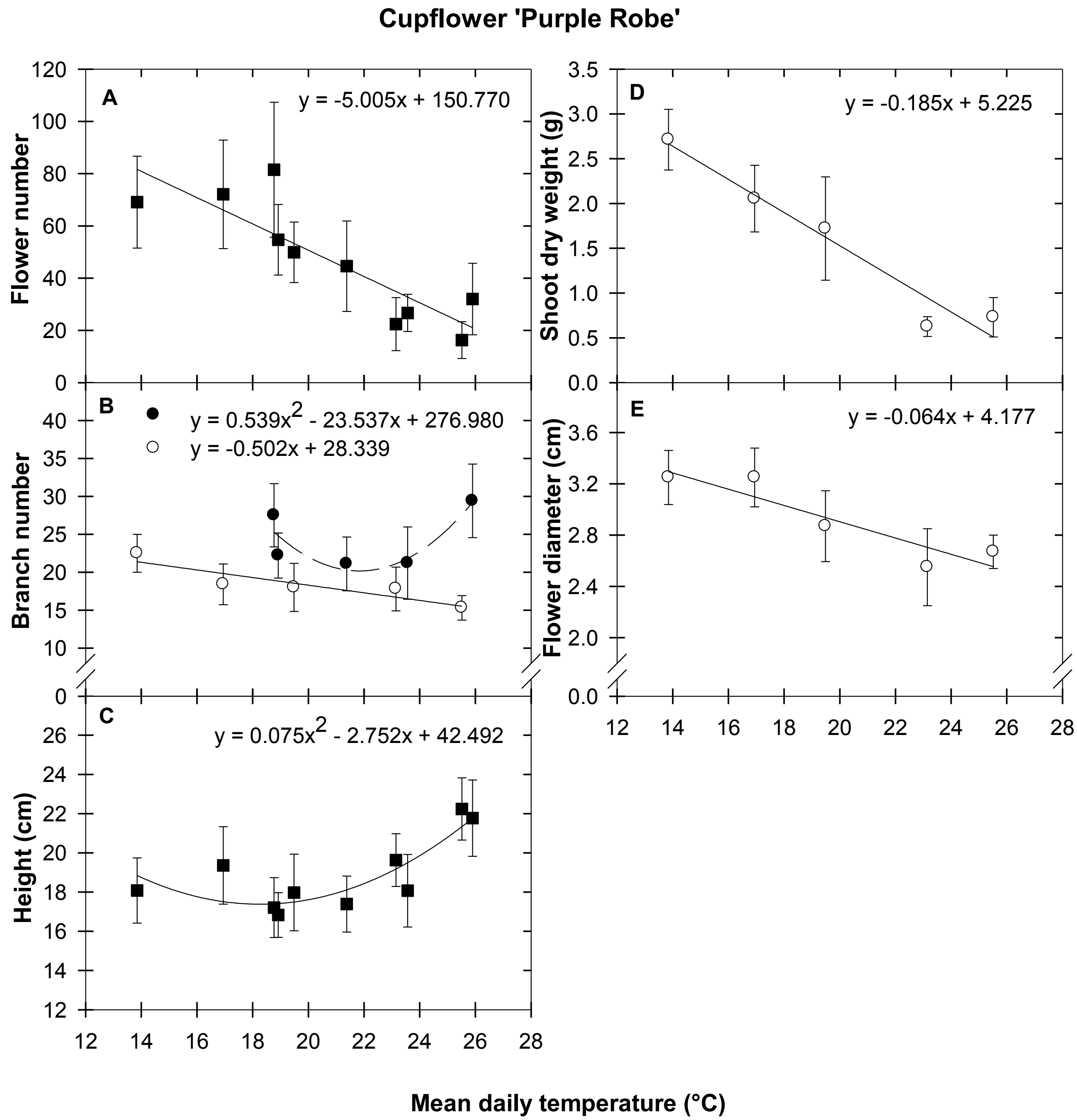

Figure 2.4. The effect of mean daily temperature on flower number (A), axillary branch number (B), height (C), shoot dry weight (D), and flower diameter (E) in cupflower ‘Purple Robe’ for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel B represent regression equations for replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

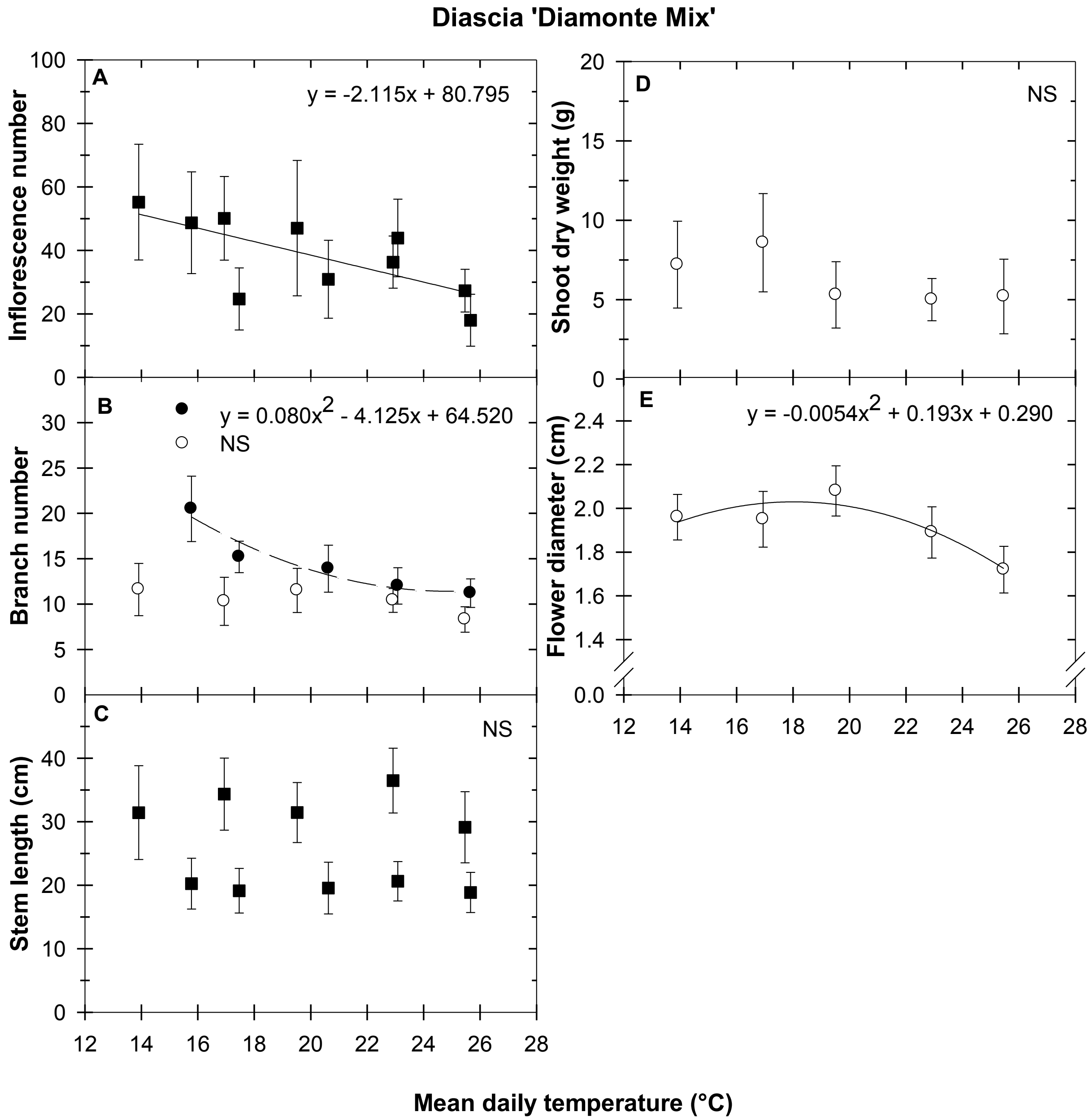

Figure 2.5. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), stem length (C), shoot dry weight (D), and flower diameter (E) in diascia 'Diamonte Mix' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. NS = nonsignificant at $P \leq 0.05$. Dashed lines in panel B represent regression equations for replication 1. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

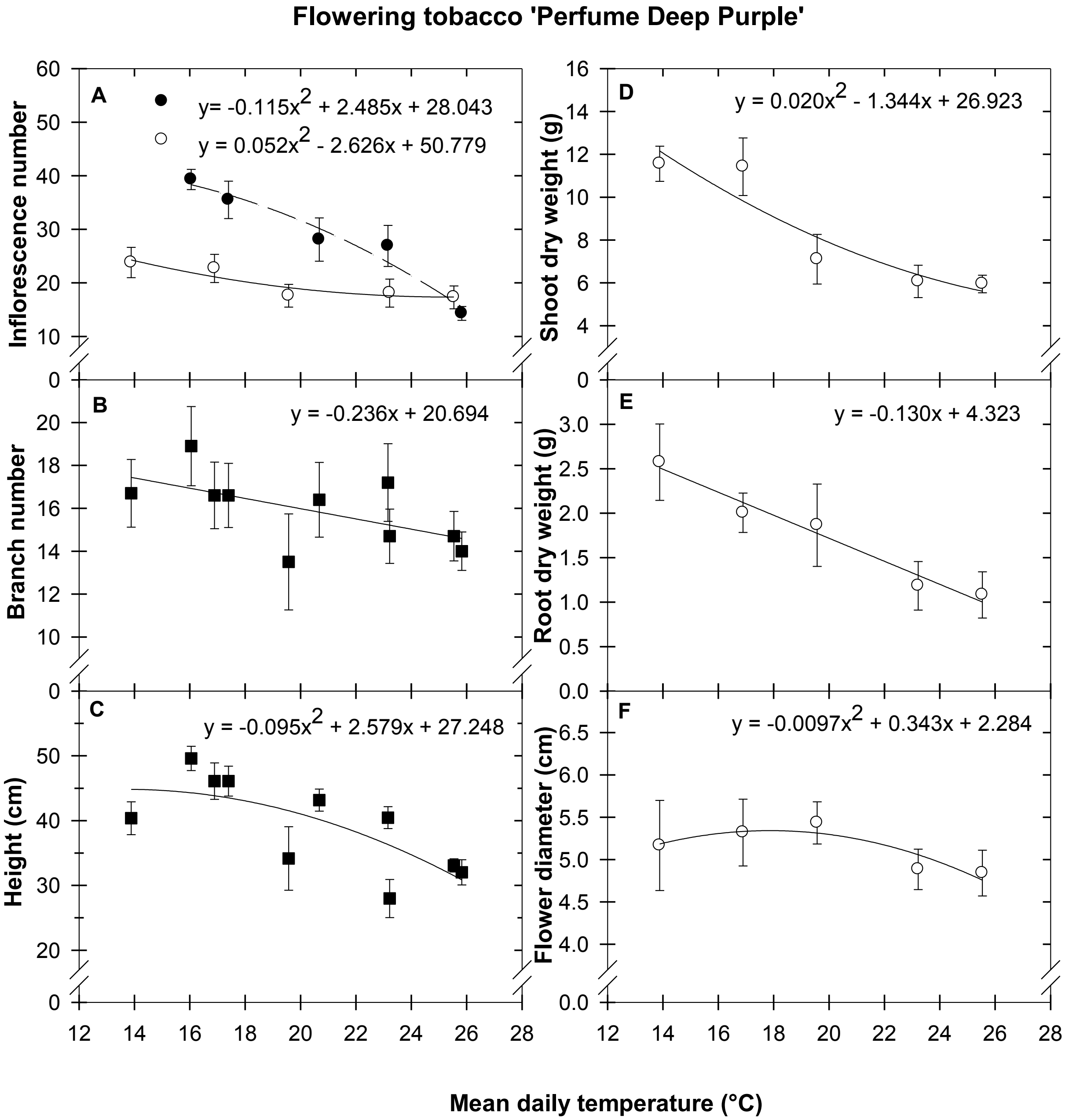

Figure 2.6. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and flower diameter (F) in flowering tobacco 'Perfume Deep Purple' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A represent regression equations for replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol{\cdot}m^{-2}{\cdot}d^{-1}$, respectively.

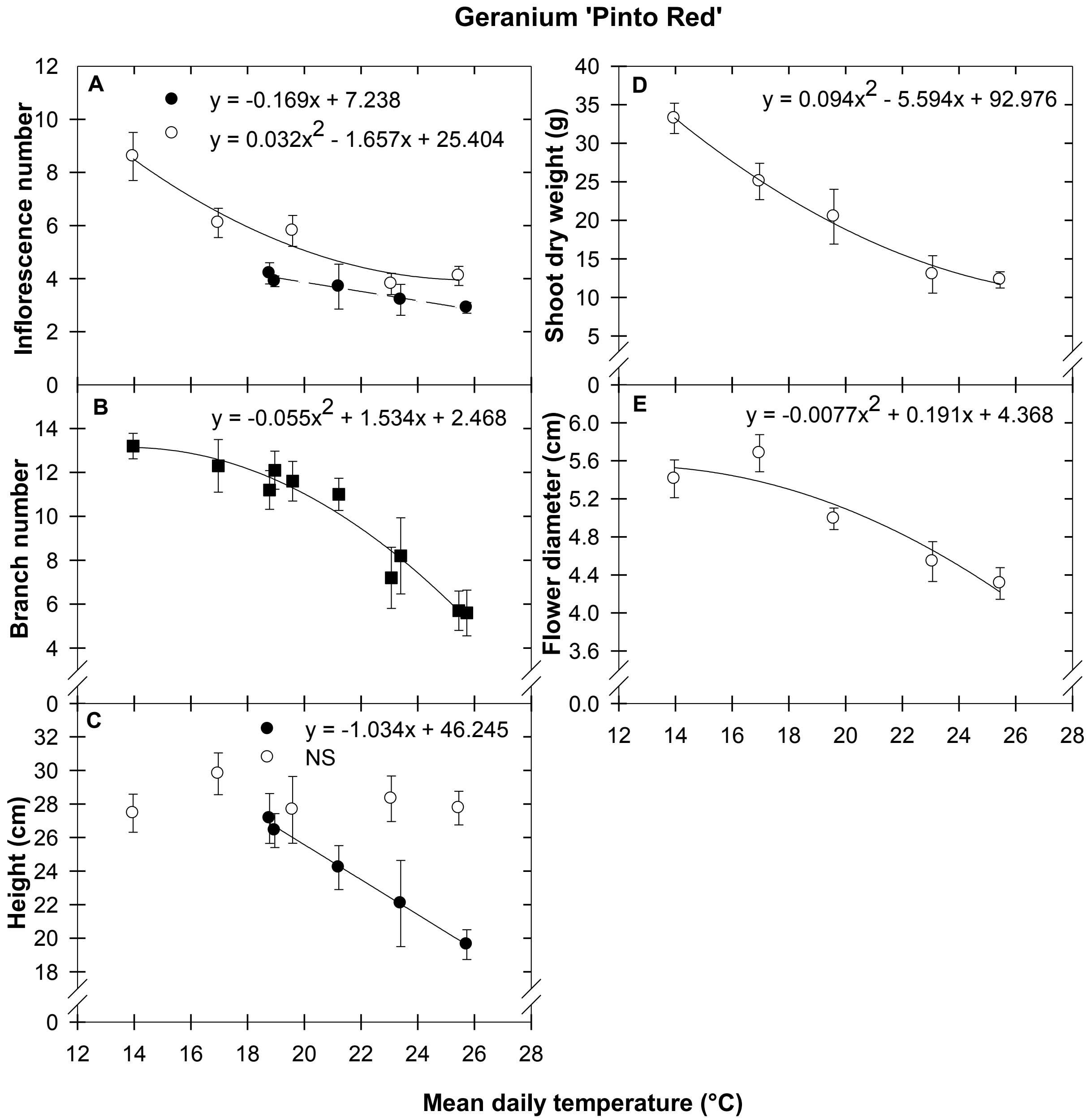

Figure 2.7. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot dry weight (D), and flower diameter (E) in geranium 'Pinto Red' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$, respectively.

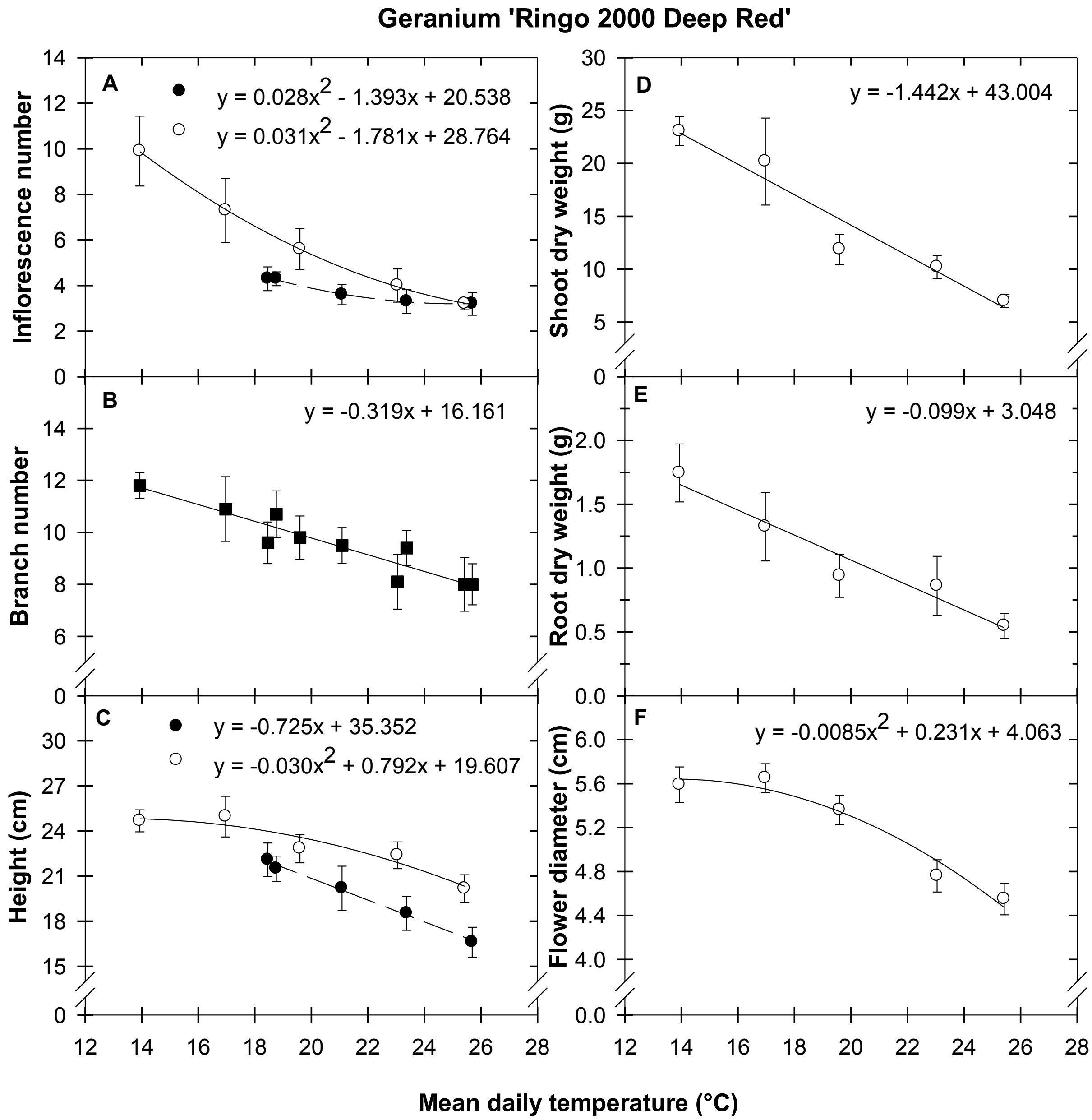

Figure 2.8. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and flower diameter (F) in geranium ‘Ringo 2000 Deep Red’ for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

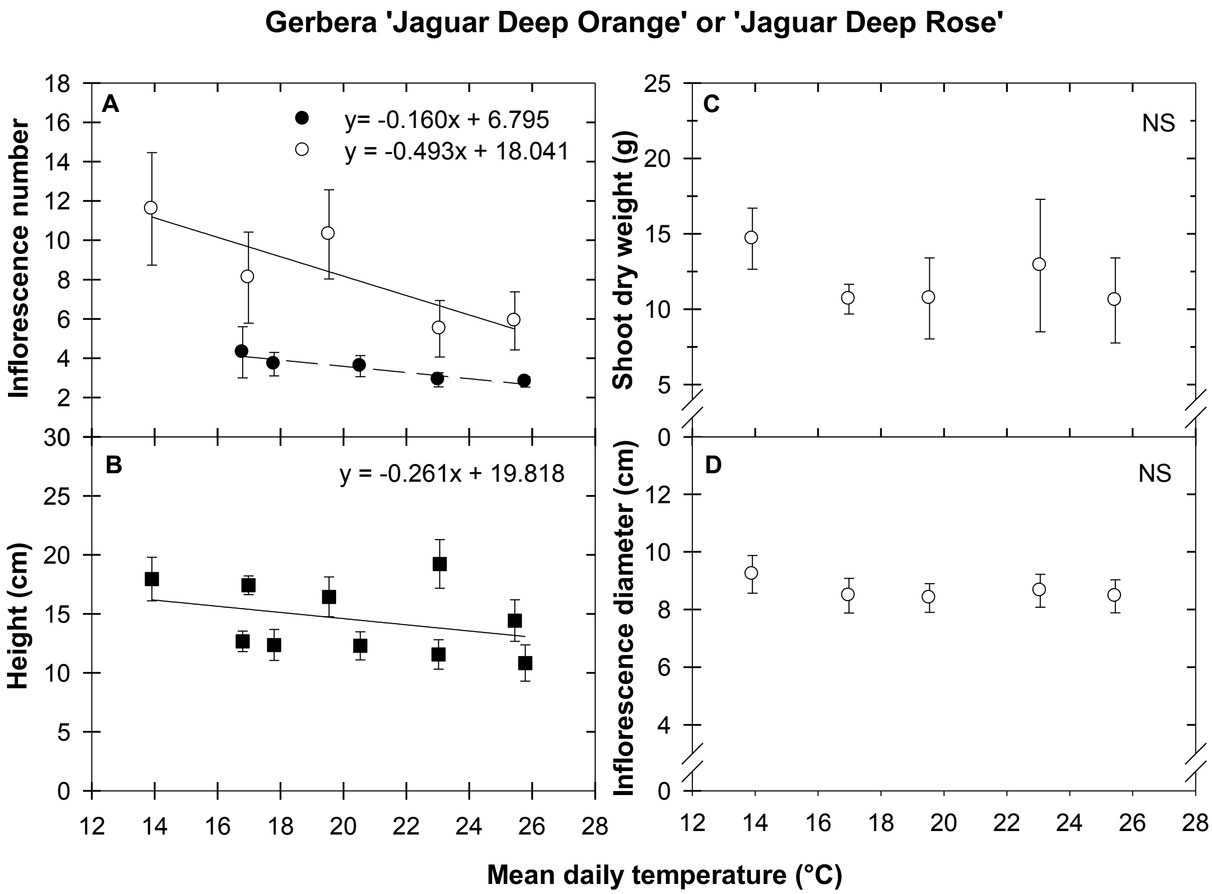

Figure 2.9. The effect of mean daily temperature on inflorescence number (A), height (B), shoot dry weight (C), and inflorescence diameter (D) in gerbera 'Jaguar Deep Orange' for replication 1 (●) or 'Jaguar Deep Rose' for replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. NS = nonsignificant at $P \leq 0.05$. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A represent regression equations for replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

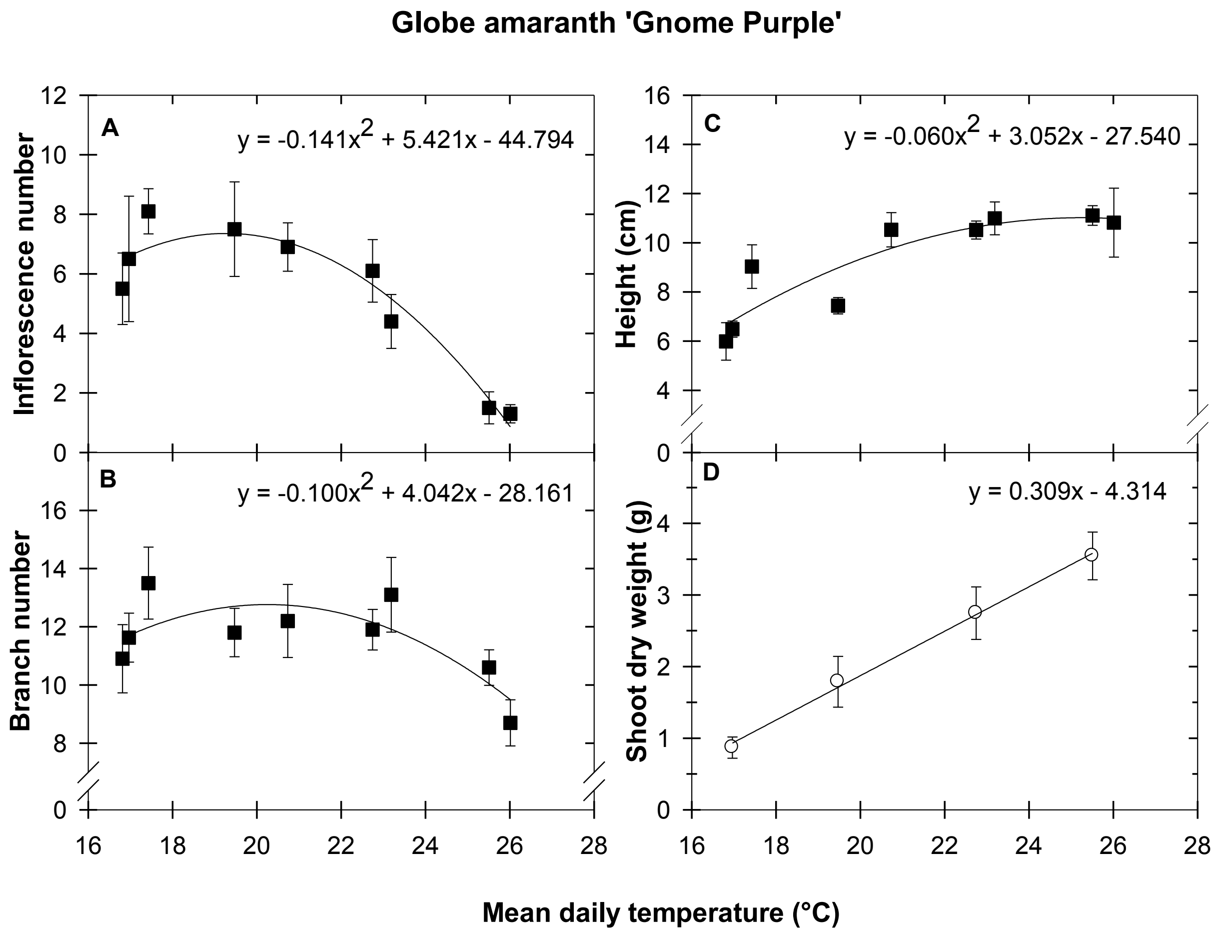

Figure 2.10. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), and shoot dry weight (D) in globe amaranth 'Gnome Purple' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. All plants died at 14 °C, and therefore data could not be collected. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

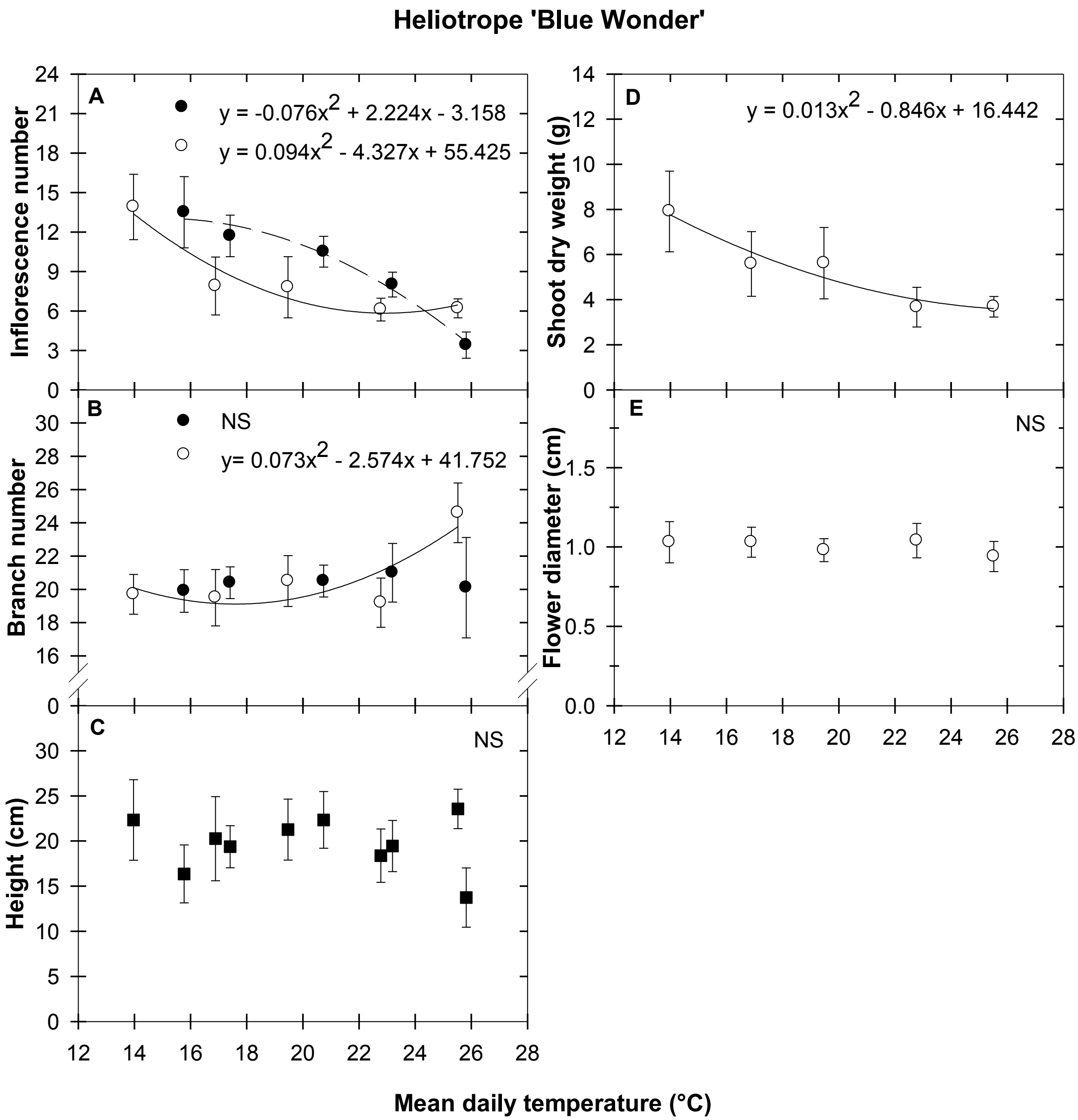

Figure 2.11. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot dry weight (D), and flower diameter (E) in heliotrope ‘Blue Wonder’ for replication 1 (●) and replication 2 (○).When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. NS = nonsignificant at $P \leq 0.05$. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A and B represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

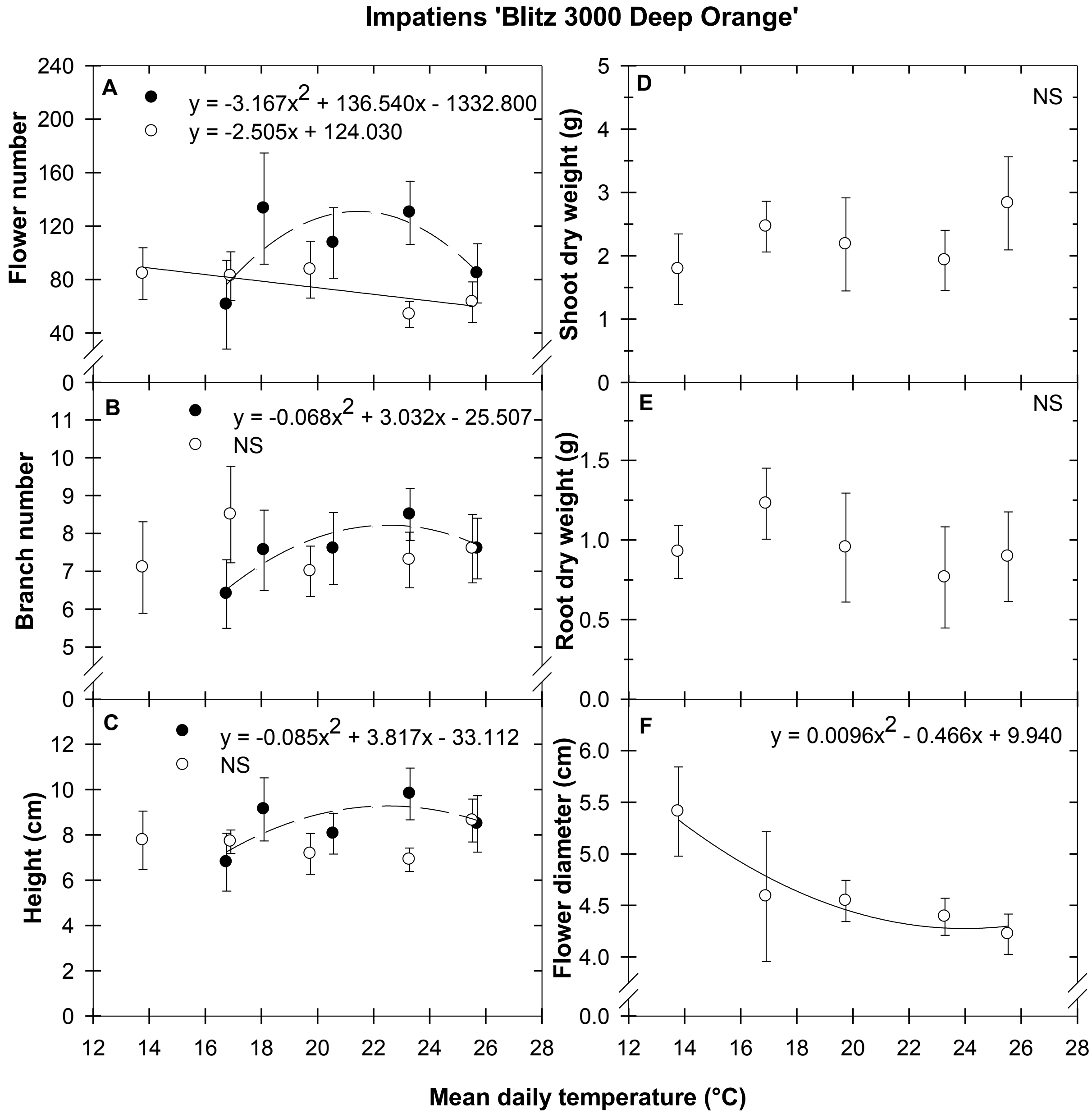

Figure 2.12. The effect of mean daily temperature on flower number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and flower diameter (F) in impatiens ‘Blitz 3000 Deep Orange’ for replication 1 (●) and replication 2 (○). NS = nonsignificant at $P \leq 0.05$. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A, B and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

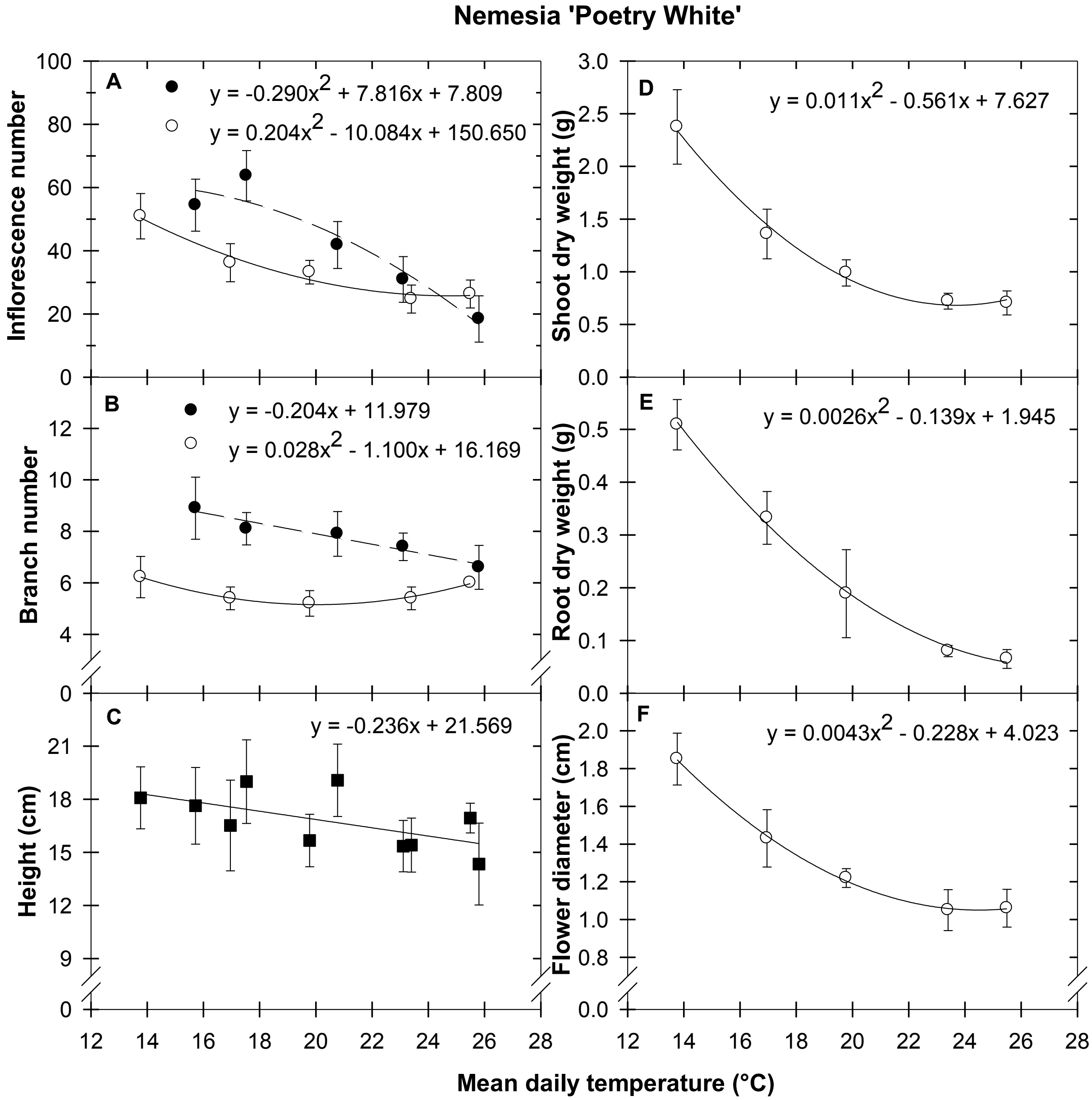

Figure 2.13. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and flower diameter (F) in nemesia 'Poetry White' for replication 1 (●) and replication 2 (○).When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A and B represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

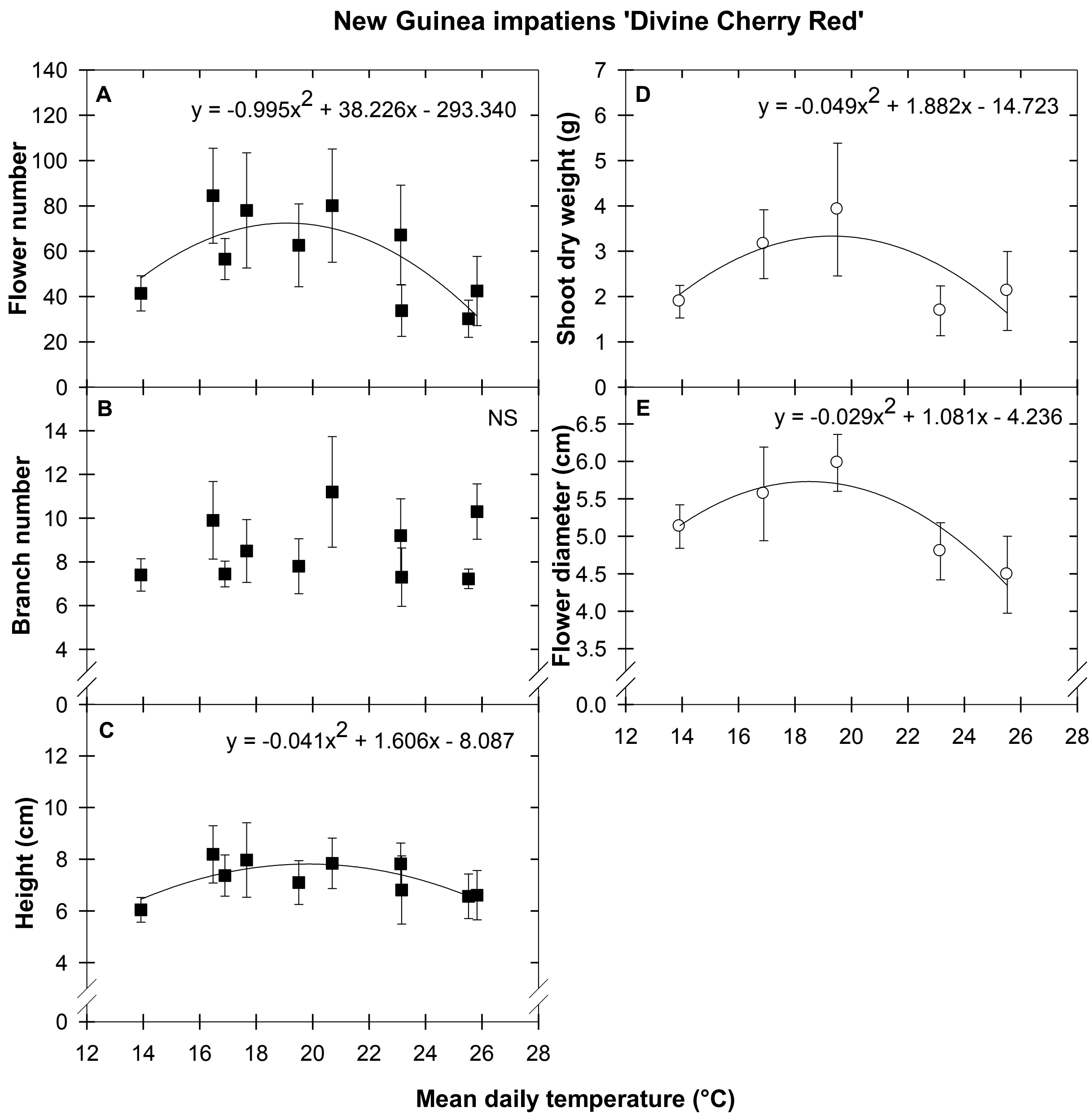

Figure 2.14. The effect of mean daily temperature on flower number (A), axillary branch number (B), height (C), shoot dry weight (D), and flower diameter (E) in New Guinea impatiens 'Divine Cherry Red' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. NS = nonsignificant at $P \leq 0.05$. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

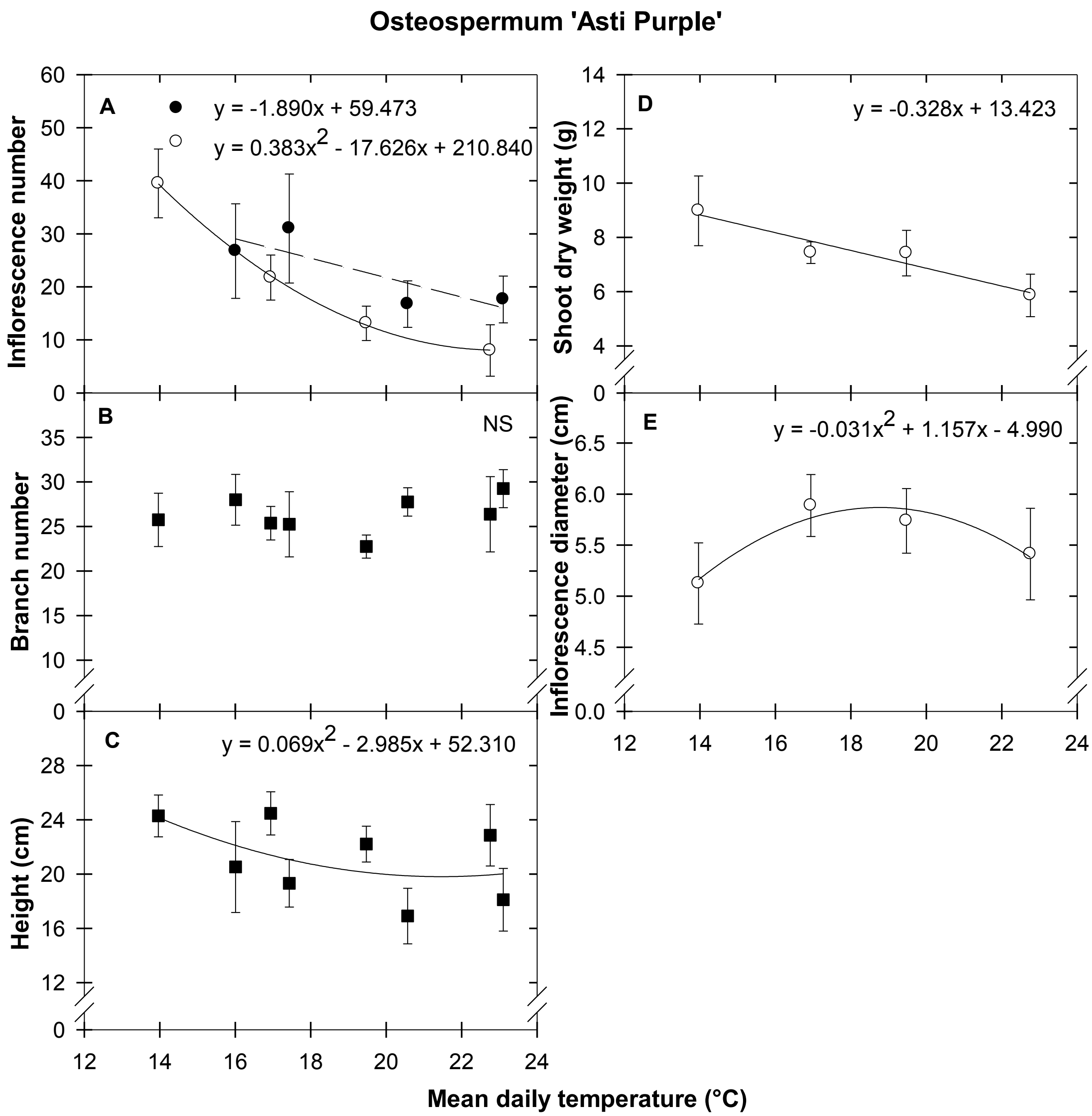

Figure 2.15. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot dry weight (D), and inflorescence diameter (E) in osteospermum ‘Asti Purple’ for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. NS = nonsignificant at $P \leq 0.05$. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A represent regression equations for replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

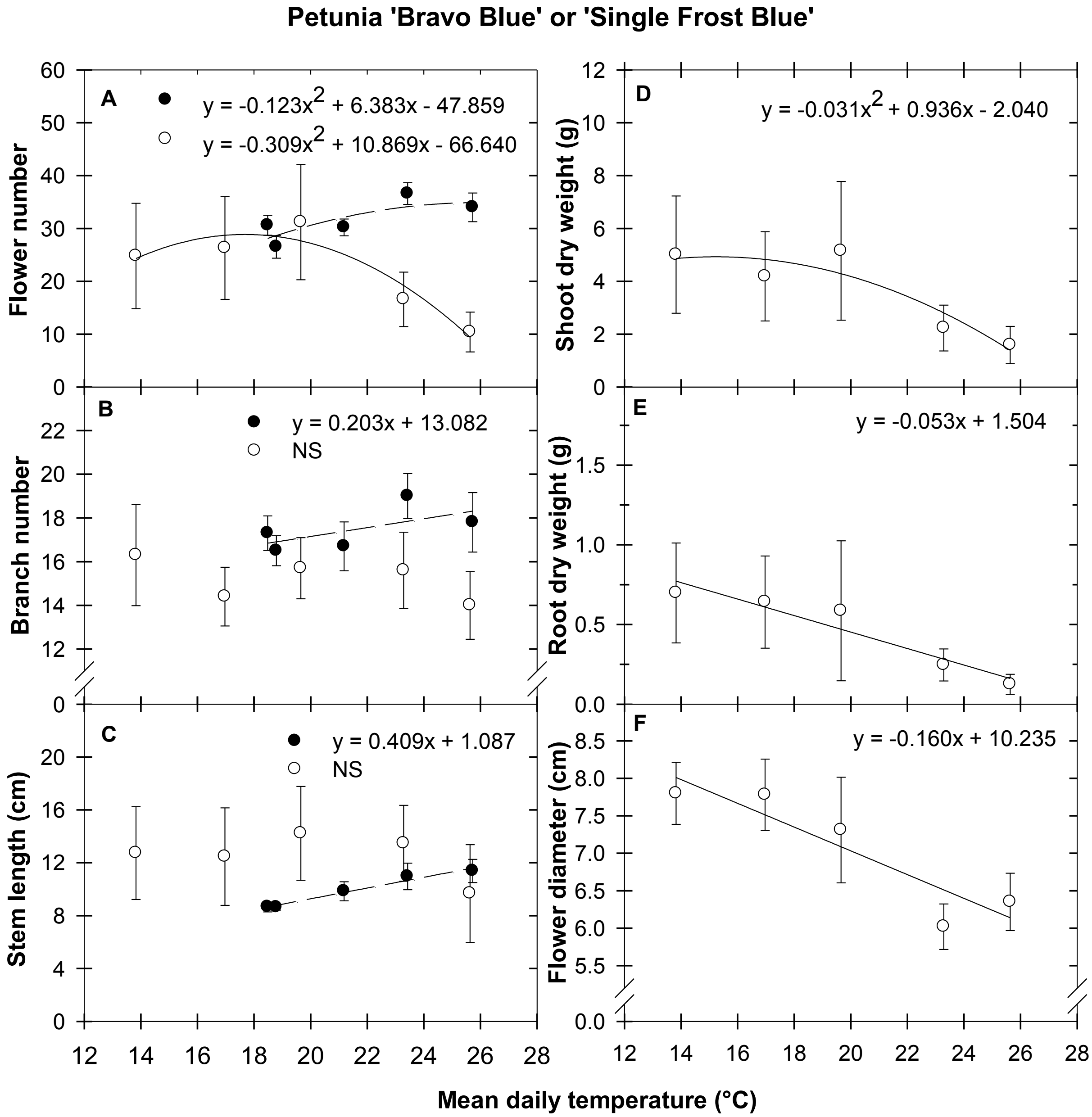

Figure 2.16. The effect of mean daily temperature on flower number (A), axillary branch number (B), stem length (C), shoot and root dry weight (D and E), and flower diameter (F) in petunia ‘Bravo Blue’ or ‘Single Frost Blue’ for replication 1 (●) and replication 2 (○). Each symbol represents the treatment means, and error bars represent 95% confidence intervals. NS = nonsignificant at $P \leq 0.05$. Dashed and solid lines in panel A, B and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol{\cdot}m^{-2}{\cdot}d^{-1}$, respectively.

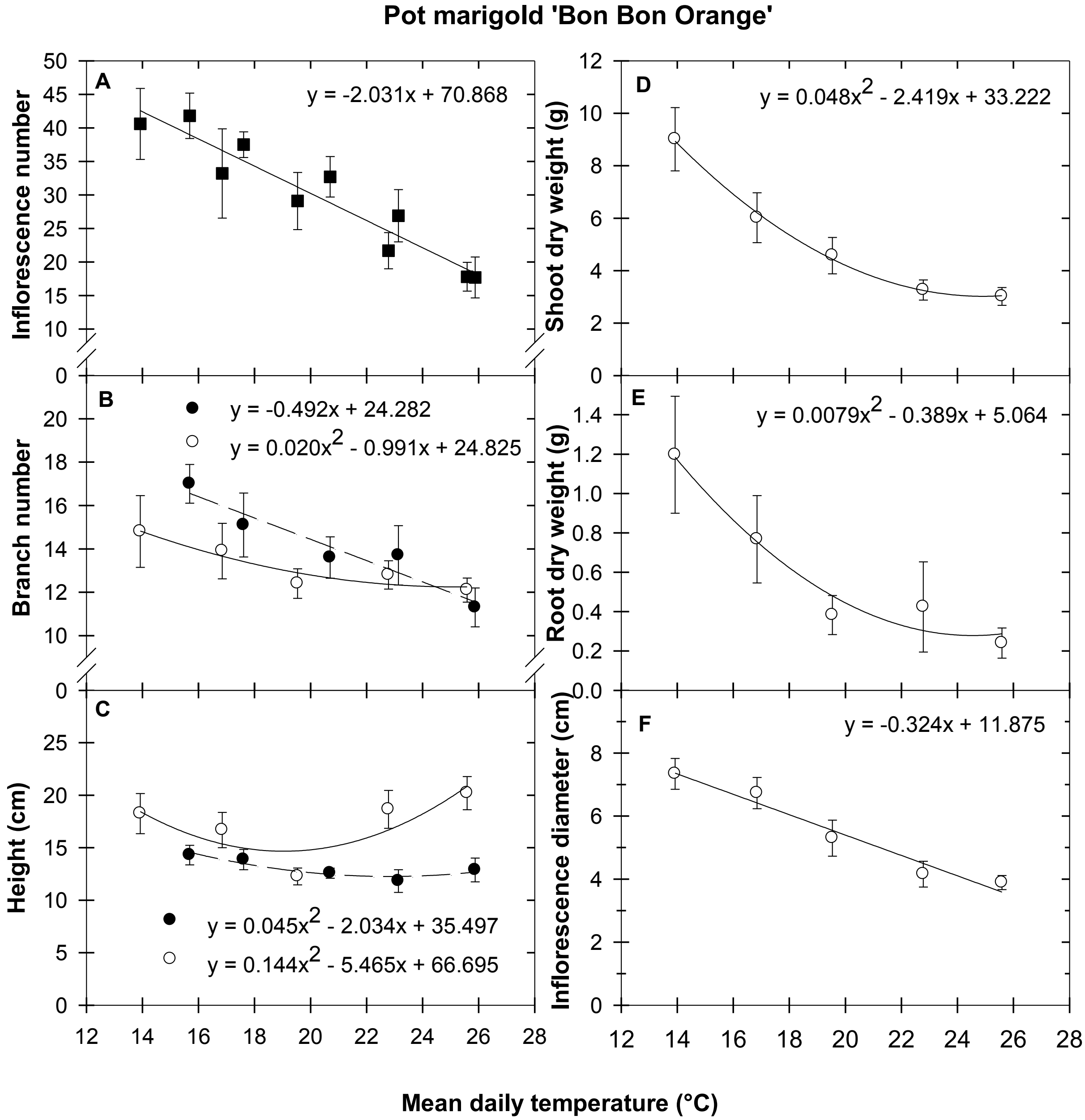

Figure 2.17. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and inflorescence diameter (E) in pot marigold ‘Bon Bon Orange’ for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel B and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

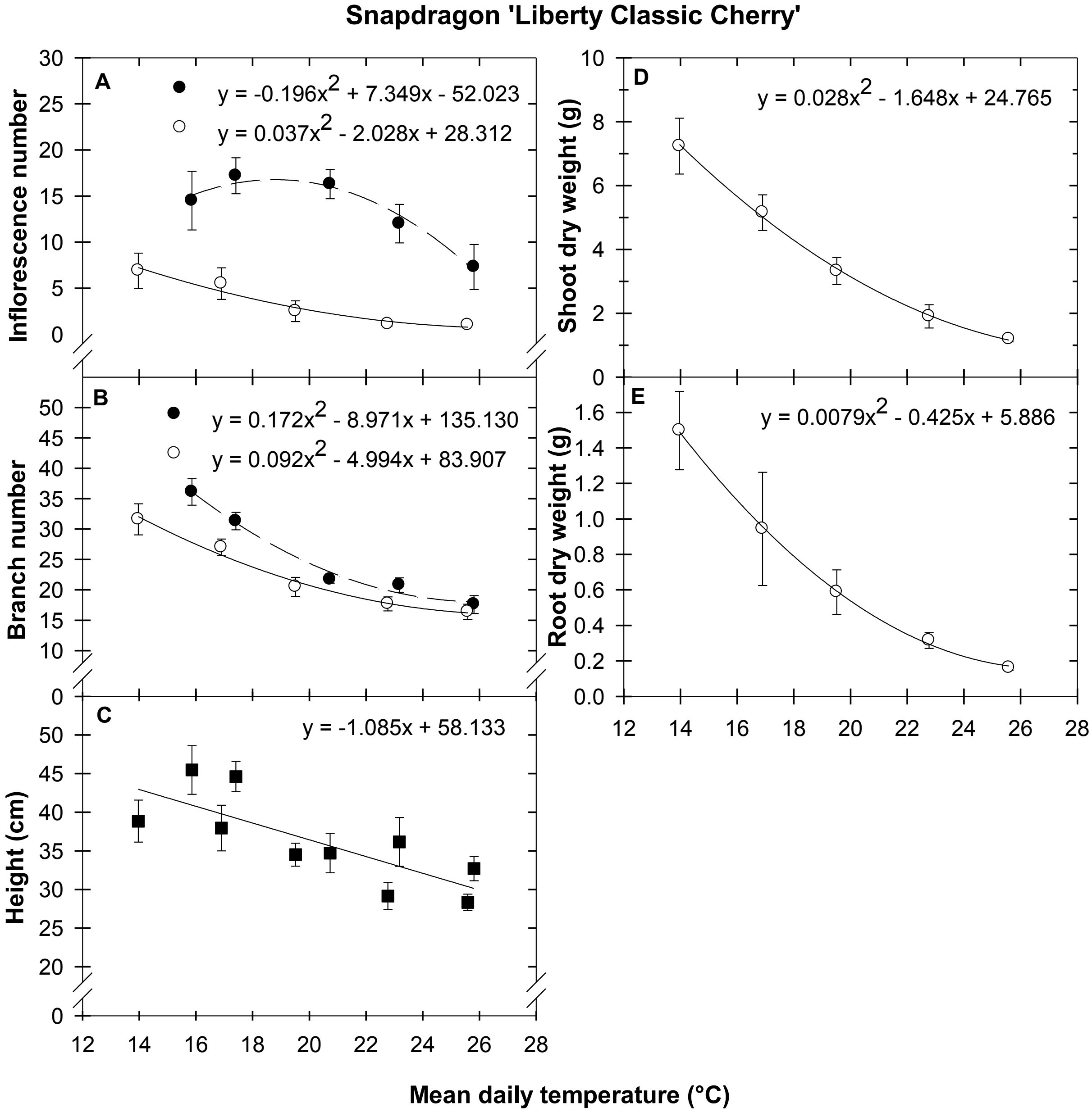

Figure 2.18. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), and shoot and root dry weight (D and E) in snapdragon 'Liberty Classic Cherry' for replication 1 (●) and replication 2 (○). Each symbol represents treatment means, and error bars represent the standard error with 95% confidence levels. Dashed and solid lines in panel A and B represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 mol·m^{-2}·d^{-1}, respectively.

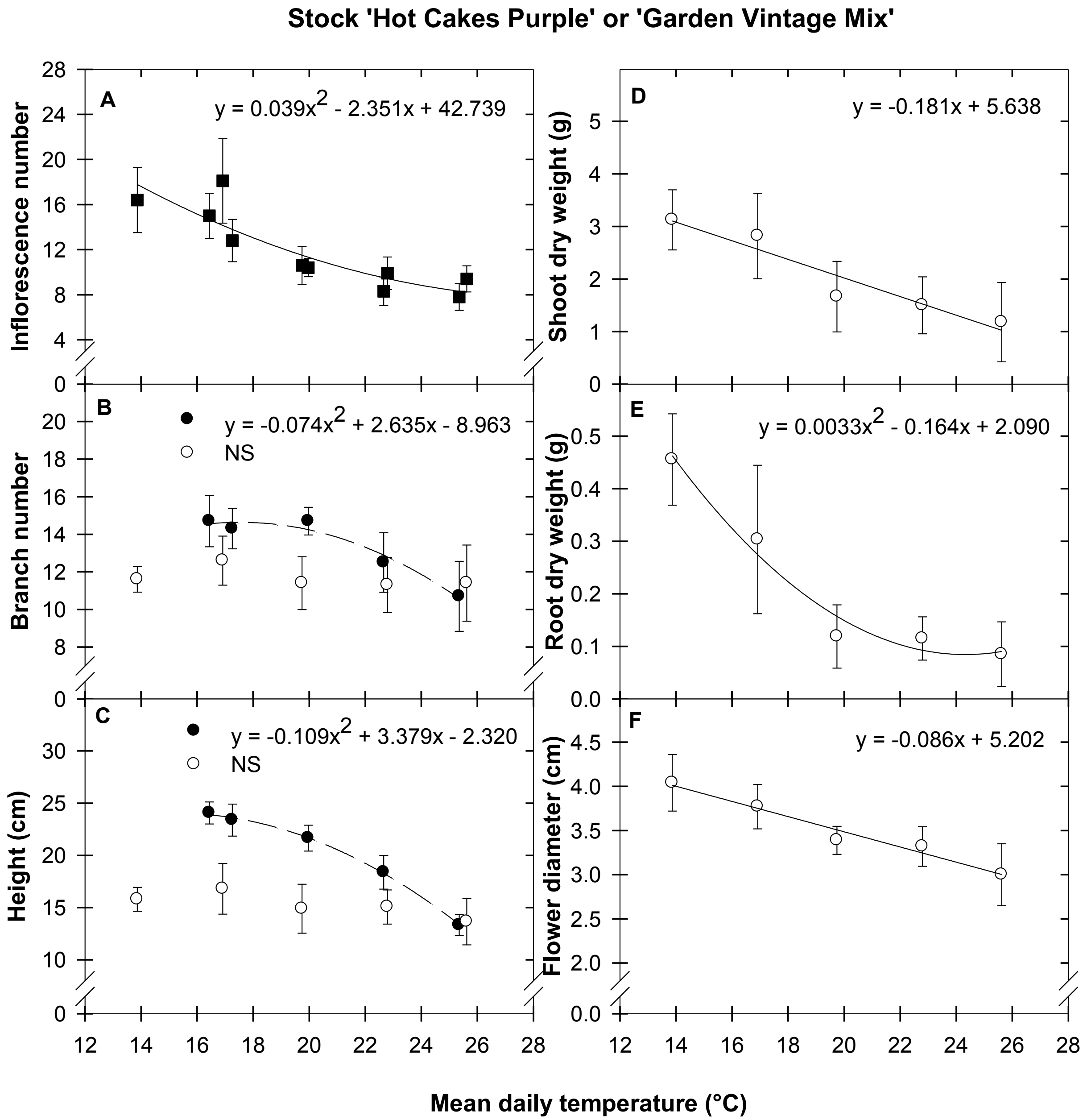

Figure 2.19. The effect of mean daily temperature on inflorescence number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and flower diameter (F) in stock 'Hot Cakes Purple' for replication 1 (●) or 'Garden Vintage Mix' for replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. NS = nonsignificant at $P \leq 0.05$. Dashed and solid lines in panel B and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

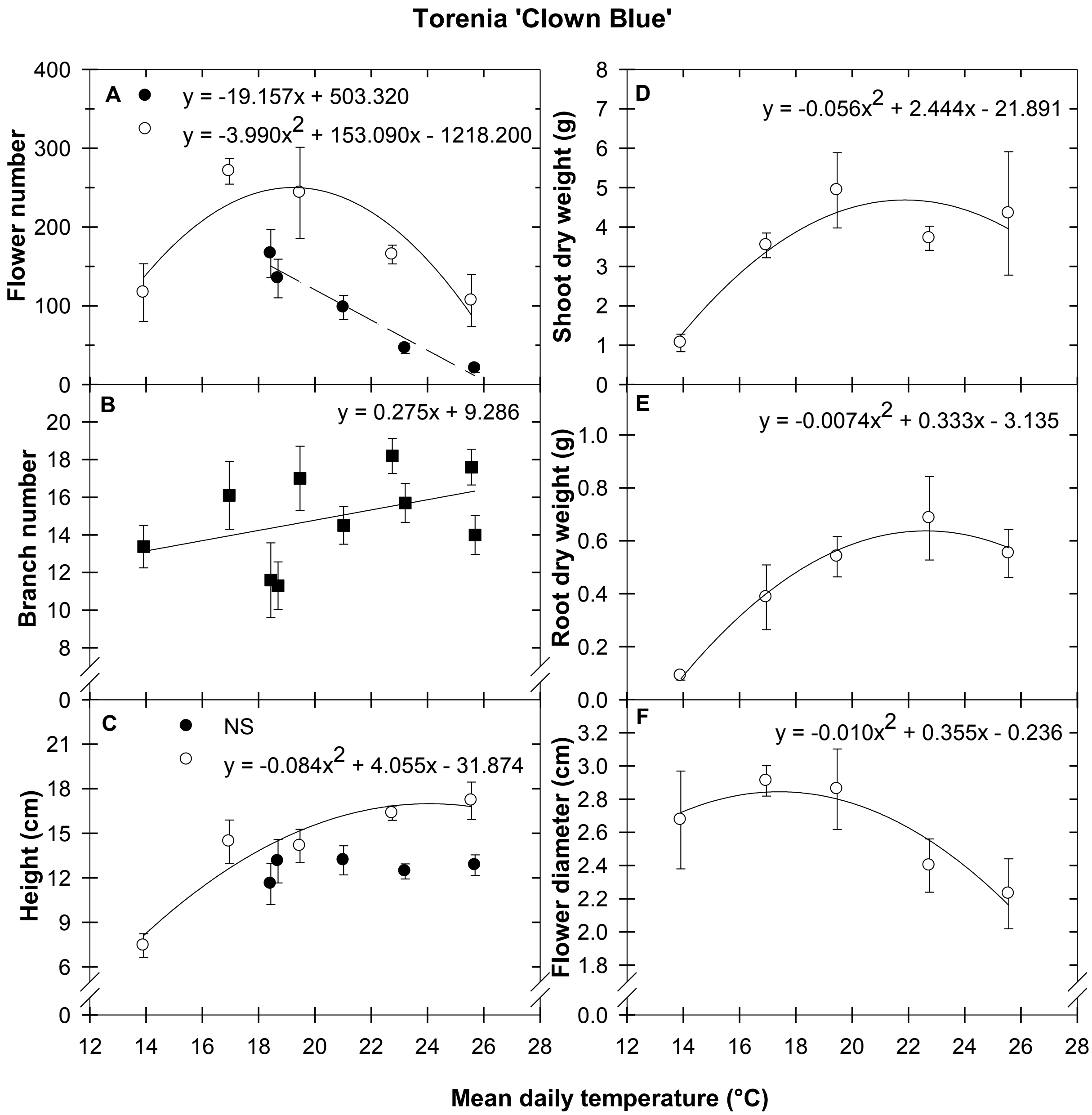

Figure 2.20. The effect of mean daily temperature on flower number (A), axillary branch number (B), height (C), shoot and root dry weight (D and E), and flower diameter (F) in torenia 'Clown Blue' for replication 1 (●) and replication 2 (○). When regression slopes were non-significant between the two replications ($P \leq 0.05$), data was pooled (■) for statistical analysis. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines in panel A and C represent regression equations for each parameter in replication 1 and 2, respectively. The mean daily light integral for replication 1 and 2 was 18 and 9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

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SECTION III

AVERAGE DAILY TEMPERATURE AND TRANSPLANT SIZE AFFECT FLOWERING TIME, QUALITY, AND ESTIMATED PROFITABILITY IN FIVE SPECIES OF ANNUAL BEDDING PLANTS

Average Daily Temperature and Transplant Size Affect Flowering time, Quality, and Estimated Profitability in Five Species of Annual Bedding Plants

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Abstract

Volatile fuel costs and declining profit margins have made it necessary for growers, especially in temperate climates, to improve their production efficiency. A shorter finish production time can potentially reduce the heating, labor and overhead costs. However, shorter crop timing is sometimes offset by reduced crop quality. We grew American marigold (*Tagetes erecta* L.), geranium (*Pelargonium* × *hortorum* L.H. Bailey), gerbera (*Gerbera jamesonii* Bolus ex Hook. f.), osteospermum [*Osteospermum ecklonis* (D.C.) Norl.], and snapdragon (*Antirrhinum majus* L.) in glass-glazed greenhouse compartments to quantify how temperature and transplant size influence flowering time and quality parameters. This information was then used to estimate the net profit per pot and per square meter week for each species. Seedlings from two different transplant size trays (128- versus 288-cell size or 36- versus 128-cell size) were transplanted in 10-cm pots and grown at constant temperature setpoints of 17 or 23 ºC and under a 16-h photoperiod provided by high-pressure sodium lamps. Days to flower from transplant, inflorescence number, inflorescence diameter, branch number, number of nodes below the first open flower, and plant height were measured at first flowering. Flowering time decreased as average daily temperature increased in all five species. American marigold, geranium and snapdragon flowered earlier when grown from a larger compared to a smaller transplant, whereas transplant size did not influence flowering time in gerbera and osteospermum. Inflorescence number and diameter was greater at 17 than 23 ºC in three and four species, respectively, whereas transplant size had little or no influence on these parameters. Estimated net profit per pot was greater at 23 ºC and with the smaller transplant size in all five species. Therefore, transplanting a larger transplant or lowering the greenhouse temperature to save on heating costs is not necessarily a profitable strategy.

Introduction

In the United States, bedding and garden plants are the largest contributors (48%) to the total value of production of all reported floriculture crops, with a 15-state wholesale value of $1.90 billion in 2011 (USDA, 2012). In temperate regions, bedding plants scheduled for spring sales are typically grown beginning in late winter, when high energy inputs are required to maintain greenhouse temperature setpoints. The cost of heating greenhouses in these climates, not surprisingly, accounts for a major share of the indirect cost of greenhouse production (Bartok, 2001). A general assumption is that lowering the greenhouse temperature during the winter can reduce the heating bills, which may not always be true, since the crop production period is lengthened at lower temperatures (Blanchard et al., 2011b).

A shorter crop production cycle in a greenhouse can reduce heating, labor and overhead expenses on a per-crop basis, and can potentially increase profitability by enabling more production cycles in a season. Although fast cropping is an appealing concept, it can result in reduced plant quality, since plants photosynthesize for a shorter duration before flowering. Poor ornamental plant quality characteristics, such as tall and weak stems, few branches, few and small flowers, and reduced biomass, can lower consumer appeal and potentially bring a lower price. Crop production time and in some cases, plant quality, can depend on the species and cultivar (Blanchard, 2009), starting plant size and characteristics (Fisher, 2006), desired finish size, average daily temperature (ADT) (Blanchard and Runkle, 2011), photosynthetic daily light integral (DLI) (Blanchard, 2009; Moccaldi and Runkle, 2007; Pramuk and Runkle, 2005b), and photoperiod (Adams et al., 1997, 1998a). Assuming a plant is grown under an inductive photoperiod, temperature is the primary environmental factor that controls plant development rate and thus, the period of time in which plants can harvest light before flowering.

The number of days (n) to reach a particular developmental event as a function of temperature can be converted to a rate by taking a reciprocal of that number of days (1/n). Average daily temperature influences flowering time by affecting flower initiation, development, or both. Many studies have quantified the influence of temperature on flowering time, and reported a decrease in days to flower (DTF) with an increase in ADT, when ADT is between the species-specific T_{min} (base temperature at or below which the flower development rate is zero) and T_{opt} (optimum temperature at which the flower development rate is maximum) (Adams et al., 1998b, 1998c, 1999; Blanchard and Runkle, 2011; Clough et al., 2001; Kanellos and Pearson, 2000; Miller and Armitage, 2002; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001; Pramuk and Runkle, 2005b). For example, an increase in ADT from 14 to 24 °C decreased flowering time by 47 d in angelonia (*Angelonia angustifolia* Benth.), 18 d in dianthus (*Dianthus chinensis* L.), and 24 d in verbena (*Verbena* × *hybrida* Groenl. & Ruempl.) (Blanchard and Runkle, 2011). A decrease in DTF with an increase in ADT is usually from faster flower development rate (Brøndum and Heins, 1993; Faust and Heins, 1994; Karlsson and Werner, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998), although some plants initiate flowers at a lower node count at higher temperatures (Adams et al., 1998b, 1998c; Mattson and Erwin, 2003). When plants are grown at an ADT above T_{opt}, the flower development rate (reciprocal of DTF) begins to decline until it reaches zero at the species-specific maximum temperature (T_{max}) (Blanchard and Runkle, 2011; Brøndum and Heins, 1993; Faust and Heins, 1994; Semeniuk, 1975).

In addition to plant development, temperature also influences plant quality parameters including flower number and size, branch number, and plant height. Several studies have reported a decrease in quality parameters of ornamental crops with an increase in ADT when grown at the same or similar average DLI (Blanchard et al., 2011a, 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001; Pramuk and Runkle, 2005b). For example, as ADT increased from 16 to 26 °C inflorescence number decreased by 80% in largeflower tickseed (*Coreopsis grandiflora* Hogg ex Sweet), 55% in Shasta daisy [*Leucanthemum* ×*superbum* (Bergmans ex J.W. Ingram)] and 75% in black-eyed Susan (*Rudbeckia fulgida* Aiton) (Yuan et al., 1998). Similarly, each degree increase in ADT linearly decreased flower diameter by 0.97 mm in tussock bellflower (*Campanula carpatica* Jacq) 'Blue Clips' (under 10.8 $mol{\cdot}m^{-2}{\cdot}d^{-1}$) (Niu et al., 2001), 1.42 cm in dahlia (*Dahlia pinnata* Cav.) 'Royal Dahlietta Yellow' (Brøndum and Heins, 1993), and branch number by 0.3 in petunia (*Petunia* × *hybrida* Vilm.-Andr.) 'Dreams Neon Rose' (Mattson and Erwin, 2003).

Many studies have investigated the influence of two or more environmental factors and their interaction on flowering time and quality of annual bedding plants (Adams et al., 1997, 1998a; Moccaldi and Runkle 2007; Pramuk and Runkle, 2005b). For example, Moccaldi and Runkle (2007) and Pramuk and Runkle (2005b) developed crop models to predict the effect of ADT and DLI on DTF and plant quality parameters such as flower number and diameter, shoot mass, and plant height. The effect of environmental factors such as ADT, DLI, and photoperiod on flowering time and plant quality parameters has been reported for numerous bedding plants, but there is little published information on the influence of transplant size and temperature on these parameters.

Bedding plants are commercially sold in different transplant sizes that commonly range from 512-cell (3.1-mL) to 36-cell (42.3-mL) trays, depending on the species and grower preferences. Practical experience and some initial research data (Fisher, 2006) indicate that a larger, more mature plant flowers earlier than a smaller, less-developed plant. A shorter crop production period from transplant has many potential advantages: lower labor, heating and overhead costs; delayed transplanting in the winter, which can reduce heating costs if outdoor temperatures later in the year are higher; and increased number of production cycles in a season. However, faster flowering from use of a larger transplant is at least partly offset by the higher price of the larger transplant (Fisher, 2006). In addition, the influence of starting size of plants on plant quality parameters has not been published to our knowledge in annual bedding plants when grown under the same environmental conditions. Therefore, research-based information was needed to quantify the differences in flowering time and plant quality, as well as further improve the reliability of scheduling bedding plants. The objectives of this research were 1) to study the effect of ADT and transplant size on flowering time and plant quality of five species of popular bedding plants, and 2) to estimate the potential change in net profit per pot and per square meter week in growing a larger versus a smaller transplant at two temperature treatments.

Materials and Methods

Plant material. Experimental protocol, data collection and data analysis were similar to that reported by Blanchard and Runkle (2011) and Pramuk and Runkle (2005b). Seedlings of American marigold (*Tagetes erecta* L. 'Inca II Mix'), geranium (*Pelargonium ×hortorum* L.H.Bailey 'Ringo 2000 Deep Red'), gerbera (*Gerbera jamesonii* Bolus ex Hook. f. 'Jaguar Deep Orange'), osteospermum [*Osteospermum ecklonis* (D.C.) Norl. 'Asti Purple'], and snapdragon (*Antirrhinum majus* L. 'Rocket Mix') were grown in two different tray sizes [128-cell (12 mL) and 288-cell (6 mL) or 36-cell (42 mL) and 128-cell], depending on species (Table 3.1), by a commercial greenhouse (C. Raker & Sons, Litchfield, MI) and received at Michigan State University (MSU) on 26 October 2010. Production was scheduled by the commercial producer such that the seedlings were ready for transplant when received at MSU. On receipt the plants were immediately transplanted and grown in greenhouses maintained at two different temperature set points.

The experiment was repeated in spring 2011 to generate data under different DLI conditions. Seedlings in this replicate were received at MSU on 3 March 2011 and were grown in a glass-glazed greenhouse at a constant temperature setpoint of 20 °C under the natural photoperiod (lat. 43 °N) until the leaf number for each species and for each transplant size was similar to that of the transplants grown previously. Once the desired leaf count was achieved (Table 3.1), the seedlings were transplanted and grown in separate glass-glazed greenhouse compartments maintained at different temperature set points.

Greenhouse environments. Seedlings were transplanted into 10-cm round containers (480-mL) filled with a peat-based medium (Suremix, Michigan Grower Products, Galesburg, MI). The seedlings were thinned to one plant per cell prior to transplant and 10 plants of each species were grown at constant temperature set points of 17 or 23 °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 (HPS) lamps from 0600 to 2200 HR that provided a *PPF* of 80 to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In each greenhouse compartment, a shielded and aspirated 0.13 mm type E thermocouple (Omega Engineering, Stamford, CT) recorded the air temperature and a line quantum sensor containing 10 photodiodes (Apogee Instruments) placed at canopy height (22 cm above bench height) measured the *PPF*. A CR10 datalogger (Campbell Scientific, Logan, UT) collected the environmental data every 10 s and hourly averages were recorded. Actual average air temperatures during the fall and spring experiments were 17.0 or 23.1 and 18.6 or 22.7 ºC, respectively. The mean DLIs during the fall and spring experiments were 10.0 and 15.0 mol·m^{-2}·d^{-1}, respectively. Average DIF values (day – night temperature) ranged from 0.3 to 0.7 ºC and 0.7 to 2.3 ºC in the fall and spring experiments, respectively. Vapor pressure deficit was maintained between 0.7 and 1.2 kPa by steam injection at night. Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing (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 Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Data collection and analysis. When each plant flowered according to the individual characteristics for each species (Table 3.1), the date of flowering was recorded and DTF from transplant was calculated for each species. Inflorescence number, inflorescence diameter, axillary branch number, number of nodes below the first open flower on the primary stem, and plant height (from media surface to tallest inflorescence) were also recorded at first open flower. Branch number and inflorescence diameter were not recorded in gerbera and snapdragon, respectively. The experiment was set up as a split-plot design; two temperature treatments (whole plot factor) were randomly assigned to the greenhouse compartments, and two transplant size (sub-plot factor) treatments were randomly assigned to the experimental units (plants) within each temperature treatment. SAS (SAS Institute, Cary, N.C.) was used to analyze the experimental data. Mean separation using Tukey's honestly significant difference test at $P \leq 0.05$ was performed on all the data to compare differences between treatments. Data were pooled when there were no significant replicate and treatment interactions.

Cost estimation. Costs were estimated for a finish market date of April 1 using the procedure described by Fisher et al. (2006). Production time was calculated based on the average days to flower for each treatment, and assumed a 16-h photoperiod and an average DLI of ≥10

$mol{\cdot}m^{-2}{\cdot}d^{-1}$. Greenhouse heating costs were estimated for Grand Rapids, MI using Virtual Grower software version 2.51 (Frantz et al., 2010; USDA−ARS, 2009). Greenhouse characteristics used for heating cost estimations were the same as those used by Blanchard et al. (2011b): eight spans 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 at US$ $0.36{\cdot}m^{-3}$, 50 % heater efficiency, no energy curtain, an air infiltration rate of 1.0 h^{-1}, and constant temperature setpoint of 17 and 23 ºC. Price of individual transplant sizes was obtained from a commercial producer (C. Raker & Sons), although prices could vary depending on volume, shipping and handling, and distributors. Each 10-cm pot was assumed to occupy 0.023 m^2 of space, which is a typical spacing used by commercial growers. A greenhouse space use efficiency of 80% was assumed, and labor and overhead expenses were estimated from Fisher (2006). The estimated labor and overhead cost of $\$3.25{\cdot}m^{-2}{\cdot}week^{-1}$ was calculated by updating the original estimate of $\$2.90{\cdot}m^{-2}{\cdot}week^{-1}$ from Fisher (2006) using the Consumer Price Index increase of 12% between 2006 and 2011 (USDL, 2012). This figure was further updated to per m^2 per week by dividing $3.25 by the space use efficiency (0.80) to give the final labor and overhead (not including heating and lighting) costs of $4.06. To estimate the net profit per pot and per square meter week, the wholesale sales price for each 10-cm pot was assumed to be $1.25 for American marigold, geranium, and snapdragon (USDA, 2012), and $1.50 for gerbera and osteospermum [the starting material was generally more expensive (Table 3.2), and these plants often have a greater commercial value]. Net profit per pot was calculated by subtracting the total cost from the wholesale price, and net profit per square meter week was calculated by dividing the net profit per square meter (number of pots per square meter × net profit per pot) by the production time in weeks. Lighting and other variable costs (pots, media, and tags), the potential change in net profit from additional crop turns or differences in plant quality (and thus, sales price) were not considered.

Results

American marigold. Flowering time decreased by 7 or 8 d for larger (128-cell) compared to smaller (288-cell) transplants; and by 12 or 13 d when plants were grown at 23 versus 17 ºC (Figure 3.1A). Inflorescence number and diameter at flowering were similar between transplant sizes, but were 68 to 70 % and 21 to 32 % greater at 17 than 23 ºC, respectively. Temperature and transplant size interacted to influence plant height, branch number, and leaf number at first flowering. Transplant size had no influence on plant height, and number of branches and leaves at 17 ºC, but smaller transplants grown at 23 ºC were taller, had greater branching, and developed more leaves than larger transplants (Figure 3.1C, D). Plant height at flowering was greater when grown at 23 ºC, irrespective of transplant size. ADT did not affect branch number and leaf number below first open flower in larger transplants, but smaller transplants formed 10% and 24% fewer branches and leaves, respectively when grown at 17 than 23 ºC.

Geranium. Temperature had a greater influence on flowering time than transplant size (Figure 3.2A). Plants grown from a 128-cell tray (with 6 leaves) flowered 1 to 5 d earlier compared to plants grown from a 288-cell tray (with 4 leaves). On the other hand, plants grown at 23 °C flowered 17 to 20 d earlier than those grown at 17 °C. Inflorescence number was similar between transplant sizes when grown at 23 ºC, but larger transplants developed significantly more inflorescences than smaller transplants when grown at 17 ºC (Figure 3.2B). Similarly, plant height was similar between transplant sizes when grown at 17 ºC, but 128-cell transplants were 10% taller than 288-cell transplants when grown at 23 ºC (Figure 3.2C). Both transplant sizes had 45 to 47% fewer inflorescences and were 10 to 16% shorter at flowering when grown at 23 compared to 17 ºC. Transplant size did not significantly influence inflorescence diameter, whereas plants grown at 23 ºC had 7 to 9% smaller inflorescences than those grown at 17 ºC (Figure 3.2E). Temperature and transplant size did not influence leaf number below the first open flower (Figure 3.2F). Branch number was not significantly affected by transplant size in the first replication, but larger transplants had greater branching in the second replication (Figure 3.2D). Similarly, ADT did not significantly influence branch number in smaller transplants, whereas lower compared to higher temperature promoted greater branching in larger transplants in the first replication.

Gerbera. Flowering time was 10 or 11 d shorter at 23 versus 17 ºC, but was not influenced by transplant size (Figure 3.3A). Temperature and transplant size did not influence inflorescence number and leaf number below the first open inflorescence (Figure 3.3B, E), whereas these parameters interacted to influence plant height at first flowering (Figure 3.3C). Plant height was greater at 23 °C for larger (36-cell) transplants, but was similar when starting from smaller (128-cell) transplants. Inflorescence diameter was greater in plants grown at 17°C than 128-cell transplants grown at 23 °C (Figure 3.3D).

Osteospermum. Transplant size had no effect on flowering time, but the higher temperature accelerated flowering time by 8 and 11 d in smaller (128-cell) and larger (36-cell) transplants, respectively (Figure 3.4A). Temperature and transplant size did not affect inflorescence number and branch number at first flowering (Figure 3.4B, D). Larger transplants grown at 23 ºC were 20% shorter that those grown at 17 ºC (Figure 3.4C). In contrast, ADT did not influence plant height at flowering in smaller transplants. Inflorescence diameter was similar between transplant sizes, but plants grown at 17 ºC had 11 to 23% larger inflorescences than those grown at 23 ºC (Figure 3.4E). Plants from 36-cell transplants and grown at 23 °C developed more leaves before flowering than either transplant size grown at 17 °C (Figure 3.4F).

Snapdragon. The higher temperature and larger (128-cell) transplant size accelerated flowering time compared to lower temperature and smaller (288-cell) transplant size (Figure 3.5A). Plants grown at 23 ºC flowered 13 or 14 d earlier than those grown at 17 ºC, whereas the larger transplants flowered 7 or 8 d earlier than the smaller transplants. Inflorescence number was variable among all treatments, but 288-cell transplants grown at 17 °C developed more inflorescences than either transplant size grown at 23 °C (Figure 3.5B). Plant height was similar between transplant sizes at 17 ºC, but smaller transplants were significantly taller than larger transplants at 23 ºC (Figure 3.5C). Plants grown at 17 ºC had 13 to 26% more branching than those grown at 23 ºC (Figure 3.5D). At 17 ºC, larger transplants formed significantly fewer branches than the smaller transplants, whereas branch number was similar between transplant sizes grown at 23 ºC. Larger transplants developed significantly fewer nodes before flowering compared to smaller transplants, irrespective of temperature (Figure 3.5E). ADT did not influence leaf number in larger transplants, whereas smaller transplants developed more leaves when grown at 17 compared to 23 ºC.

Economic analysis. On a per-pot basis, the estimated net profit was usually higher (or the net loss was lower) when starting with smaller transplants and growing at the higher temperature (Table 3.2). For example, in American marigold, maximum estimated net profit per pot was 162% greater when smaller transplants were grown at 23 ºC than when larger transplants were grown at 17 ºC. In gerbera and osteospermum, larger transplants resulted in a net loss per pot regardless of the growing temperature. In geranium, a net loss per pot was estimated for both transplant sizes when grown at 17 versus 23 ºC. Interestingly, in American marigold and snapdragon, the estimated net profit per square meter week was similar between transplant sizes at 23 ºC, but was 8 to 12% lower for larger compared to smaller transplants grown at 17 ºC.

Discussion

Among the five species studied, transplanting a larger versus a smaller transplant decreased flowering time in American marigold, geranium (only at 17 ºC), and snapdragon. In these species, the initial leaf number at transplant and transplant production period (time from seed sow until plants were ready for transplanting) were positively correlated, whereas there was a negative correlation between flowering time and initial leaf number ($P < 0.0001$). For example, in snapdragon, larger transplants flowered 7- or 8-d earlier, but had a 5- or 6-d longer transplant production period compared to smaller transplants. Therefore, the total time from seed sow to flowering was similar between transplant sizes in these species. Although the total production period was not affected by transplant size, transplanting a larger compared to a smaller transplant may be more cost-effective, since production costs per transplant are relatively low for young plants given their high density. Consistent with these results, Fisher (2006) reported a 2- to 3-week delay in flowering time when transplanting a smaller transplant (84- versus 50-cell tray). The magnitude of difference in flowering time between the two transplant sizes reported by Fisher (2006) was greater than that observed in our study, possibly due to a greater difference in development between the two transplant sizes (initial leaf number not reported). Interestingly, in gerbera and osteospermum, initial leaf number was similar between transplant sizes (128-cell versus 36-cell) and therefore, transplant size did not influence DTF in these species.

All plants grown at 23 ºC flowered faster than those grown at 17 ºC. This increase in temperature had a greater effect on flowering time than increasing the transplant size. For many floriculture crops, an increase in ADT linearly increased the flowering rate, when ADT was above the species-specific T_{min} and at, or below, T_{opt} (Adams et al., 1997; Clough et al, 2001; Whitman et al., 1997; Yuan et al., 1998). For example, the rate of progress towards flowering increased linearly as temperature increased from 15 to 26 °C for largeflower tickseed, blanketflower (*Gaillardia ×grandiflora* Van Houtte), Shasta daisy, and black-eyed Susan (Yuan et al., 1998). An increase in flowering time from a decrease in ADT may be due to a developmental delay in flowering when flowering is induced at a lower node (Adams et al., 1998b, 1998c; Mattson and Erwin, 2003), but typically it is from a slower rate of flower development (Blanchard and Runkle, 2011; Brøndum and Heins, 1993; Faust and Heins, 1994; Karlsson and Werner, 2001; Pietsch et al., 1995).

In our study, the lower temperature (17 ºC) developmentally delayed flowering time in snapdragon only in the smaller transplants. In contrast, osteospermum transplants grown at 17 ºC formed fewer nodes before flowering than those grown at 23 ºC, although flowering occurred earlier at 23 ºC. A similar response was observed in American marigold, but only in the smaller transplants. Consistent with our results, Blanchard (2009) reported a decrease in leaf number below the first open inflorescence with a decrease in ADT in African marigold 'Antigua Primrose'. In some species, an increase in leaf number from an increase in ADT could be attributed to an increase in leaf development rate, and not delayed flower initiation (Adams et al., 1998c). In addition, larger transplants formed significantly fewer leaves than smaller transplants in American marigold (only at 23 ºC) and snapdragon. This and previous results suggest that larger transplants of American marigold and snapdragon could have already initiated flowers.

Transplant size had little or no effect on inflorescence number and diameter in this study. On the other hand, inflorescence number and diameter were significantly greater at 17 ºC in 3 and 4 species, respectively. These responses to ADT are consistent with previous studies on bedding plants (Blanchard et al., 2011a, 2011b; Mattson and Erwin, 2003; Moccaldi and Runkle, 2007; Niu et al., 2000, 2001). For example, celosia (*Celosia argentea* L.), impatiens (*Impatiens walleriana* Hook. f.), and petunia 'Wave Purple' and 'Easy Wave Coral Reef' plants grown at 17 versus 23 ºC and under a DLI of 10.0 $mol \cdot m^{-2} \cdot d^{-1}$ had 7%, 63%, and 8 to 18% greater inflorescences, respectively (Blanchard and Runkle, 2011; Pramuk and Runkle, 2005a). Similarly, flower size was 33 to 53% greater in pansy (*Viola ×wittrockiana* Gams.) when plants were grown at 17 ºC compared to 23 ºC and under a range of DLI conditions (Niu et al., 2000). An increase in flower number and diameter at lower temperatures could be attributed to the longer time that plants harvested light before flowering (Pramuk and Runkle, 2005a; Oh et al., 2010), higher net photosynthetic rate (van Iersel; 2003), greater import of photosynthates into the developing buds (Dinar and Rudich, 1985) and/ or an increase in leaf number (and thus branch number) below the first open flower (Mattson and Erwin, 2003; Warner and Erwin, 2006).

Smaller transplants had significantly greater branching only in American marigold grown at 23 ºC and snapdragon at 17 ºC. Therefore, in most instances, transplant size had no effect on lateral branching. Branch number was greater in plants grown at 17 ºC than 23 ºC in geranium (only in the first replication) and snapdragon, whereas American marigold transplants formed comparatively fewer branches when grown at 17 ºC. Many researchers have reported an increase in branch number with a decrease in ADT in several species, including balloon flower [*Platycodon grandiflorus* (Jacq.) A. DC.] 'Astra Blue' (Park et al., 1998), fuchsia (*Fuchsia × hybrida* hort. ex Siebold & Voss) (Erwin et al., 1991), pansy (Mattson and Erwin, 2003; Warner and Erwin, 2006) and petunia (Mattson and Erwin, 2003). In some cases, at higher temperatures, a decrease in branch number was correlated with a decrease in leaf number below the first open flower (Mattson and Erwin, 2003). Among the species we studied, a decrease in branch number was positively correlated ($P < 0.001$) with a decrease in leaf number below the first open inflorescence in American marigold and snapdragon. In addition, a shorter production period in larger transplants and plants grown at 23 ºC could potentially reduce plant quality in these species.

In American marigold and snapdragon, smaller transplants were significantly taller than larger transplants when grown at 23 ºC. Plant height of geranium, snapdragon, and osteospermum (larger transplants only) at flowering was greater at 17 ºC compared to 23 ºC, whereas an opposite occurred in gerbera (larger transplants only) and American marigold. ADT and DIF (day – night temperature) can influence plant height by affecting leaf number below the first flower and internode length, respectively (Clough et al., 2001; Erwin et. al., 1991; Erwin and Heins, 1990; Mattson and Erwin, 2003). Higher temperatures developmentally accelerate flowering in some species (Mattson and Erwin, 2003), which can potentially decrease plant height (Clough et al., 2001) due to fewer nodes formed prior to flowering. Among the five species we studied, a decrease in plant height was positively correlated with a decrease in leaf number below the first open inflorescence in American marigold and snapdragon. Similarly, 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* Moretti) (Moe and Mortensen, 1992b). In our study, although the greenhouse temperature setpoints were constant, the day temperatures were sometimes higher than the night temperatures and the magnitude was generally greater at 17 than at 23 °C. The mean DIF values were generally small in this experiment (0.3 to 2.3 °C), but occasional exposure to high daytime temperatures, especially during the spring replication, could have contributed to an increase in plant height at lower temperatures (Whitman et al., 1997). The effects of transplant size on flowering characteristics cannot be compared to previous work, since to our knowledge this has not been reported in annual bedding plants.

The net profit was greater, or the net loss per pot was less, when plants were grown at 23 compared to 17 °C irrespective of transplant size. Heating cost estimations by Blanchard and Runkle (2009) indicate that in some cases, less energy for heating is consumed on a per-crop basis by growing at a higher temperature because production time is shorter. For example, petunia 'Wave Purple' flowered 17 d earlier at 23 °C than at 17 °C, and for a greenhouse in Grand Rapids, MI and a market date of April 1, 22% less energy for heating was predicted by growing the crop at the higher temperature (Blanchard and Runkle, 2009). In addition, a shorter production period can reduce labor and overhead expenses and can enable the production of more crops, assuming they can be marketed.

In addition, growing a larger transplant (128- versus 288-cell or 36- versus 128-cell size) was either less profitable or resulted in a net loss/ greater net loss per pot and per square meter week, except for American marigold and snapdragon grown at 23 °C. Although larger transplants reduced flowering time in some species, the decrease in heating, labor and overhead costs was generally offset by the higher price of the larger transplant. In contrast to our results, Fisher et al. (2006) reported that using a larger transplant was more profitable. However, in their study, the larger transplant (50-cell size) accelerated flowering by 2 to 3 weeks compared to the smaller one (84-cell size), whereas in our study the difference in flowering time was ≤ 8 d between transplant sizes. Therefore, although a larger transplant may flower earlier, it may not always be profitable. This economics depends upon individual grower and transplant characteristics such as, the magnitude of difference in maturity (leaf number) and flowering time between transplant sizes, plant spacing, demand for greenhouse space, heating labor and overhead costs, and higher price/shipping costs of the larger transplant. The influence of transplant size on plant development and quality depends on the magnitude of difference in development between transplant sizes, and also the environmental conditions during transplant production (Pramuk and Runkle, 2005a). Further location-specific research is needed to identify the minimum difference in development between transplant sizes that can justify the higher price of the larger transplant, since this economics is so situational. In addition, more research is required on how environmental conditions such as DLI and photoperiod during transplant production influence flower initiation in different transplant sizes, and therefore subsequent flowering characteristics.

Table 3.1. Time from seed sow to transplant, mean leaf no. at transplant, and characteristics used to determine flowering date for five bedding plant species in two experimental replicates. Seedlings were grown in 36-, 128-, or 288-cell trays.

	Time from seed sow to transplant (d)			Mean leaf no. at transplant			
Species	288	128	36	288	128	36	Flowering characteristics
American marigold 'Inca II Mix'	21 or 22	28 or 29	–[z]	4	6	–	1 inflorescence with ≥50% of the ray flowers reflexed
Geranium 'Ringo 2000 Deep Red'	33 or 35	39 or 46	–	4	6	–	5 flowers open on an inflorescence
Gerbera 'Jaguar Deep Orange'	–	45	45	–	7	7	1 inflorescence with all of the ray flowers reflexed
Osteospermum 'Asti Purple'	–	35 or 46	15 or 36	–	9	9	1 inflorescence with ray flowers reflexed
Snapdragon 'Rocket Mix'	33 or 42	39 or 47	–	6	9	–	2 flowers open on an inflorescence

[z]Transplant sizes not included in the experiment.

Table 3.2. Estimated production costs and net profits when starting with two transplant sizes (36-, 128-, or 288-cell trays) in the production of five bedding plant species grown at 17 or 23 °C for first flowering on April 1. Heating costs were calculated using Virtual Grower software for Grand Rapids, MI. Labor and overhead costs are estimated from Fisher (2006). See materials and methods for information on production cost and net profit estimation. Production time is the average days to flower, and assumes a 16-h photoperiod and a mean DLI of ≥10 $mol \cdot m^{-2} \cdot d^{-1}$.

Average temperature (°C)	Production time (d)		Estimated cost per pot (US$): Heating		Transplants		Labor and overhead		Total cost		Net profit per pot		Net profit per square meter week	
American marigold 'Inca Mix II'														
Transplant size:	288	128	288	128	288	128	288	128	288	128	288	128	288	128
17	57	49	$0.15	$0.12	$0.17	$0.35	$0.76	$0.65	$1.08	$1.12	$0.17	$0.13	$0.91	$0.81
23	44	37	$0.15	$0.12	$0.17	$0.35	$0.59	$0.49	$0.91	$0.96	$0.34	$0.29	$2.35	$2.38
Geranium 'Ringo 2000 Deep Red'														
Transplant size:	288	128	288	128	288	128	288	128	288	128	288	128	288	128
17	70	65	$0.19	$0.18	$0.21	$0.41	$0.93	$0.87	$1.33	$1.46	–$0.08	–$0.21	–$0.35	–$0.98
23	49	48	$0.16	$0.16	$0.21	$0.41	$0.65	$0.64	$1.02	$1.21	$0.23	$0.04	$1.43	$0.25
Gerbera 'Jaguar Deep Orange'														
Transplant size:	128	36	128	36	128	36	128	36	128	36	128	36	128	36
17	57	56	$0.15	$0.15	$0.54	$0.83	$0.76	$0.75	$1.45	$1.73	$0.05	–$0.23	$0.27	–$1.47
23	46	46	$0.15	$0.15	$0.54	$0.83	$0.61	$0.61	$1.30	$1.59	$0.20	–$0.09	$1.32	–$0.60
Osteospermum 'Asti Purple'														
Transplant size:	128	36	128	36	128	36	128	36	128	36	128	36	128	36
17	51	52	$0.13	$0.13	$0.54	$0.83	$0.68	$0.69	$1.35	$1.65	$0.15	–$0.15	$0.90	–$0.89
23	43	41	$0.14	$0.13	$0.54	$0.83	$0.57	$0.55	$1.25	$1.51	$0.25	–$0.01	$1.77	–$0.07

Table 3.2. (cont'd).

Average temperature (°C)	Production time (d)		Estimated cost per pot (US$) Heating		Transplants		Labor and overhead		Total cost		Net profit per pot		Net profit per square meter week	
						Snapdragon 'Rocket Mix'								
Transplant size:	288	128	288	128	288	128	288	128	288	128	288	128	288	128
17	56	48	$0.15	$0.12	$0.15	$0.33	$0.75	$0.64	$1.05	$1.09	$0.20	$0.16	$1.09	$1.01
23	42	35	$0.14	$0.11	$0.15	$0.33	$0.56	$0.47	$0.85	$0.91	$0.40	$0.34	$2.90	$2.96

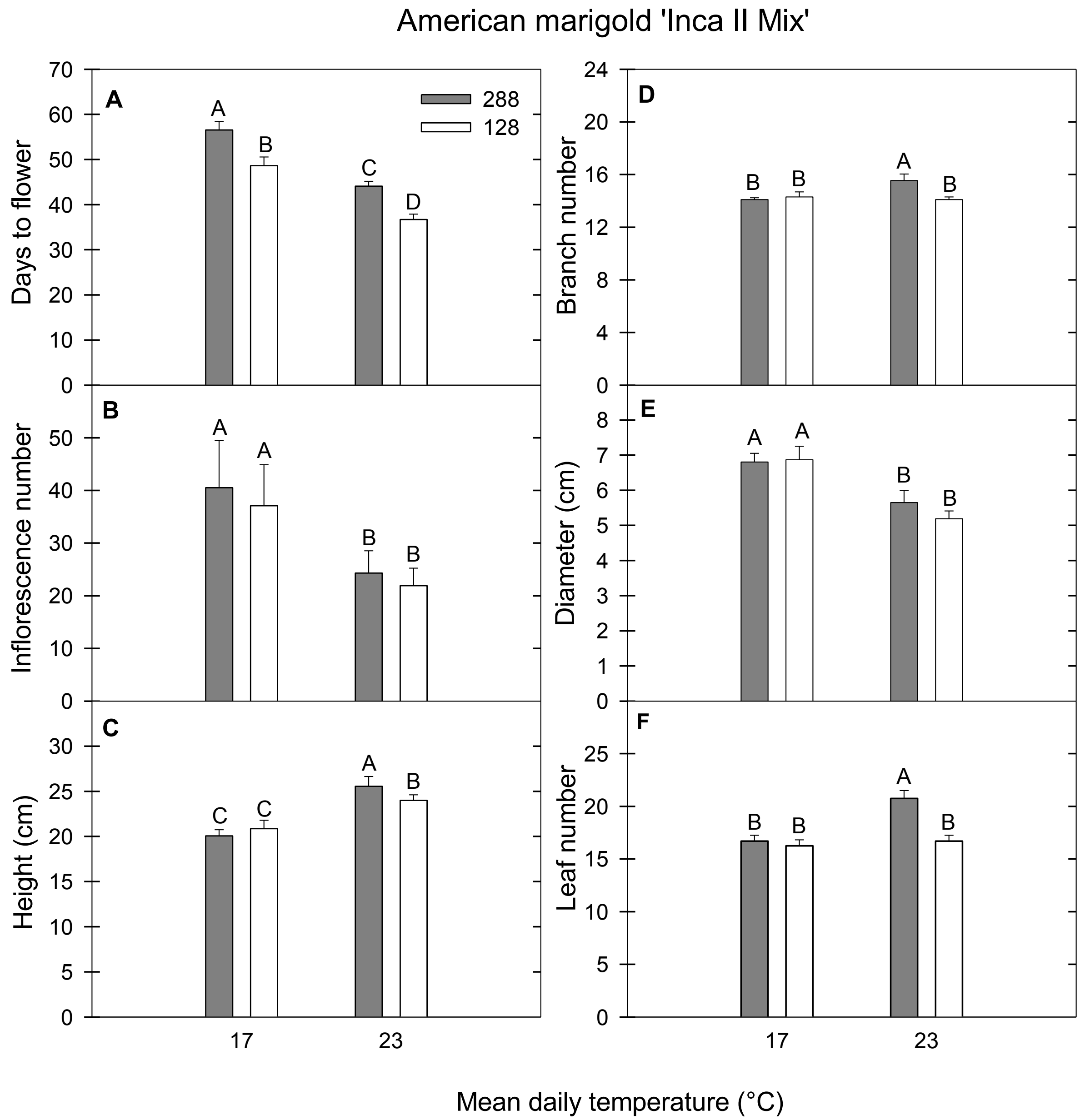

Figure 3.1. The effect of starting transplant size (288- or 128-cell trays) on flowering characteristics of American marigold ‘Inca II Mix’ grown at 17 or 23 °C. Data were pooled between two experimental replications when there were no replicate and treatment interactions ($P \leq 0.05$). Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Mean DLIs during the fall and spring experiments were 10.0 and 15.0 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

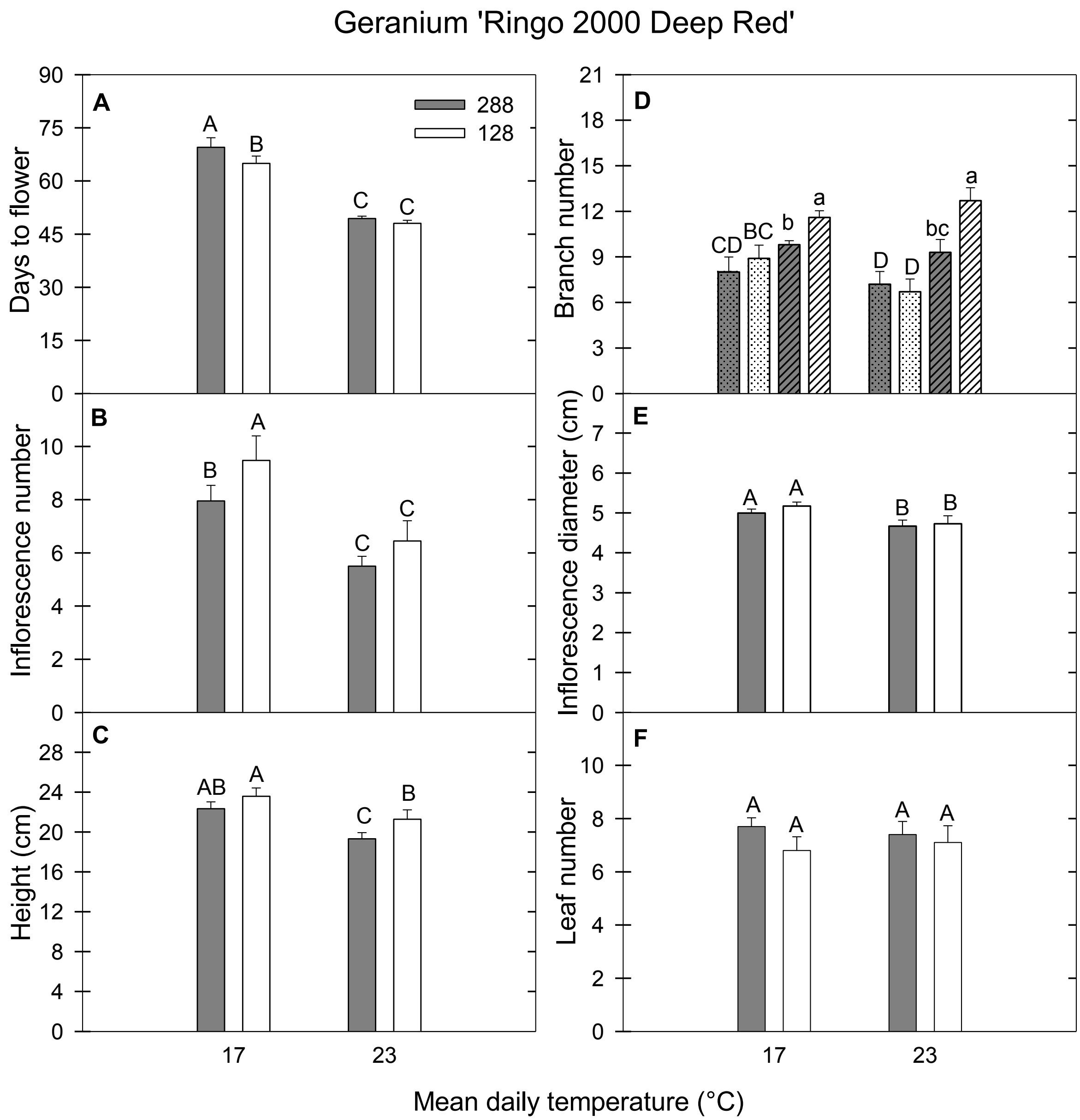

Figure 3.2. The effect of starting transplant size (288- or 128-cell trays) on flowering characteristics of geranium ‘Ringo 2000 Deep Red’ grown at 17 or 23 °C. Data were pooled between two experimental replications when there were no replicate and treatment interactions ($P \leq 0.05$). When the interaction was significant, data are separately presented for fall (dots) and spring (stripes) replications. Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Mean DLIs during the fall and spring experiments were 10.0 and 15.0 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

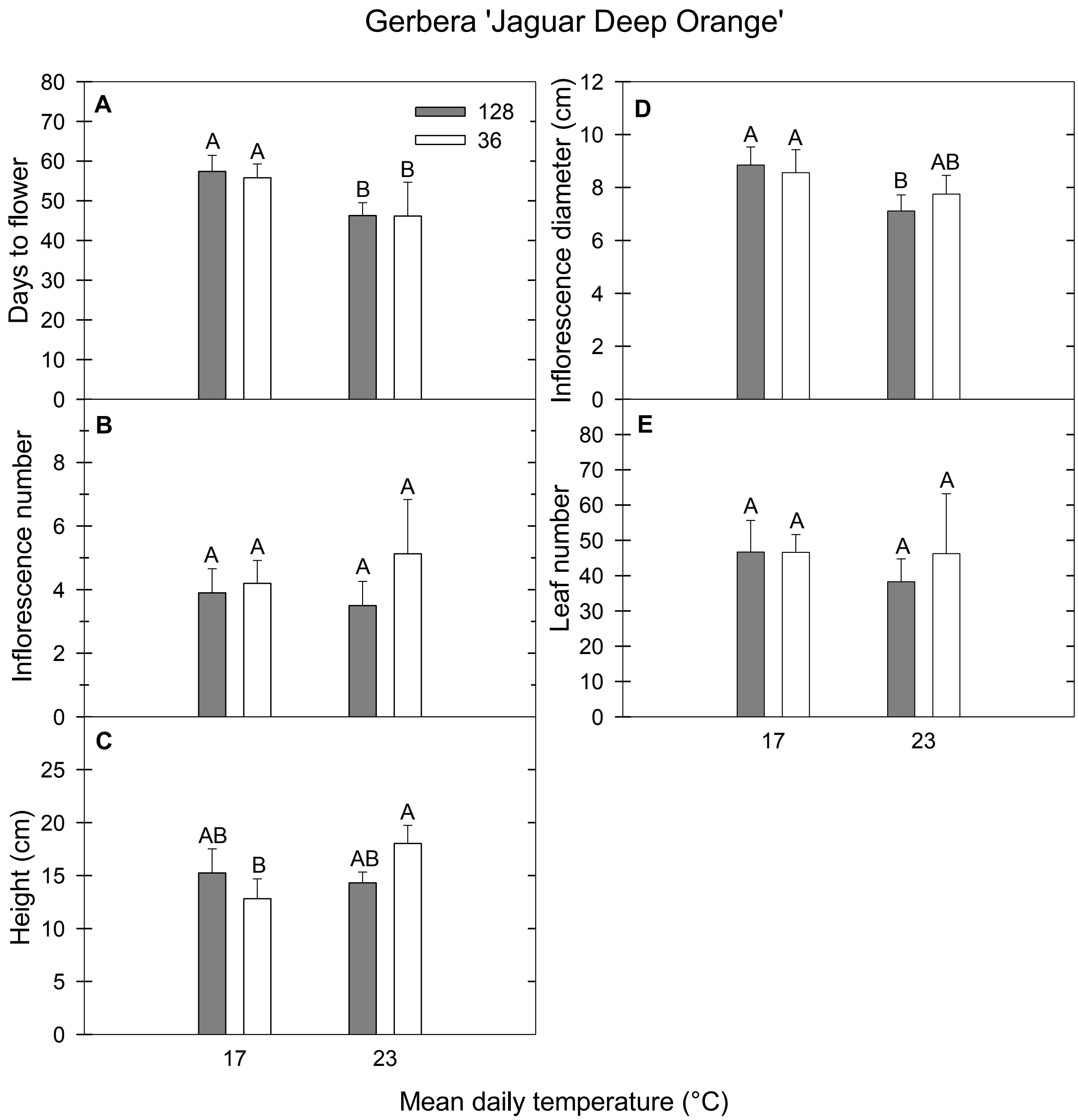

Figure 3.3. The effect of starting transplant size (128- or 36-cell trays) on flowering characteristics of gerbera 'Jaguar Deep Orange' grown at 17 or 23 °C. Data were pooled between two experimental replications when there were no replicate and treatment interactions ($P \leq 0.05$). When the interaction was significant, data are separately presented for fall (dots) and spring (stripes) replications. Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Mean DLIs during the fall and spring experiments were 10.0 and 15.0 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively.

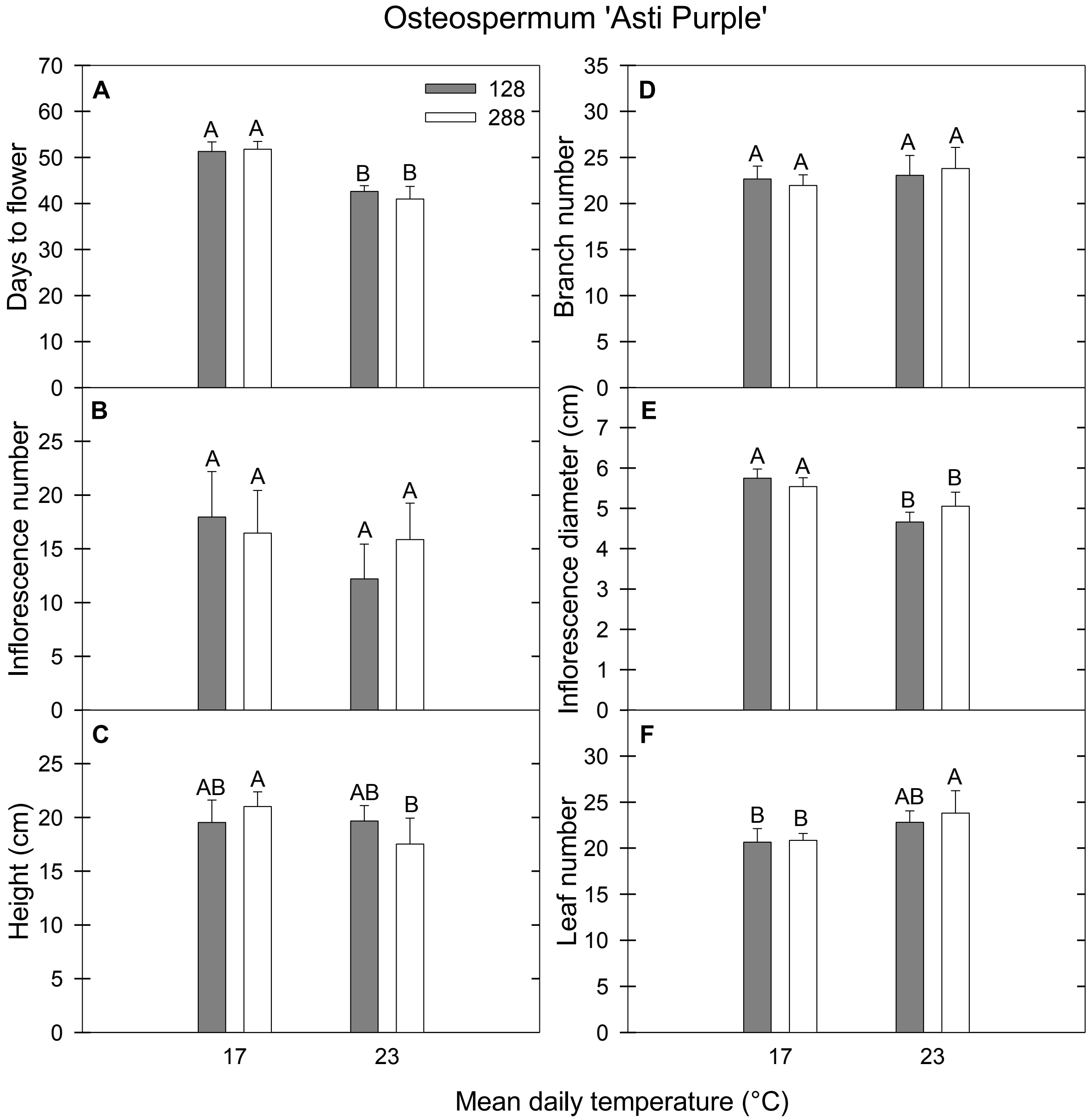

Figure 3.4. The effect of starting transplant size (128- or 36-cell trays) on flowering characteristics of osteospermum 'Asti Purple' grown at 17 or 23 °C. Data were pooled between two experimental replications when there were no replicate and treatment interactions ($P \leq 0.05$). When the interaction was significant, data are separately presented for fall (dots) and spring (stripes) replications. Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Mean DLIs during the fall and spring experiments were 10.0 and 15.0 mol·m^{-2}·d^{-1}, respectively.

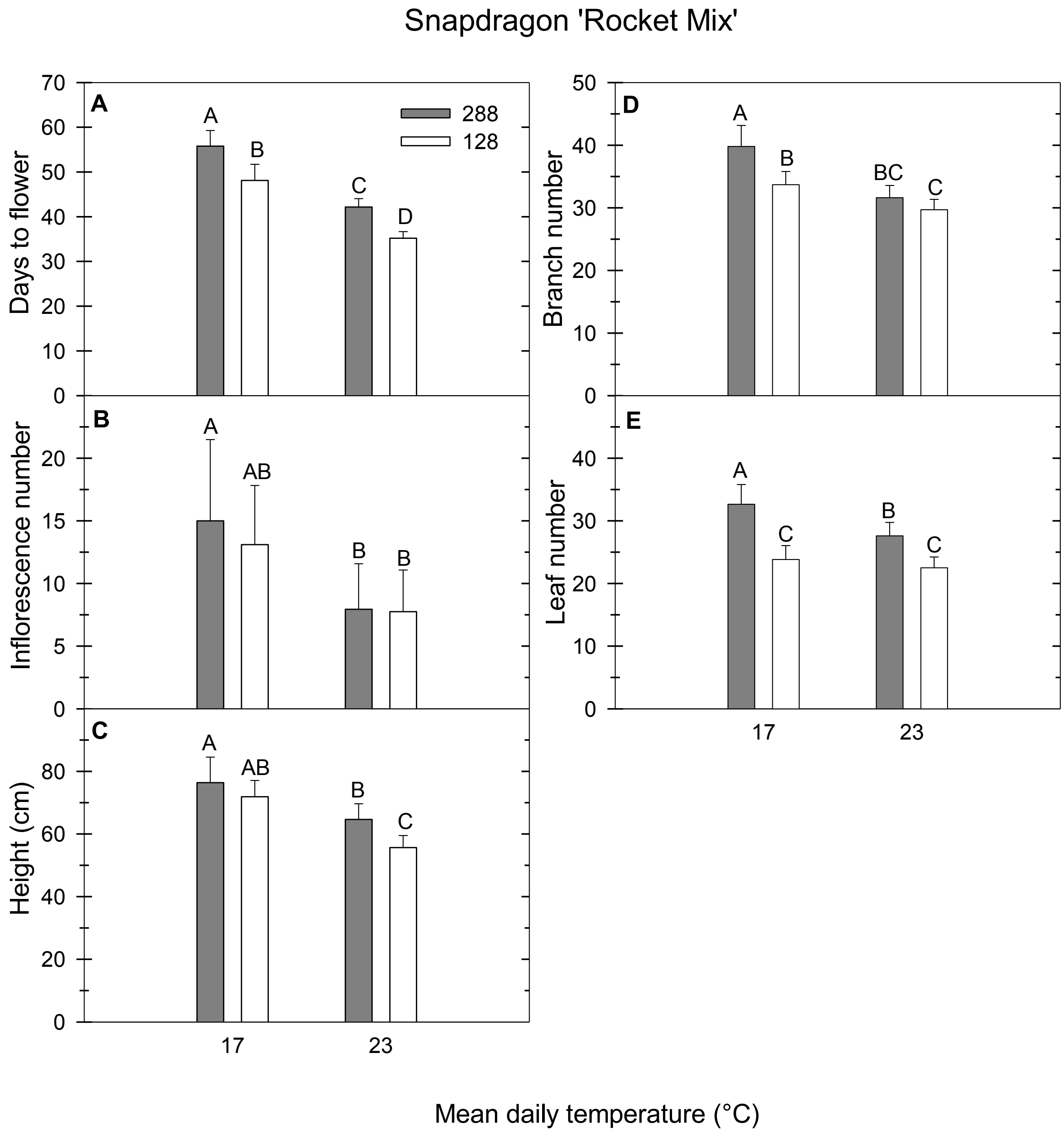

Figure 3.5. The effect of starting transplant size (288- or 128-cell trays) on flowering characteristics of snapdragon ‘Rocket Mix’ grown at 17 or 23 °C. Data were pooled between two experimental replications when there were no replicate and treatment interactions ($P \leq 0.05$). When the interaction was significant, data are separately presented for fall (dots) and spring (stripes) replications. Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Mean DLIs during the fall and spring experiments were 10.0 and 15.0 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

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SECTION IV

DETERMINING THE PHOTOPERIOD-SENSITIVE STAGES OF DEVELOPMENT AND THE EFFECT OF TEMPERATURE AND PHOTOPERIOD ON FLOWERING IN THREE PETUNIA CULTIVARS

Determining the Photoperiod-Sensitive Stages of Development and the Effect of Temperature and Photoperiod on Flowering in Three Petunia Cultivars

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Abstract

Petunia ×*hybrida* Vilm.-Andr. is a facultative long day (LD) plant and is typically commercially produced in temperate climates beginning in late winter, when the natural photoperiod is short. Greenhouse growers in these climates often use low-intensity, LD lighting to promote flowering in this species. Limiting LD lighting to periods of photoperiod sensitivity can promote flowering, while potentially reducing lighting costs and undesirable stem extension. We performed reciprocal transfer experiments with petunia 'Easy Wave Neon Rose', 'Improved Wave Purple' and 'Classic Wave Purple', in which plants with 4, 6, 8, 10, or 12 leaves were moved from inductive LDs to non-inductive short days (SDs), and vice versa, to determine when these varieties become sensitive to photoperiod. In a separate experiment, the effects of average daily temperature and photoperiod on the flowering of petunia were quantified. Plants were grown in glass-glazed greenhouses at 14 or 20 ºC and with a 10- or 16-h photoperiod created by a combination of a truncated 9-h natural day extended with light from incandescent lamps. Developmentally, 'Easy Wave Neon Rose' became receptive to photoperiod after unfolding ≤4 leaves, whereas 'Classic Wave Purple' and 'Improved Wave Purple' became photoperiod-sensitive after unfolding >8 leaves. Flowering was fastest in plants grown under LDs and at 20 ºC for all petunia varieties. For example, 'Easy Wave Neon Rose', 'Classic Wave Purple' and 'Improved Wave Purple' plants flowered 31, 49, or 59 d earlier, respectively when grown at 20 ºC with LDs compared to 14 ºC with SDs. However, plants that flowered earliest had fewer flower buds (except in 'Classic Wave Purple') and branches. In 'Easy Wave Neon Rose' and 'Improved Wave Purple', LDs had less of a promotive effect when grown at 14 ºC than at 20 ºC.

Introduction

Annual bedding and garden plants that are commercially grown in temperate regions have a narrow sales period in late spring, which necessitates precise scheduling of flowering in these species. Flower initiation and development is a complex function of average daily temperature (ADT), daily light integral (DLI), and for photoperiodic crops, photoperiod (Adams et al., 1998a; Blanchard et al., 2011; Kacsperski et al., 1991). Several studies have investigated the influence of two or more of these environmental factors on the flowering characteristics of annual bedding plants (Adams et al., 1996, 1997, 1998; Moccaldi and Runkle 2007; Pramuk and Runkle, 2005b). For example, Adams et al. (1997) reported a linear increase in the rate of progress towards flowering in pansy (*Viola ×wittrockiana* Gams.) with an increase in ADT, DLI, and photoperiod up to an optimum. Interestingly, DLI and particularly ADT can influence crop responses to photoperiod by modifying the length of the juvenile phase (Adams et al., 1999). Leaves of photoperiodic plants perceive changes in daylength to induce flowering (Thomas and Vince-Prue, 1997), while ADT mainly influences the plant development rate (Blanchard and Runkle, 2011).

Photoperiodic floral induction depends upon the length of the juvenile phase and the minimum number of inductive cycles necessary for floral initiation (Warner, 2009). The juvenile phase is the early stage of plant development during which flowering can not be induced regardless of the environmental conditions (Thomas and Vince-Prue, 1997). The length of the juvenile phase, and the minimum number of inductive cycles required for floral induction in mature plants, depends upon the species, cultivar, and growing temperature (Adams et al., 1999, 2003; Verheul et al., 2005; Warner, 2009). For example, at 20 ºC, the juvenile phase lasted from 9 to 12 d after emergence in celosia (*Celosia argentea* L.; Warner, 2009), and 25 to 40 d in snapdragon (*Antirrhinum majus* L.; Adams et al., 2003) depending on the cultivar. In addition, there is considerable variation in the minimum number of inductive cycles required for flowering among species. For example, some short day (SD) plants such as, whiteedge morning-glory [*Pharbitis nil* (L.) Roth], and red goosefoot (*Chenopodium rubrum* L.) can be induced to flower by a single inductive cycle (Thomas and Vince-Prue, 1997), whereas others such as strawberry (*Frageria* L.) require at least 21 SDs for floral induction (Verheul et al., 2005).

Some photoperiodic species exhibit a photoperiod-sensitive phase during development, which comes after the juvenile phase and before a second photoperiod-insensitive phase during the later stages of development (Adams et al., 1999; Warner, 2009). For example, in celosia and petunia (*Petunia* ×*hybrida* Vilm.-Andr.) 'Express Blush Pink' grown at ≈ 20 ºC, the photoperiod sensitive phase was ≈ 9 to 45 d and 16 to 56 d after emergence, respectively (Adams et al., 1999; Warner, 2009). The phases of photoperiod sensitivity can be determined by reciprocal transfer experiments, in which plants are transferred from long days (LDs) to SDs, and vice versa, at different stages in plant maturity (Adams et al., 1999, 2003; Munir et al., 2010). This technique has been used in several field and ornamental crops, such as maize (*Zea mays* L.; Kiniry et al., 1983), barley (*Hordeum vulgare* L.; Roberts et al., 1988), soybean [*Glycine max* (L.) Merr.; Wilkerson et al., 1989], opium poppy (*Papaver somniferum* L.; Wang et al., 1997), celosia (Warner, 2009), chrysanthemum (*Dendranthema* ×*grandiflorum* Kitam.; Adams et al., 1998), petunia (Adams et al., 1999), and snapdragon (Adams et al., 2003; Munir et al., 2010).

Many researchers have analyzed the plastochron index (leaf number before first open flower) data when flowering was terminal, in addition to flowering time data, to separate the effects of photoperiod on flower induction and flower development (Adams et al., 1998b, 2003). Although photoperiod primarily influences flower induction, in some species, it also affects flower bud development rate. For example, snapdragon 'Bells' transferred from LDs to SDs during early flower development flowered 4 d later than those grown under continuous LDs (Adams et al., 2003). Similarly, transferring chrysanthemum plants from SDs to LDs during early flower development delayed flowering and resulted in distorted, abnormal flowers (Adams et al., 1998b). Interestingly, some species with visible flower buds, such as garden balsam (*Impatiens balsamina* L.), soybean, and perilla (*Perilla* L.), revert to vegetative growth when transferred from inductive to non-inductive conditions (Han et al., 2006; Lam and Leopold, 1961; Pouteau et al., 1997). This reversion is primarily due to a lack of meristem commitment and a rapidly diminishing floral signal in previously induced leaves. This is evident from a positive correlation between the amount of induction and the timing of reversion (Pouteau et al., 1997), and also from a decrease in the number of flowers initiated under a non-inductive photoperiod (Lam and Leopold, 1961).

In addition to the flowering time, plant quality parameters (e.g., flower bud number, branch number or shoot mass) can be influenced by the timing and duration (number) of inductive photoperiods in some species (Damann and Lyons, 1993; Imamura et al., 1966; Warner, 2009). For example, increasing the duration of SD exposure from 5 to 30 d when celosia plants had developed only one true leaf, increased the inflorescence number by 175% (Warner, 2009). A similar trend occurred in celosia plants with 2 or 3 leaves, whereas inflorescence number in plants with 4 or 5 leaves was not influenced by the duration of SDs. In contrast, flower number, branch number and shoot mass decreased as the duration of SDs increased from 1 to 12 d in celosia plants exposed to SD before expansion of the first leaf pair. Knowledge of the effects of timing and duration of photoperiod on flowering characteristics of photoperiodic species can allow commercial growers to balance crop timing with acceptable plant quality.

Petunia ×hybrida, derived from a cross between *P. axillaris* and *P. integrifolia* (Stehmann et al., 2009) is among the top ten bedding plants produced in the United States, with a reported 15-state wholesale value of $132 million in 2011 (USDA, 2012). There are over 360 petunia cultivars available in the United States (Kelly et al., 2007), most of which are sold in flats, hanging baskets, or pots (USDA, 2012). Several studies have categorized petunia as a facultative long day (LD) plant (Adams et al., 1998a; Piringer and Cathey, 1960; Warner, 2010), since plants flowered earlier when grown under LDs compared to short days (SDs). For example, Adams et al. (1998) reported a linear increase in rate of progress towards flowering (reciprocal of days to flower, DTF) of petunia 'Express Blush Pink' with an increase in photoperiod from 8 to 14.4 $h \cdot d^{-1}$. Similarly, all four petunia species evaluated by Warner (2010) flowered 8 to 21 d earlier, and developed 14 to 22 fewer leaves prior to flowering, when grown under LDs versus SDs. In temperate climates, petunias are typically grown beginning in late winter, when the ambient photoperiods are short, which necessitates the use of LD lighting to promote flowering in this species. Limiting LD lighting to periods of photoperiod sensitivity can promote flowering, while potentially reducing lighting costs and undesirable stem extension (Adams et al., 2001). However, plant quality is often positively correlated with flowering time, and sometimes with the leaf number below first open flower (Blanchard and Runkle, 2011; Pramuk and Runkle, 2005a, Warner, 2009). Previous studies investigating photoperiod sensitivity in petunia 'Express Blush Pink' indicates that this variety has a distinct photoperiod-senstive phase. However, some petunia 'Wave' cultivars can reportedly revert to vegetative growth when grown under non-inductive conditions during early flower development (S. Padhye, pers. comm.).

In addition to photoperiod, temperature also influences the flowering time in petunia, such that as ADT increases within a species-specific range, rate of progress towards flowering linearly increases (Adams et al., 1998a; Blanchard et al., 2011). The flowering rate of petunia 'Easy Wave Coral Reef' and 'Wave Purple' increased by 0.003 and 0.002, respectively with each degree rise in temperature from 14 to 26 ºC (Blanchard et al., 2011). Some researchers have studied the interaction effects of temperature and photoperiod on photoperiod receptivity, T_{opt} for flowering, and flowering characteristics in a few petunia varieties (Adams et al., 1996, 1998a, 1999). In some petunia varieties ADT can influence seedling sensitivity to photoperiod by modifying the length of the juvenile phase; an increase in ADT from 13.7 to 22.3 ºC decreased the juvenile phase of petunia 'Express Blush Pink' from 21 to 13 d (Adams et al., 1999). Similarly, an increase in photoperiod from 8 $h \cdot d^{-1}$ to 14.4 $h \cdot d^{-1}$ linearly increased T_{opt} for flowering in petunia 'Express Blush Pink' from 20.7 ºC to 23.4 ºC (Adams et al., 1998a). Adams et al. (1996) reported a temperature and photoperiod interaction on flowering time and morphogical characteristics in trailing petunias 'Malve' and 'White'. The effect of photoperiod on flowering time of these trailing petunia varieties was greater when plants were grown at a higher versus a lower temperature. Similarly, the effect of temperature on the rate of progress towards flowering was greater when plants were grown under LDs than SDs. However, this response to temperature and photoperiod may vary between petunia varieties, since Adams et al. (1998a) observed little or no interaction in the effects of temperature and photoperiod on the flowering characteristics in petunia 'Express Blush Pink'. Therefore, the objectives of this study were: 1) to determine the precise timing and minimum duration of inductive LDs to achieve 100% flowering in petunia, and 2) to study the effect of temperature and photoperiod interaction on petunia flowering characteristics.

Materials and Methods

Growth chamber treatments and culture. Experimental protocol, data collection and analysis were similar to that reported by Blanchard and Runkle (2011). Seeds of petunia 'Easy Wave Neon Rose', 'Classic Wave Purple', and 'Improved Wave Purple' were sown in 36-cell (42.3-mL) plug trays on 27 December 2011 by a commercial greenhouse (C. Raker & Sons, Litchfield, MI) and received at Michigan State University (MSU) on 4 January 2012. On receipt, the seedlings were unfolding their first leaf and were thinned to one plant per cell. They were then grown in a controlled environment chamber at a constant temperature setpoint of 20 ºC ± 2 ºC under a 16-h long day (LD; 0700 to 2300 HR) at a photosynthetic photon flux (*PPF*) of 140 $\mu mol \cdot m^{-2} \cdot s^{-1}$, or for a 10-h short day (SD; 0700 to 1700 HR) at a *PPF* of 220 $\mu mol \cdot m^{-2} \cdot s^{-1}$ provided by a combination of cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and incandescent lamps (INC, Philips, Somerset, NJ). The different light intensities were used so that the daily light integral (DLI) for both photoperiodic treatments was ≈ 8 $mol \cdot m^{-2} \cdot d^{-1}$. The light intensity and plant temperature were checked periodically with an instantaneous quantum sensor (Apogee Instruments Inc., Logan, UT) at canopy height and a hand-held infrared thermometer (Tel-Fast 2, Tel-Tru, Rochester, NY), respectively. The desired light intensities were maintained by replacing and/or lowering the lamps when required. The temperature setpoint was lowered by 1 to 2 ºC in the environment chamber with the 10-h photoperiod when plant temperature was > 20 ºC. Plugs were irrigated by hand as necessary with acidified well water (140 $mg \cdot L^{-1}$ titratable alkalinity of $CaCO_3$) containing ($mg \cdot L^{-1}$) 95, 34, and 29 Ca, Mg, and S, and 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).

Expt 1. Reciprocal photoperiodic transfers at different stages of development on flowering. Sixteen plants of each cultivar were randomly selected and transferred from LD to SD, and vice versa, when they averaged 4, 6, 8, and 10 leaves, which occurred 13 to 26 d after the start of photoperiodic treatments (Table 4.1). A leaf was included when it had uncurled and was at least half expanded. In addition, 16 plants per cultivar were grown under continuous LD or SD until they attained 12 leaves. When plants in all the treatments attained an average of 12 leaves (24 to 30 d after start of treatments), they were transplanted into 10-cm round containers (480-mL) filled with a peat-based medium (Suremix, Michigan Grower Products, Galesburg, MI). Ten plants per treatment were selected for uniformity and grown at a constant set point of 20 °C with a 10-h photoperiod in a glass-glazed greenhouse. The actual average air temperature and DLI in the greenhouse during the experiment were 21.1 ºC and 10.4 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. Treatments were completely randomized between and within greenhouse benches. The experiment was arranged as a split-plot design; two photoperiods (whole plot factor) were randomly assigned to the controlled environment chambers, and five leaf number (sub-plot factor) treatments were randomly assigned to the experimental units (plants) within each photoperiod.

Expt 2. Temperature and photoperiod interaction on flowering. Fifty plants per cultivar were grown in a controlled environment chamber at 20 ºC under LDs as previously described. When the plants attained an average of 8 leaves, forty plants were selected for uniformity and transplanted into 10-cm round pots (480-mL) and grown at constant temperature set points of 14 or 20 °C in separate glass-glazed greenhouses under a SD or LD. Ten plants were randomly assigned to each combination of temperature and photoperiod treatment. The experiment was arranged as a split-plot design; two temperatures (whole plot factor) were randomly assigned to the greenhouses, and two photoperiods (sub-plot factor) were randomly assigned to the experimental units (plants) within each temperature treatment. The actual average air temperatures were 15.9 and 20.7 ºC and the mean DLI was 10.0 $mol·m^{-2}·d^{-1}$ in the greenhouses during the experiment.

Greenhouse culture and environments. All plants were treated with a 250 ml paclobutrazol (Piccolo, Fine Americas Inc., Walnut Creek, CA) drench at 5 $mg·L^{-1}$ 7 to 10 d after transplant to inhibit extension growth. In the greenhouse, plants were grown under a 10-h SD or a 16-h LD. Under all lighting regimens, plants were grown under a 9-h (0800 to 1700 HR) truncated natural photoperiod (lat. 43 °N) using blackcloth and supplemental lighting (at 100 to 120 $\mu mol·m^{-2}·s^{-1}$) from high-pressure sodium lamps when the outside light intensity was < 290 $\mu mol·m^{-2}·s^{-1}$. The 9-h photoperiod was extended by incandescent lamps (at 1 to 3 $\mu mol·m^{-2}·s^{-1}$) to create the SD (1700 to 1800 HR) and LD (1700 to 2400 HR) photoperiod. The air temperature and *PPF* in each greenhouse were recorded by a shielded and aspirated 0.13 mm type E thermocouple (Omega Engineering, Stamford, CT), and a line quantum sensor containing 10 photodiodes (Apogee Instruments) placed at canopy height (22 cm above bench height), respectively. A datalogger (CR-10, Campbell Scientific, Logan, UT) collected the environmental data every 10 s and hourly averages were recorded. Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing ($mg·L^{-1}$) 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 Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Data collection and analysis: Plants were considered in flower when the first flower fully opened on each plant. At first flowering, the date was recorded and days to flower from transplant were calculated. Flowering position (terminal or lateral), flower and flower bud number, axillary branch number, and length of the longest lateral were also recorded at first open flower. When flowering was on the primary stem, the number of leaves below the first open flower was recorded, whereas when the first flower opened on a lateral branch, the total leaf number (flowering lateral + primary stem below flowering lateral) was counted. In addition, flower and flower bud number two weeks after flowering were recorded in Expt. 2. Plants that did not flower within 90 d (Expt. 1) or 100 d (Expt. 2) of transplant were considered nonflowering. Some plants demonstrated abnormal flowering characteristics, and were not included in the statistical anaysis to allow for an unbiased treatment comparison. SAS (SAS Institute, Cary, N.C.) was used to analyze the experimental data. Mean separation using Tukey's honestly significant difference test at $P \leq 0.05$ was performed on all the data to compare differences between treatments. Data from treatments that had ≤30% flowering is not presented, except flowering percentage.

Results

Expt 1. The effect of reciprocal photoperiodic transfers at different stages of development on flowering. Essentially all 'Easy Wave Neon Rose' and 'Improved Wave Purple' flowered within 90 d after transplant in all the treatments (Figures 4.1A, C). As leaf number of 'Classic Wave Purple' at photoperiodic transfer increased, flowering percentage decreased from 100 to 0 when plants were transferred from SD to LD, but increased from 0 to 40% during the reciprocal transfer (Figure 4.1B). Although 'Classic Wave Purple' plants that flowered in this experiment had 6 to 8 flower buds at first flowering, additional open flowers were not observed after the first flower opened (personal observation). For the parameters measured in this study, significant treatment effects occurred only in 'Easy Wave Neon Rose' (Figures 4.1, 4.2). However, reciprocal photoperiodic transfers at different stages of development did not influence stem length (Figure 4.2D) and flowering position (data not presented) in this variety.

'Easy Wave Neon Rose' plants that unfolded 10 or 12 leaves under SDs flowered significantly later than plants transferred to LDs after unfolding 4 leaves, or initially grown under LDs until they attained 6 or more leaves (Figure 4.1D). In general, flowering time increased with increase in leaf number at transfer from SD to LD, but not for the reciprocal transfer. Similarly, leaf number below the first open flower and lateral branch number generally increased with an increase in leaf number at transfer from SD to LD for 'Easy Wave Neon Rose', but not for the reciprocal transfer (Figures 4.2A, G). For example, plants grown under SDs until they attained 4, 10, or 12 leaves developed 13, 20, or 21 leaves and 17, 22, or 21 branches, prior to flowering. In addition, 'Easy Wave Neon Rose' plants transferred from SD to LD after the 4-leaf stage had greater branching and formed more leaves than those subjected to the reciprocal transfer at a similar stage of development. Flower number of 'Easy Wave Neon Rose' was similar within each photoperiodic treatment, but plants that unfolded 10 leaves under SDs had a significantly greater flower number than those initially grown under LDs until they attained 4 to 8 leaves (Figure 4.1G).

Expt 2. Temperature and photoperiod interaction on flowering. All plants of all three varieties flowered when grown under a 16-h LD (Figures 4.3A-C). In contrast, under a 10-h SD, flowering percentage was 100%, 20 to 60%, or 90 or 100% in 'Easy Wave Neon Rose', 'Classic Wave Purple', and 'Improved Wave Purple', respectively. Flowering was delayed the most in all the petunia varieties when grown at 14 ºC and under a 10-h photoperiod (Figures 4.3D-F). For example, 'Easy Wave Neon Rose', 'Classic Wave Purple' and 'Improved Wave Purple' plants flowered 31, 49, or 59 d earlier, respectively, when grown at 20 ºC with LDs compared to 14 ºC with SDs. Among the petunia varieties studied, temperature and photoperiod interacted to influence the flowering position only in ‘Easy Wave Neon Rose’ (data not presented). For example, lateral flowering occurred in 90 or 100% of ‘Easy Wave Neon Rose’ plants grown under SDs. In contrast, the first flower opened terminally in 50% or 100% of ‘Easy Wave Neon Rose’ plants when grown under LDs at 14 ºC or 20 ºC, respectively.

Temperature did not influence leaf number below the first open flower in all three varieties, irrespective of photoperiod (Figures 4.3G-I). Except in ‘Easy Wave Neon Rose’, there was a developmental delay in flowering under SDs, irrespective of ADT. Branching was greater in all three varieties under SDs compared to LDs, regardless of ADT (Figures 4.4A-C). Temperature did not influence branch number at flowering in ‘Classic Wave Purple’ and ‘Improved Wave Purple’ under either photoperiod; and in ‘Easy Wave Neon Rose’ under SDs. However, ‘Easy Wave Neon Rose’ plants grown LDs had 30% greater branching at 14 ºC compared to 20 ºC.

The effect of temperature and photoperiod on flower number at first flowering and two weeks after flowering varied among varieties (Figures 4.4D-I). ‘Easy Wave Neon Rose’ and ‘Improved Wave Purple’ plants grown under SDs generally had a greater flower number than plants under LDs, whereas the opposite occurred in ‘Classic Wave Purple’. Flower number recorded at flowering and two weeks after flowering was similar between temperature treatments for ‘Easy Wave Neon Rose’ grown under SDs, and ‘Improved Wave Purple’ grown under LDs. In contrast, ‘Easy Wave Neon Rose’ and ‘Classic Wave Purple’ plants grown under LDs, and ‘Improved Wave Purple’ grown under SDs, had a greater flower number (at and 2 weeks after flowering) at 14 ºC compared to 20 ºC. Except in ‘Classic Wave Purple’ plants grown at 20 ºC with SDs, all the petunia varieties studied had 51 to 226% more flower buds 2 weeks after flowering than those recorded at first flowering. Flower bud abortion was observed in all the petunia varieties grown under SDs in this study, but data was not recorded.

Discussion

Petunia 'Easy Wave Neon Rose' became receptive to inductive LDs very early in development (≤ 4 leaves), since the leaf number below the first open flower was similar for plants grown under continuous LDs until flowering (at 20 ºC), and those transferred to SDs after unfolding 4 to 12 leaves under LDs (Figures 4.2 and 4.3G). A similar leaf number below the first open flower in 'Easy Wave Neon Rose' grown under different photoperiods further demonstrates that these plants were induced prior to unfolding 8 leaves. Flowering time was greater in plants grown under SDs after induction compared to those grown under continuous LDs until flowering, although they all flowered at a similar leaf number (Figures 4.1 and 4.3B). We speculate that flower bud abortion or delayed development under non-inductive photoperiod may have delayed flowering in previously induced plants. Flower bud abortion or delayed development under non-inductive photoperiods has been reported in some crops such as chrysanthemum, butterfly flower (*Asclepias tuberosa* L.), dahlia (*Dahlia pinnata* Cav.), and snapdragon (Adams et al., 1998b; 2003; Albrecht and Lehmann, 1991; Brøndum and Heins, 1993). Brøndum and Heins (1993) observed complete flower bud abortion in the facultative SD plant dahlia when grown at 25 ºC under non-inductive photoperiods (>14 h).

'Improved Wave Purple' and 'Classic Wave Purple' became sensitive to photoperiod after unfolding 8 leaves, since plants transplanted at the 8-leaf stage and grown under LDs developed significantly fewer leaves prior to flowering than those grown under SDs, irrespective of ADT. Although leaf number and DTF were not significantly influenced by the reciprocal transfer treatments in ‘Improved Wave Purple’, plants transferred to LDs earlier in development (before unfolding 10 leaves) or transferred to SDs later in development (with 10 or 12 leaves) generally formed fewer leaves (35 to 39) compared to the remaining treatments (43 to 48). ‘Improved Wave Purple’ plants with 10 leaves received 4 LDs (Table 1), which was probably not sufficient for floral induction. Incomplete floral induction may have caused the variability observed in leaf number and DTF data recorded for this variety.

‘Classic Wave Purple’ demonstrated a strong photoperiodic response in this study. For example, nearly all of the plants transferred to LDs after unfolding 4 or 6 leaves flowered, whereas only 40% of those unfolding 12 leaves under LDs flowered (Figures 4.1B). Interestingly, Adams et al. (1998) reported that chrysanthemum plants exposed to LDs prior to SDs (inductive) required fewer SDs for flowering compared to those grown under continuous SDs. For example, chrysanthemum plants grown under 53 LDs and then transferred to inductive SDs flowered after 49 SDs, whereas those grown under continuous SDs required 57 SDs for flowering. This may be due to increased sensitivity to inductive conditions with plant age, since 7-d old arabidopsis (*Arabidopsis thaliana* Heynh.) plants needed 5 LDs to induce flowering, whereas only a single inductive cycle was sufficient to induce flowering in 20-d old plants (Mozley and Thomas, 1995). The progressive decrease in flowering percentage with an increase in plant age when transferred to LDs, and vice versa, suggests that similar to ‘Improved Wave Purple’, plants may not have received a sufficient number of LDs for floral induction. In addition, ‘Classic Wave Purple’ plants that flowered under SDs (at 20 ºC) in both experiments did not develop additional flowers (data not presented), which suggests that induced plants reverted to a vegetative state under non-inductive conditions.

Flowering was delayed at 14 ºC compared to 20 ºC in all the petunia varieties studied, irrespective of photoperiod. This was expected, since several studies have reported a decrease in days to flower (DTF) with an increase in ADT in petunia (Adams et al., 1996; 1998a; Blanchard et al., 2011; Kaczsperski et al., 1991; Warner, 2010). For example, *Petunia ×hybrida* 'Snow Cloud' and 'Mitchell' flowered 22 d and 35 d earlier, respectively, at 20 ºC than at 14 ºC when grown under a 16- or 18-h photoperiod and a DLI of 13 or 16.5 $mol \cdot m^{-2} \cdot d^{-1}$ (Kaczsperski et al., 1991; Warner, 2010). Similarly, Blanchard et al. (2011) reported a 24 or 25 d delay in flowering time in petunia 'Easy Wave Coral Reef' and 'Wave Purple' when grown at 14 ºC versus 20 ºC and under a DLI of 10 $mol \cdot m^{-2} \cdot d^{-1}$.

Interestingly, temperature modified the flowering response to photoperiod in all the petunia varieties studied. Temperature had a greater effect on flowering time under LDs than SDs, whereas the LD response decreased at 14 ºC compared to 20 ºC in this study. Growing plants at 14 versus 20 ºC delayed flowering by 18% or 95% in 'Easy Wave Neon Rose' and by 15% or 110% in 'Improved Wave Purple' when grown under SDs or LDs, respectively. Similarly, LDs promoted flowering by 18% or 95% in 'Easy Wave Neon Rose' and by 66% or 202% in 'Improved Wave Purple' when grown at 14 or 20 ºC, respectively. This response was particularly strong in 'Classic Wave Purple', which demonstrated a nearly obligate LD response at 20 ºC, whereas a majority of plants flowered under SDs at 14 ºC, and nonflowering plants had visible buds. These results are consistent with those reported by Adams et al. (1996) in trailing petunias; growing petunia 'Malve' at 14 versus 20 ºC delayed the flowering time by 30% under an 8-h photoperiod and 72% under a 16-h photoperiod. Similarly, 16-h LDs compared to 10-h SDs decreased the predicted flowering time of this variety by 88% at 20 ºC and by 42% at 14 ºC.

Except for flower number in 'Classic Wave Purple' and leaf number in 'Easy Wave Neon Rose' in Expt. 2, treatments that promoted flowering generally had a lower quality (flower and branch number) and leaf number at flowering. Similarly, a positive correlation between flowering time, leaf number below the first open flower, and plant quality was reported by Warner (2009) in celosia. Faster flowering is sometimes offset by reduced plant quality in many species, since plants intercept light for a shorter duration (Pramuk and Runkle, 2005a; Warner, 2009). A decrease in DTF from 43 d under 4 $mol \cdot m^{-2} \cdot d^{-1}$ to 33 d under 14 $mol \cdot m^{-2} \cdot d^{-1}$, decreased the leaf number, flower number, and dry weight by 39, 84, and 56%, respectively (Pramuk and Runkle, 2005a). In addition, branch number, flower number at flowering and 2 weeks after flowering was greater for plants grown at 14 ºC compared to 20 ºC, regardless of photoperiod. These responses to ADT are consistent with previous studies in petunia (Adams et al., 1996; Blanchard et al., 2011; Kaczperski et al., 1991). For example, petunia 'Wave Purple' and 'Easy Wave Coral Reef' plants grown at 14 versus 20 ºC and under a DLI of 10.0 $mol \cdot m^{-2} \cdot d^{-1}$ had 17 and 6% greater inflorescences, respectively (Blanchard et al., 2011). Similarly, Kaczperski et al. (1991) reported a quadratic decrease in the number of lateral shoots with an increase in ADT from 10 to 30 ºC.

In general, the length of the juvenile phase, the minimum number of cycles required for floral induction, and flowering responses to temperature and photoperiod varied among the petunia varieties studied. Previous studies in celosia, snapdragon, and whiteedge morning-glory have reported a similar varietal difference in photoperiodic behavior (Adams et al., 2003; Imamura et al., 1966; Warner, 2009). For example, the juvenile stage in snapdragon varied from 9.9 leaves in 'Chimes' to 28.8 leaves in 'Annabel' (Adams et al., 2003). Similarly, 1, 2, and 10

SDs were required to induce flowering in whiteedge morning-glory ‘Kidachi’, ‘Nepal’, and ‘Africa’, respectively (Imamura et al., 1966).

Petunia ‘Easy Wave Neon Rose’ became sensitive to photoperiod after unfolding ≤4 leaves, whereas ‘Classic Wave Purple’ and ‘Improved Wave Purple’ became sensitive after unfolding >8 leaves. However, the duration of the juvenile phase may be confounded with the number of inductive cycles required for flowering in this study, especially since plant age may influence sensitivity to photoperiod in some species (Mozley and Thomas, 1995). Further research using limited inductive photoperiod at regular intervals during development may help identify the precise juvenile phase and minimum number of inductive cycles needed for complete floral induction. In addition, flower bud abortion observed under non-inductive conditions in this study suggests that flower bud development in the petunia varieties studied is sensitive to photoperiod, although some petunia varieties may have a distinct photoperiod-sensitive phase (Adams et al., 1999). Experiments using reciprocal transfers until flowering may be performed on additional popular petunia varieties to identify the photoperiod sensitive phases.

Table 4.1. Days from start of photoperiodic treatments to reciprocal transfer at different stages of development (leaf number) in three petunia cultivars during the transplant stage.

	Leaf number at photoperiodic transfer				
Petunia cultivar	4	6	8	10	12
Easy Wave Neon Rose	13	16	19	22	25
Classic Wave Purple	13	19	22	26	30
Improved Wave Purple	13	16	19	21	24

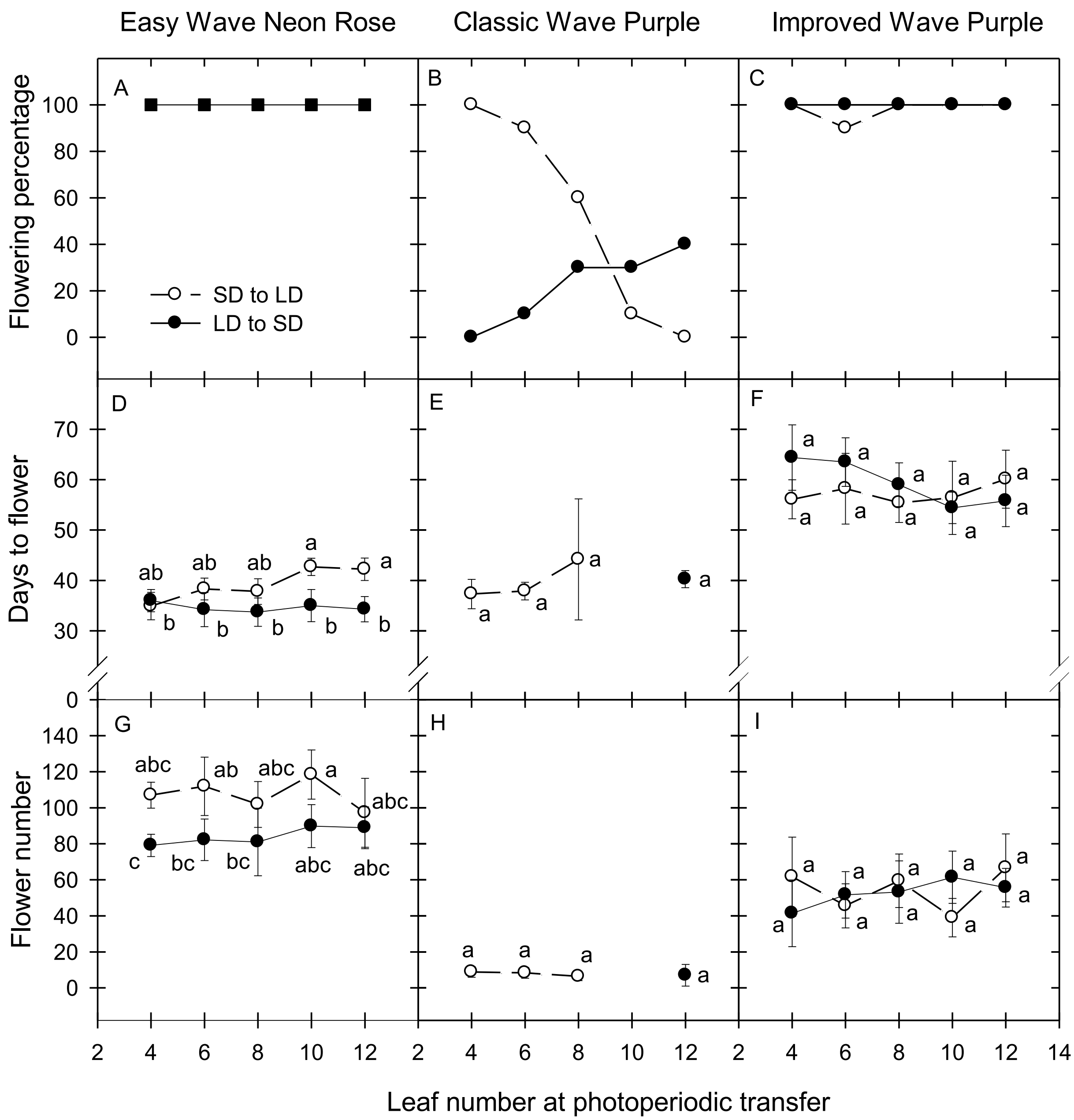

Figure 4.1. The effect of transferring plants at different stages of development (leaf number) from long days (LD, 16 h·d^{-1}) to short days (SD, 10 h·d^{-1}) (●), and from SD to LD (○) during the transplant stage on flowering characteristics of three petunia varieties. Plants were transplanted at 12-leaf stage and grown in a greenhouse maintained at a constant setpoint of 20 °C with a 10 h photoperiod. Each symbol represents the treatment means, and error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Treatments that had ≤ 30% flowering are not shown, except for flowering percentage.

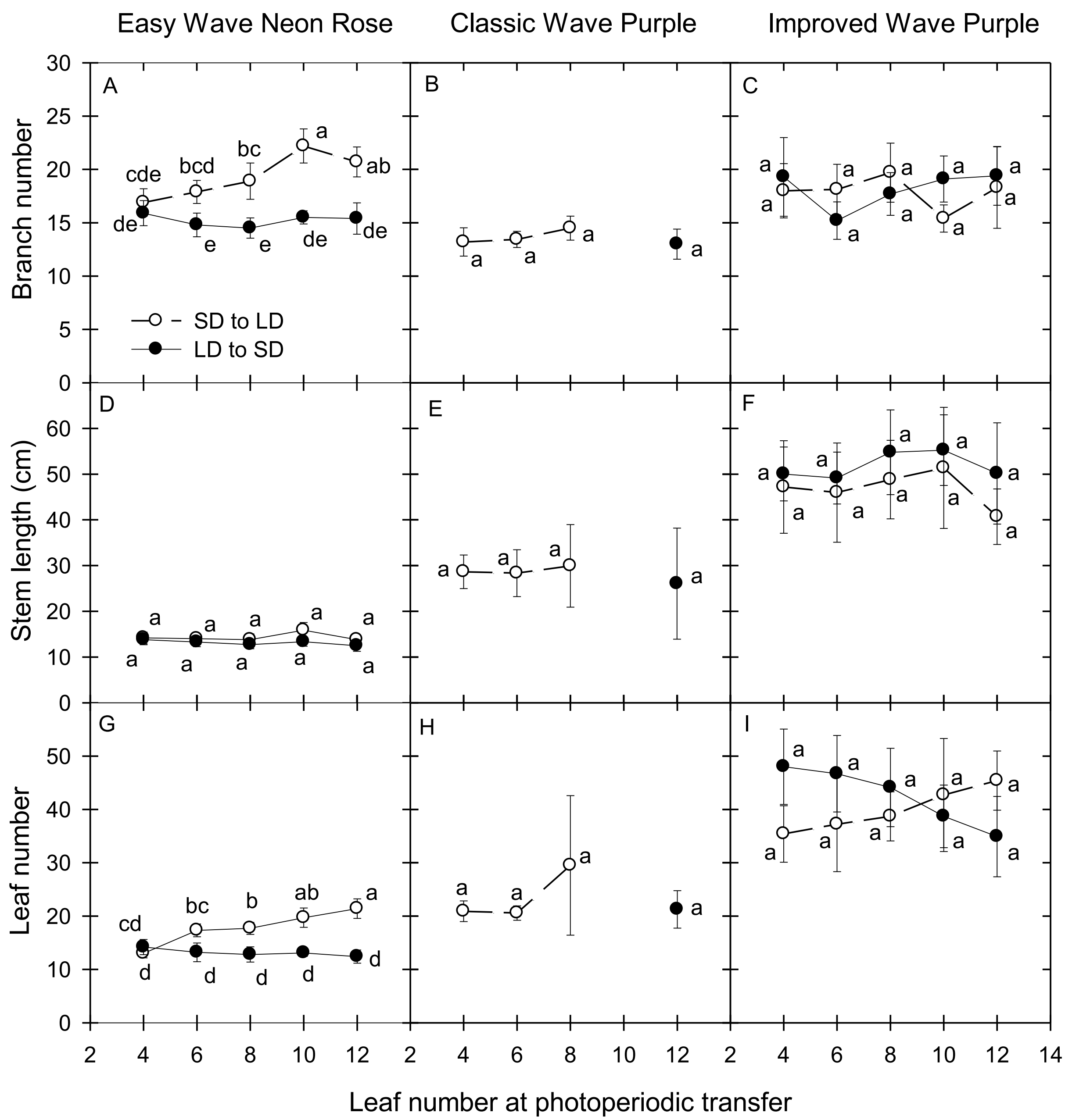

Figure 4.2. The effect of transferring plants at different stages of development (leaf number) from long days (LD, 16 h·d^{-1}) to short days (SD, 10 h·d^{-1}) (●), and from SD to LD (○) during the transplant stage on flowering characteristics of three petunia varieties. Plants were transplanted at 12-leaf stage and grown in a greenhouse maintained at a constant setpoint of 20 °C with a 10 h photoperiod. Each symbol represents the treatment means, and error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Treatments that had ≤ 30% flowering are not shown.

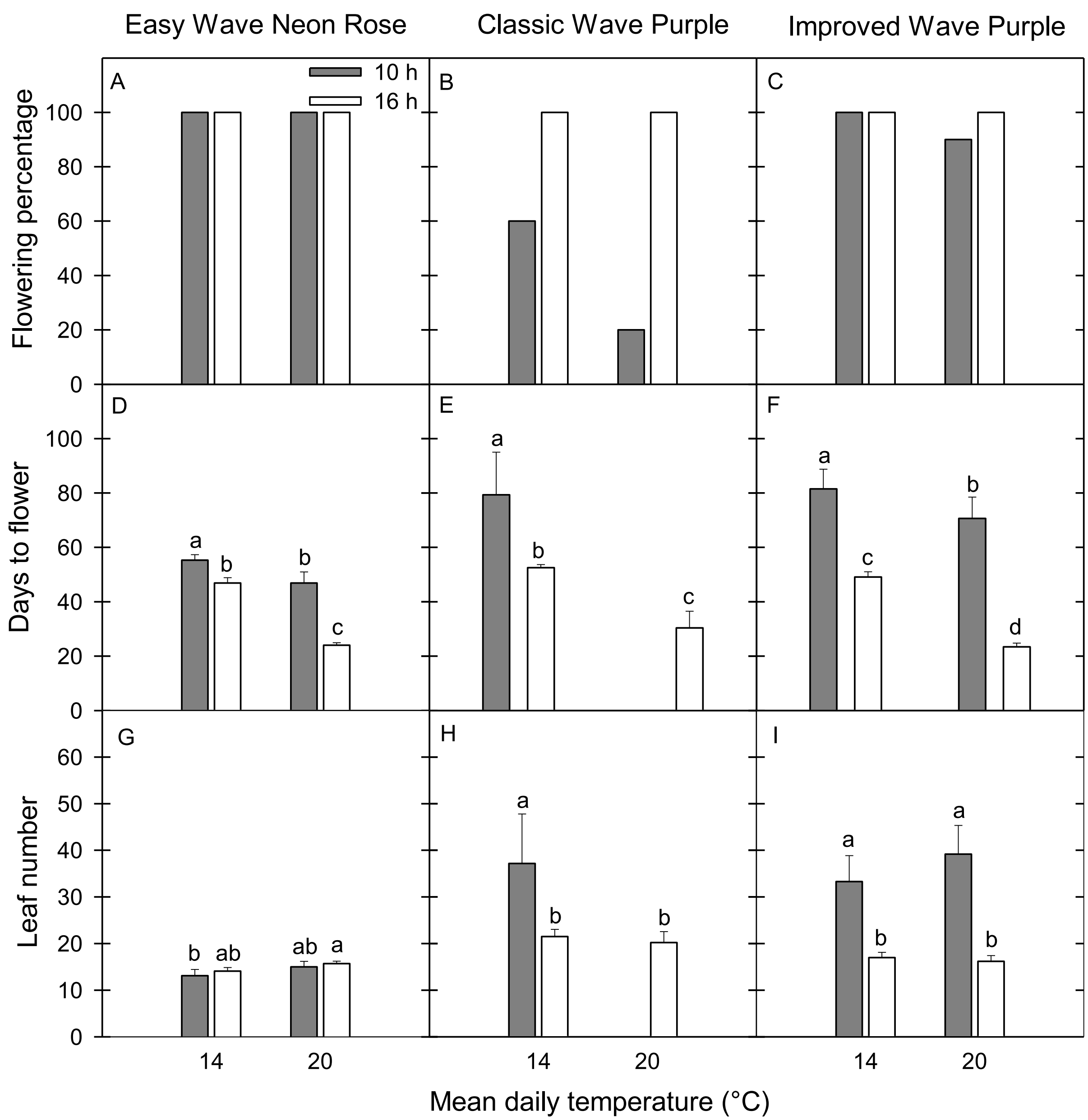

Figure 4.3. The effect of photoperiod (10 or 16 h·d^{-1}) on flowering characteristics of three petunia varieties grown at 14 or 20 °C. Plants were initially grown at a constant setpoint of 20 °C with a 16 h photoperiod in an environmental growth chamber, and then transplanted when they averaged 8 leaves. Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Treatments that had ≤ 30% flowering are not shown, except for flowering percentage.

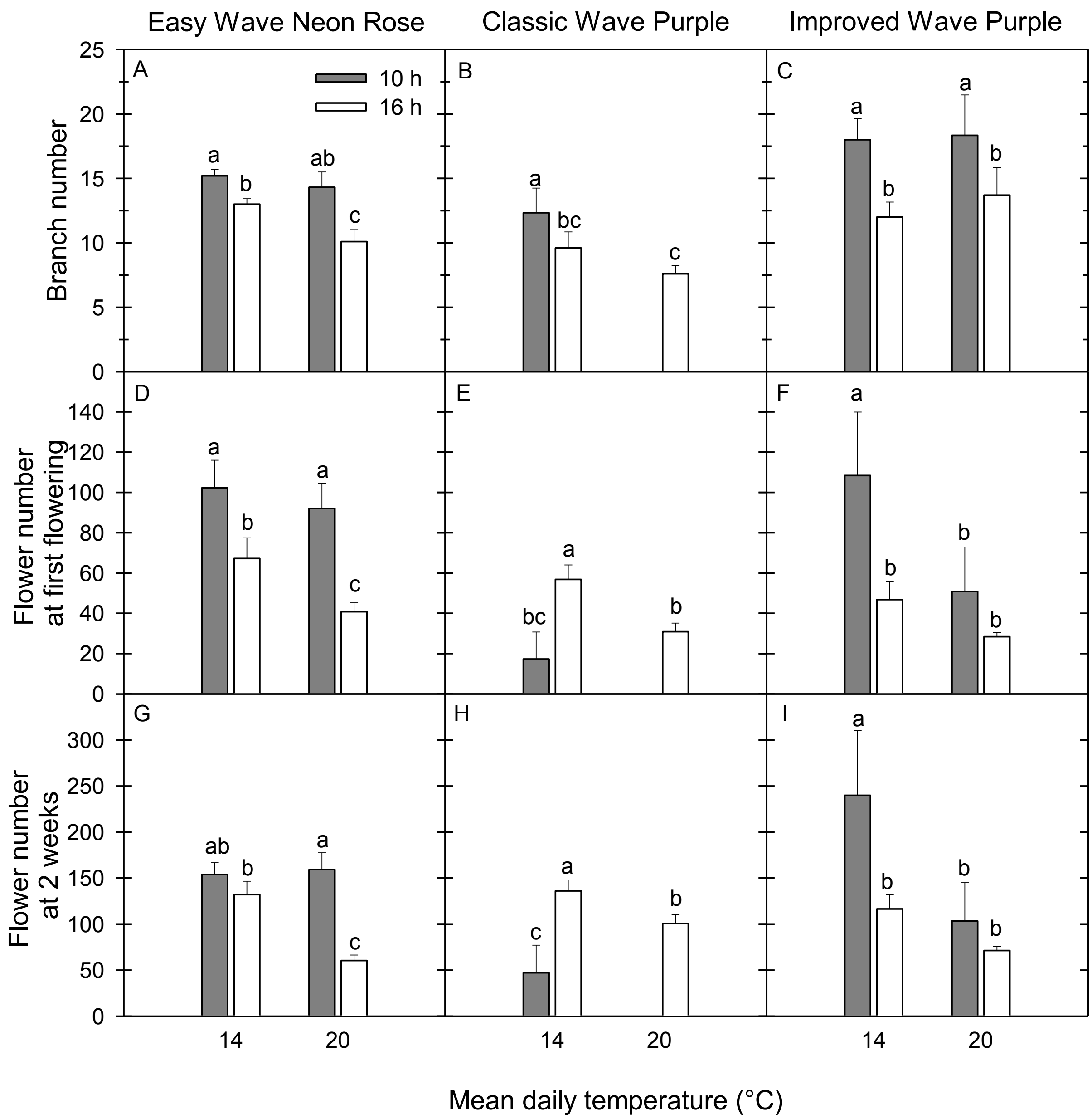

Figure 4.4. The effect of photoperiod (10 or 16 h·d^{-1}) on flowering characteristics of three petunia varieties grown at 14 or 20 °C. Plants were initially grown at a constant setpoint of 20 °C with a 16 h photoperiod in an environmental growth chamber, and then transplanted when they averaged 8 leaves. Error bars represent the standard errors. Means followed by the same letter are not statistically different ($P \leq 0.05$). Treatments that had ≤ 30% flowering are not shown.

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APPENDIX

MODELING PLANT DEVELOPMENT AND QUALITY PARAMETERS OF 16 PETUNIA VARIETIES IN RESPONSE TO AVERAGE DAILY TEMPERATURE UNDER TWO DAILY LIGHT INTERGRAL ENVIRONMENTS

Research Objective

The objectives of this study were to quantify and model the influence of average daily temperature (ADT) on flowering characteristics of 16 Wave varieties of petunia under two photosynthetic daily light integral (DLI) conditions.

Materials and Methods

Plant material. Experimental protocol and data collection and analysis were similar to that reported by Blanchard and Runkle (2011) and Pramuk and Runkle (2005). On 10 January 2011, seeds of petunia (*Petunia ×hybrida* Vilm.-Andr.) 'Easy Wave Blue', 'Easy Wave Burgundy Star', 'Easy Wave Neon Rose', 'Easy Wave Pink', 'Easy Wave Plum Vein', 'Easy Wave Red Improved', 'Easy Wave Violet', 'Easy Wave White', 'Shock Coconut', 'Shock Denim', 'Shock Wave Purple, 'Tidal Wave Silver', 'Wave Blue', 'Wave Pink', 'Wave Purple Classic', and 'Wave Purple Improved' were sown in 288-cell (6-mL) plug trays by a commercial greenhouse (C. Raker & Sons, Litchfield, MI). After germination, seedlings were received at Michigan State University (MSU) on 20 January 2011 and grown in controlled environment chambers until deemed ready for transplant.

Growth chamber treatments and environment. Seedlings were grown in the controlled environment chambers at a constant temperature setpoint of 20 ºC under a *PPF* of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ DLI ≈ 10 $mol \cdot m^{-2} \cdot d^{-1}$) provided by a combination of cool-white fluorescent (CWF; F96T12CWVHO; Philips, Somerset, NJ) and incandescent lamps (INC, Philips, Somerset, NJ) with a 16-h photoperiod. The light intensity was checked periodically with an instantaneous quantum sensor (Apogee Instruments Inc., Logan, UT) at canopy height and adjustments were made by replacing and/or lowering the lamps when required. Plugs were hand-irrigated as necessary with acidified well water (140 mg·L^{-1} titratable alkalinity of $CaCO_3$) containing (mg·L^{-1}) 95, 34, and 29 Ca, Mg, and S, respectively, and supplemented with a water-soluble fertilizer providing (mg·L^{-1}) 62 N, 6 P, 62 K, 7 Ca, 0.5 Fe, 0.3 Cu, Mn, and Zn, and 0.1 B and Mo (MSU Well Water Special; GreenCare Fertilizers Inc., Kankakee, IL).

Greenhouse treatments and environment. After 28 d from seed sowing, seedlings with six to eight leaves were transplanted into 10-cm round (480-mL) containers filled with a peat-based medium (Suremix, Michigan Grower Products, Galesburg, MI). The mean leaf number at transplant was recorded for each variety. Seedlings were thinned to one plant per cell prior to transplant and 20 plants of each species were grown in separate glass-glazed greenhouse compartments at constant temperature set points of 12, 15, 18, 21, or 24 °C and 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 (HPS) lamps. Plants were treated with a 250 ml paclobutrazol (Piccolo, Fine Americas Inc., Walnut Creek, CA) drench at 4 mg·L^{-1} 7 to 10 d after transplant to inhibit extension growth. In each temperature treatment, plants were grown under two DLIs with 10 plants under each temperature and DLI combination. A low DLI was created by using ambient light with 50% shade curtains (OLS 50; Ludvig Svensson Inc., Charlotte, NC) and supplemental lighting from HPS lamps that provided a *PPF* of 25 to 50 µmol·m^{-2}·s^{-1} at canopy height (22 cm above bench height). Plants under the high DLI treatment were grown under ambient light without a shade curtain and with supplemental HPS lighting that provided a *PPF* of 80 to 100 µmol·m^{-2}·s^{-1} at canopy height. The HPS lamps were programmed to turn on when outside light intensity was <290 µmol·m^{-2}·s^{-1} and turn off at >580 µmol·m^{-2}·s^{-1} by an environmental computer system (Priva Intégro 724; Priva, Vineland Station, Ontario, Canada). In each greenhouse compartment, a shielded and aspirated 0.13 mm type E thermocouple (Omega Engineering, Stamford, CT) recorded the air temperature and a line quantum sensor containing 10 photodiodes (Apogee Instruments) placed at canopy height (22 cm above bench height) measured light intensity. A CR10 datalogger (Campbell Scientific, Logan, UT) collected the environmental data every 10 s and hourly averages were recorded. Actual average air temperatures in the greenhouse during the experiment were 12.7, 15.0, 18.1, 21.0, or 23.4 ºC. Mean DLI under the low and high DLI treatments were 7.1 and 13.7 $mol \cdot m^{-2} \cdot d^{-1}$, respectively. Vapor pressure deficit was maintained at 1.2 kPa by steam injection at night (2200 to 0800 HR). Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing ($mg \cdot L^{-1}$) 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 Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Data collection and analysis: Plants were considered in flower when the first flower fully opened on each plant. At first flowering, the date was recorded and days to flower from transplant were calculated. Flower and flower bud number, axillary branch number, and length of the longest lateral were also recorded at first open flower. When flowering was on the primary stem, the number of nodes below the first open flower was recorded, whereas when the first flower opened on a lateral branch, the total node number (flowering lateral + primary stem below flowering lateral) was counted. The experiment was arranged as a split-plot design; five temperatures (whole plot factor) were randomly assigned to the greenhouse compartments, and two DLI treatments (sub-plot factor) were randomly assigned to the experimental units (plants) within each temperature treatment.

SAS (SAS Institute, Cary, N.C.) was used to analyze the experimental data. Linear and quadratic regression (REG procedure) analysis was used to generate equations to describe the effect of ADT on plant quality parameters under low and high DLI conditions. Linear regression analysis was independently performed on the flowering rate data generated under the two DLIs, and the slope and intercept values generated from these equations were used to calculate the estimated base temperatures (T_{min}) for each species (Roberts and Summerfield, 1987). Many researchers have estimated the T_{min} and described the flowering time response as a function of ADT using linear regression when T_{min} < ADT < T_{opt} (optimum temperature) (Clough et al., 2001; Niu et al., 2000, 2001; Pietsch et al., 1995; Whitman et al., 1997; Yuan et al., 1998):

$$1/\text{d to flower} = b_0 + b_1 \times \text{ADT} \quad (1)$$

where 1/d to flower = the rate of progress towards flowering, b_1 = slope, b_0 = intercept, and ADT = average daily temperature (°C) above T_{min} and below T_{opt}. Given that the developmental rate at T_{min} is zero, equation (1) can be used to calculate T_{min}:

$$T_{min} = -\, b_0 / b_1 \quad (2)$$

where T_{min} = temperature at or below which the flower development rate is zero.

Results

Flower development rate linearly increased with an increase in ADT from 12 to 24 ºC for all the petunia Wave varieties included in this study, and the nature of this response varied among the varieties (Figures 5.1-5.16A). For example, each degree increase in temperature from 12 to 24 ºC increased the rate of progress towards flowering from 0.0014 in ‘Easy Wave Pink’ to 0.0024 in ‘Shock Wave Purple’ (Figure 5.4 and 5.11). Linear models adequately described the effect of temperature on flowering rate in all the varieties studied, since the temperatures used in this experiment (12 to 24 ºC) were between T_{min} and T_{opt} for these varieties. The coefficients of determination generated for the linear models (r^2) ranged from 0.55 to 0.95 (data not presented). In some varieties, the variability in flowering time response differed between DLI treatments, which considerably influenced the r^2 values. For example, the r^2 values of ‘Shock Wave Denim’ varied from 0.81 under high DLI to 0.63 under low DLI mainly due to greater variability under the low DLI treatment (Figure 5.10A). The higher DLI accelerated flowering compared to the lower DLI in all the varieties irrespective of ADT (Figures 5.1-5.16A), and the absolute magnitude of this response was generally greater at lower temperatures. For example, ‘Shock Wave Denim’ plants grown under the higher DLI flowered 9 d and 29 d earlier at 24 ºC and 12 ºC, respectively (Figure 5.10A).

The estimated T_{min} for flower development rate varied among the petunia Wave varieties, and in some cases, also with the DLI (Figures 5.1-5.16A). For example, T_{min} ranged from 1.7 ºC to 7.7 ºC under the high DLI and from 3.5 to 7.5 under the low DLI for ‘Easy Wave Neon Rose’ and ‘Wave Pink’, respectively (Figures 5.3 and 5.14A). Except in ‘Wave Pink’ and ‘Wave Purple Improved’, T_{min} was 0.5 to 3.8 ºC higher under the low DLI conditions (Figures 5.1–5.16A). Petunia varieties in which the estimated T_{min} was ≤ 4 ºC regardless of the DLI were ‘Easy Wave Blue’, ‘Easy Wave Neon Rose’, ‘Easy Wave Pink’, and ‘Wave Blue’. Those with an estimated T_{min} between 4 to 8 ºC were ‘Easy Wave Red Improved’, ‘Shock Wave Coconut’, ‘Shock Wave Purple’, ‘Tidal Wave Silver’, ‘Wave Pink’, ‘Wave Purple Classic’, and ‘Wave Purple Improved’. The estimated T_{min} for some varieties, such as ‘Easy Wave Burgundy Star’, ‘Easy Wave Plum Vein’, ‘Easy Wave Violet’, ‘Easy Wave White’, and ‘Shock Wave Denim’, was ≤ 4 ºC under high DLI, but between 4 to 8 ºC under low DLI. There was a positive correlation ($P < 0.0001$) between the estimated T_{min} and delay in flowering time when plants were grown at 12 versus 24 ºC. For example, the percentage delay in flowering time when plants were grown at 12 ºC compared to 24 ºC was 177 to 181% in ‘Wave Pink’ (T_{min} = 7.5 to 7.7 ºC), and 90 to 108% in ‘Easy Wave Pink’ (T_{min} = 2.0 to 3.8 ºC).

In all petunia varieties grown under the low DLI treatment, flower number increased as ADT decreased from 24 to 12 ºC (Figures 5.1-5.16B). For example, as ADT decreased from 24 to 12 ºC, flower bud number increased by 121 and 143% in 'Tidal Wave Silver' and 'Easy Wave Violet', respectively. However, under the higher DLI, a similar decrease in ADT increased flower number for only 6 of the 16 varieties studied (Figures 5.3, 5.6, 5.7, 5.14-5.16). An optimum temperature for flower bud number was observed under the high DLI for 'Easy Wave Blue', 'Easy Wave Burgundy Star', 'Easy Wave Pink', 'Easy Wave Plum Vein', 'Easy Wave White', 'Shock Wave Denim', and 'Wave Blue' (Figures 5.1, 5.2, 5.4, 5.5, 5.8, 5.10, 5.13B). There was no significant relationship between ADT and flower number in 'Shock Wave Coconut', 'Shock Wave Purple', and 'Tidal Wave Silver' when grown under the high DLI environment (Figures 5.9, 5.11, 5.12B).

Lateral branch number was inversely related with ADT in 13 and 15 of the 16 petunia varieties grown under the high and low DLI conditions, respectively (Figures 5.1-5.16C). For example, within the temperature range studied, branch number in Easy Wave Violet linearly increased by 25 and 45% under the high and low DLI conditions, respectively. In 'Easy Wave Burgundy Star' grown under the low DLI, and 'Easy Wave Plum Vein', 'Easy Wave White, and 'Shock Wave Denim' grown under high DLI, branch number increased as temperature decreased until an optimum temperature, beyond which it decreased (Figures 5.2, 5.5, 5.8, 5.10C). In general, the high DLI treatment had a promotive effect on flower bud number and branch number, particularly at the moderate and higher temperatures, in most petunia varieties.

As ADT increased from 12 to 24 ºC, stem length decreased in 'Easy Wave Blue', 'Easy Wave Burgundy Star', 'Easy Wave Pink', 'Easy Wave Plum Vein', 'Easy Wave Violet', 'Easy Wave White', and 'Shock Wave Coconut' when grown under the low DLI (Figures 5.1, 5.2, 5.4, 5.5, 5.7, 5.8, 5.9). Under the same DLI conditions, stem length of 'Easy Wave Red Improved', 'Shock Wave Denim', 'Shock Wave Purple', 'Tidal Wave Silver', 'Wave Pink', and 'Wave Purple Classic' first decreased and then increased with ADT. In contrast, there was no significant effect of ADT on stem length in 'Easy Wave Neon Rose', 'Wave Blue', and 'Wave Purple Improved' (Figures 5.3, 5.6, 5.10-5.16D). ADT had varying effects on stem length among the petunia varieties grown under the high DLI (Figures 5.1-5.16D). For example, stem length was inversely correlated with ADT in 'Easy Wave Improved Red' and 'Shock Wave Coconut', whereas an opposite trend was observed in 'Easy Wave Neon Rose'. In 'Easy Wave Plum Vein' and 'Wave Pink', stem length first decreased with ADT, and then increased. In contrast, there was no significant relationship between ADT and stem length in the remaining 11 petunia varieties grown under the high DLI treatment. Plants grown at ≤14 ºC and under the low DLI had the longest lateral stems at flowering compared to all other treatments.

There was a developmental delay in flowering time (i.e., plants developed more nodes) with a decrease in temperature in ten petunia varieties grown under the high DLI and six varieties under the low DLI (Figures 5.1-5.16E). In contrast, ADT did not significantly influence node number in 'Easy Wave Plum Vein', 'Easy Wave Red Improved', 'Easy Wave Violet', and 'Shock Wave Coconut', regardless of the DLI (Figures 5.5-5.7, 5.9E). Similarly, there was no significant relationship between node number and ADT in 'Easy Wave Burgundy Star' and 'Shock Wave Denim' when grown under the low DLI; and 'Easy Wave Blue', 'Easy Wave Neon Rose', 'Easy Wave Pink', 'Easy Wave White', 'Wave Blue', and 'Wave Purple Improved' when grown under the high DLI (Figures 5.1-5.4, 5.8, 5.10, 5.13, 5.16E).

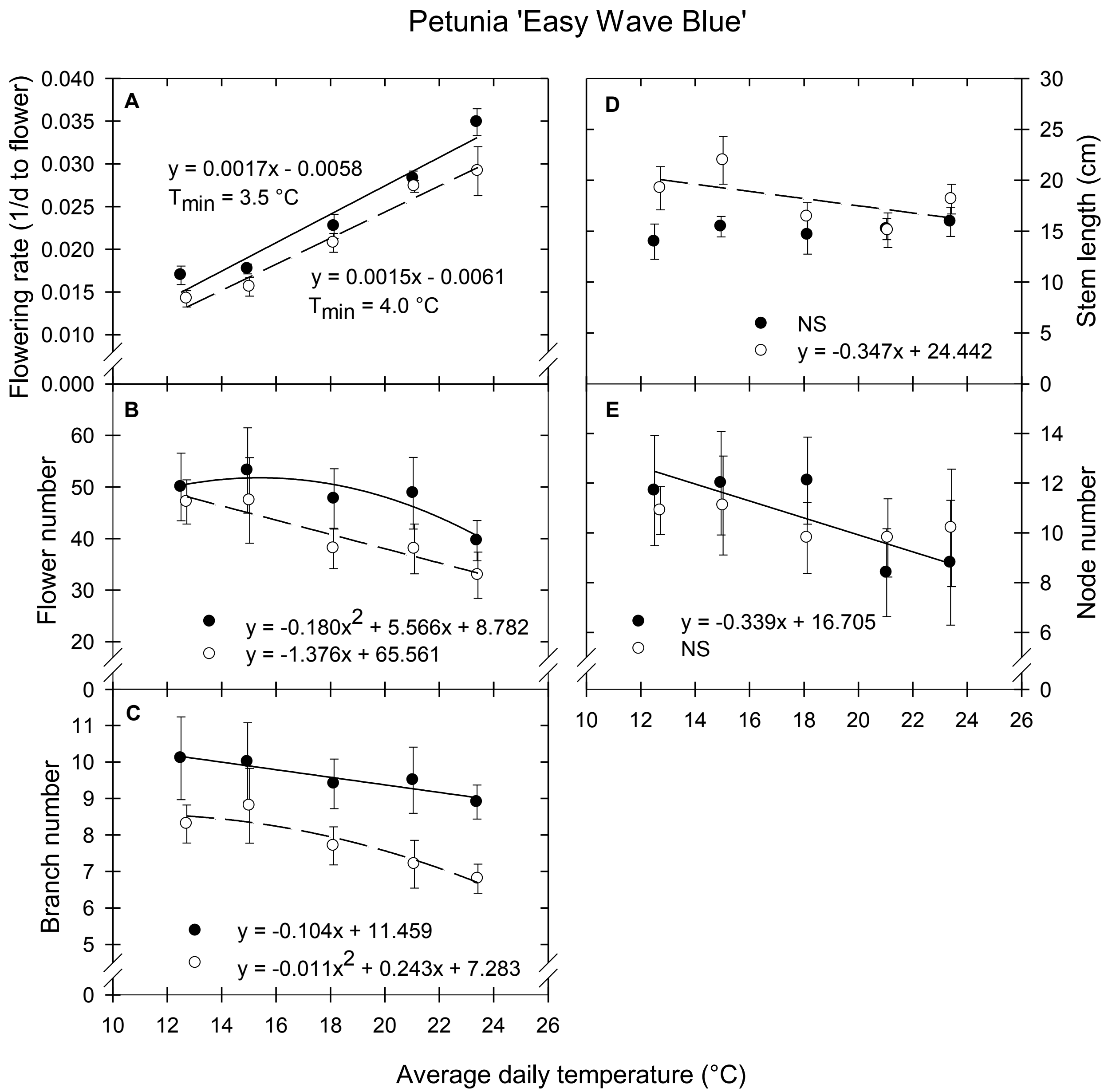

Figure 5.1. The effect of average daily temperature on flowering characteristics of petunia 'Easy Wave Blue' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at *P* > 0 .05.

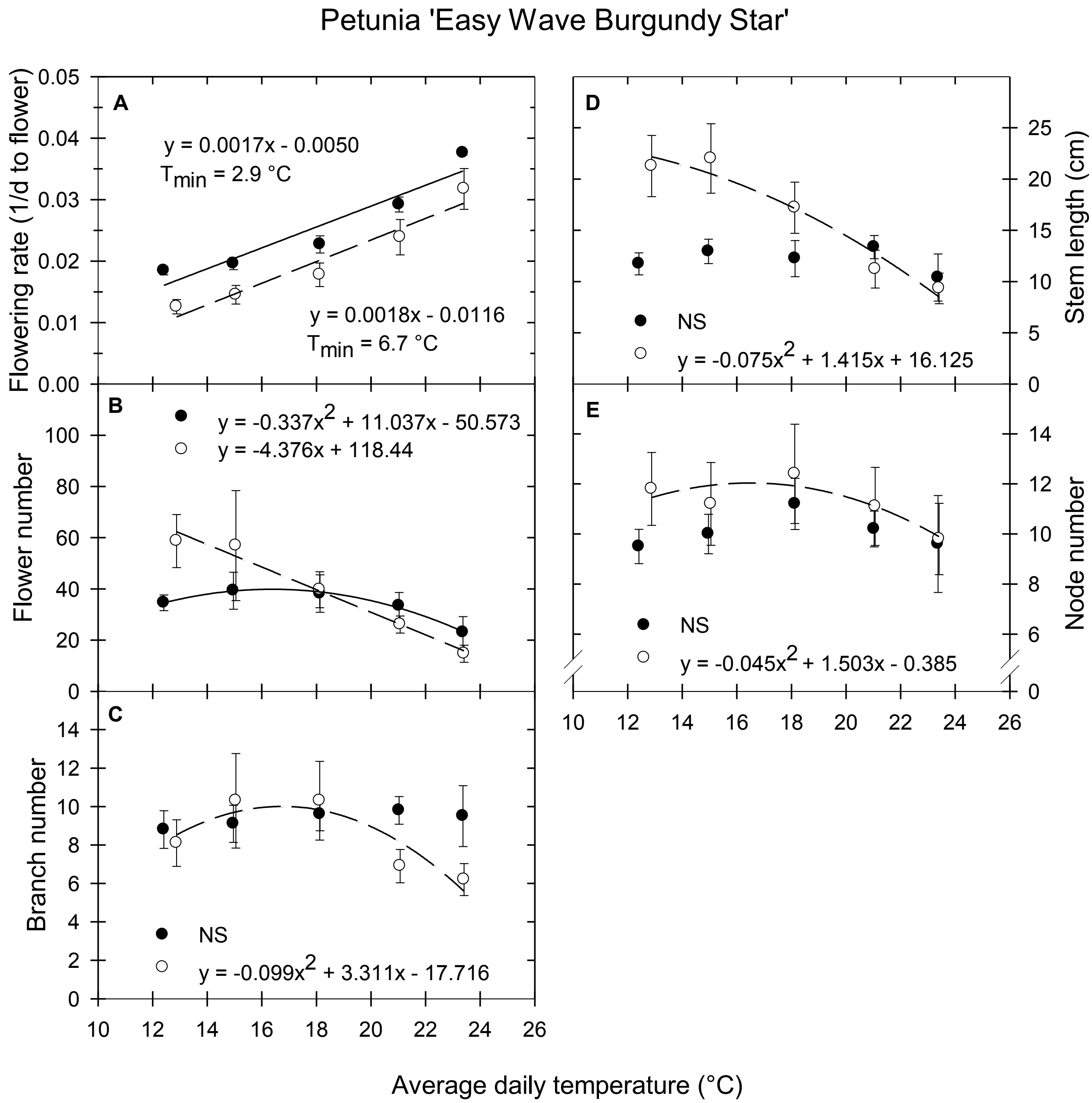

Figure 5.2. The effect of average daily temperature on flowering characteristics of petunia 'Easy Wave Burgundy Star' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at $P > 0\ .05$.

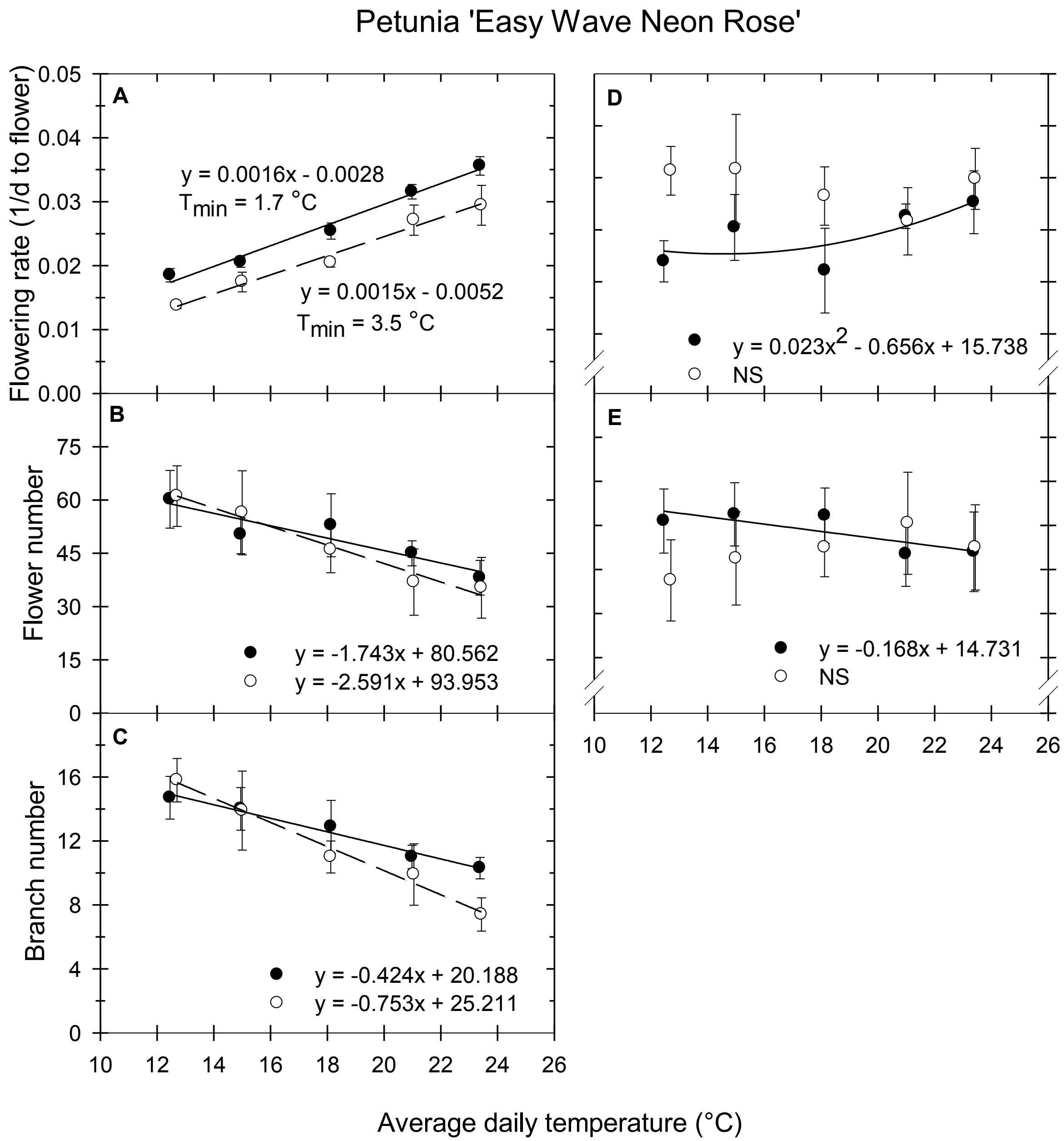

Figure 5.3. The effect of average daily temperature on flowering characteristics of petunia 'Easy Wave Neon Rose' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at $P > 0$ .05.

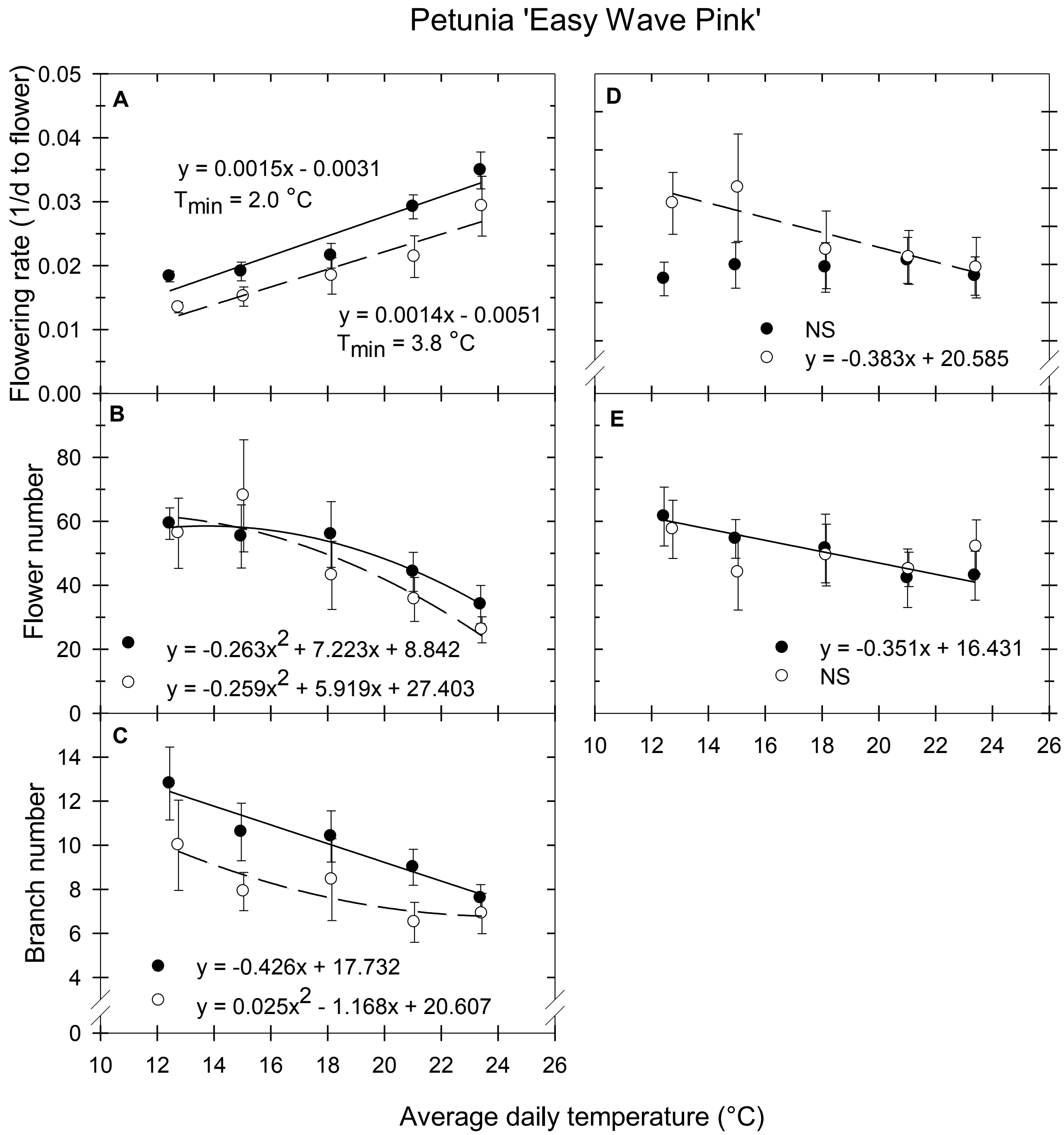

Figure 5.4. The effect of average daily temperature on flowering characteristics of petunia ‘Easy Wave Pink’ grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at *P* > 0 .05.

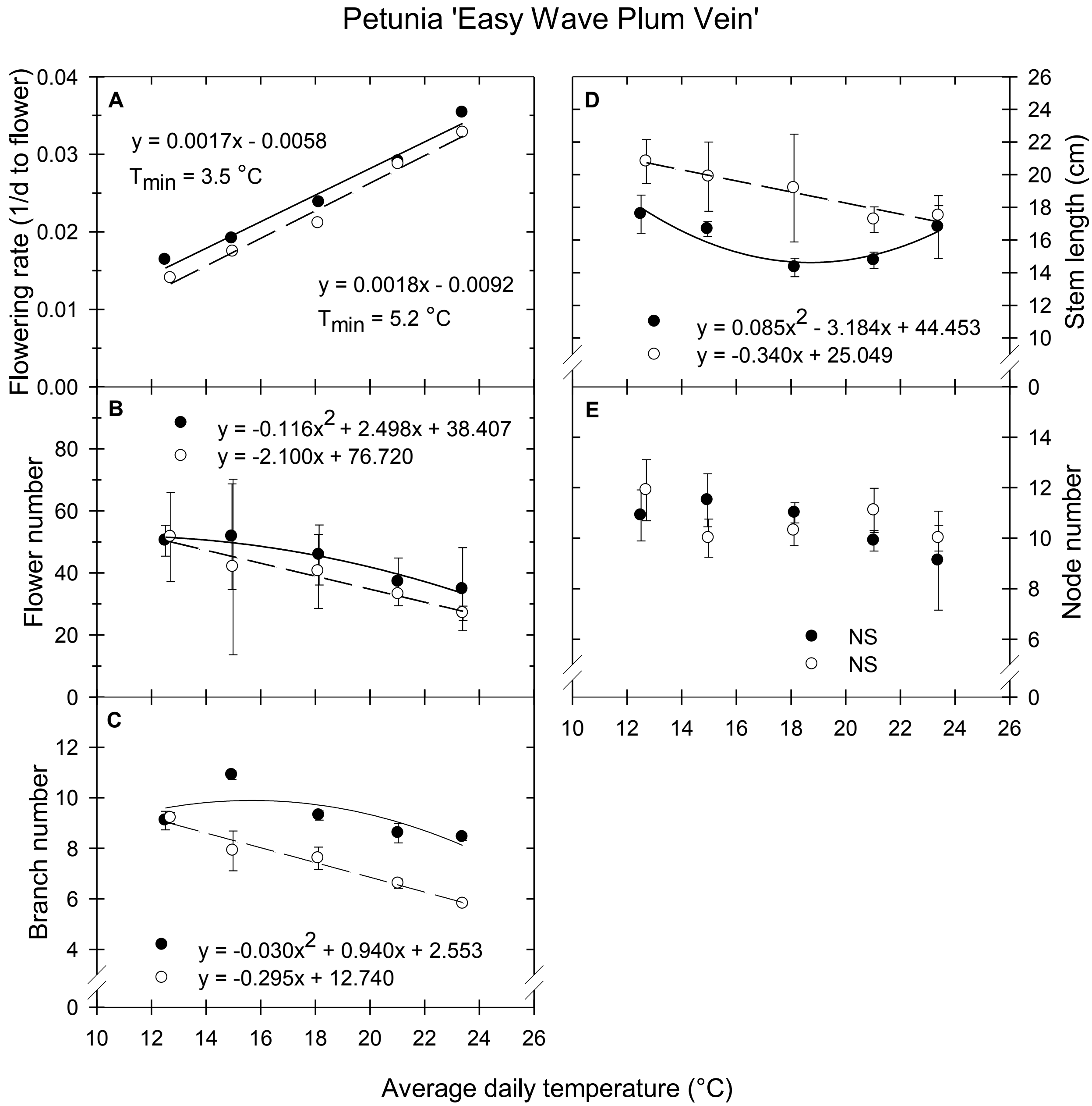

Figure 5.5. The effect of average daily temperature on flowering characteristics of petunia ‘Easy Wave Plum Vein’ grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at P > 0 .05.

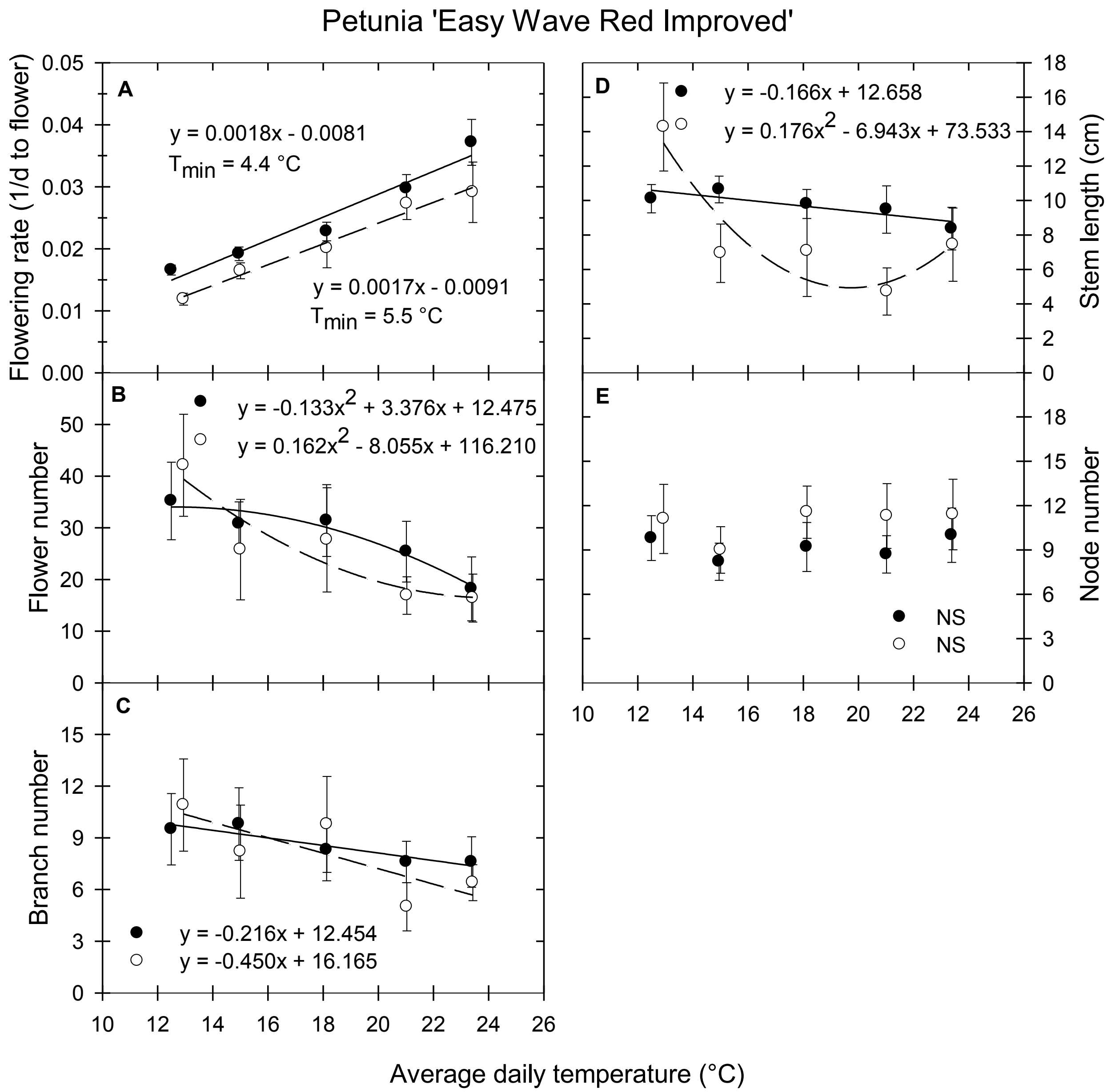

Figure 5.6. The effect of average daily temperature on flowering characteristics of petunia ‘Easy Wave Red Improved’ grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at *P* > 0 .05.

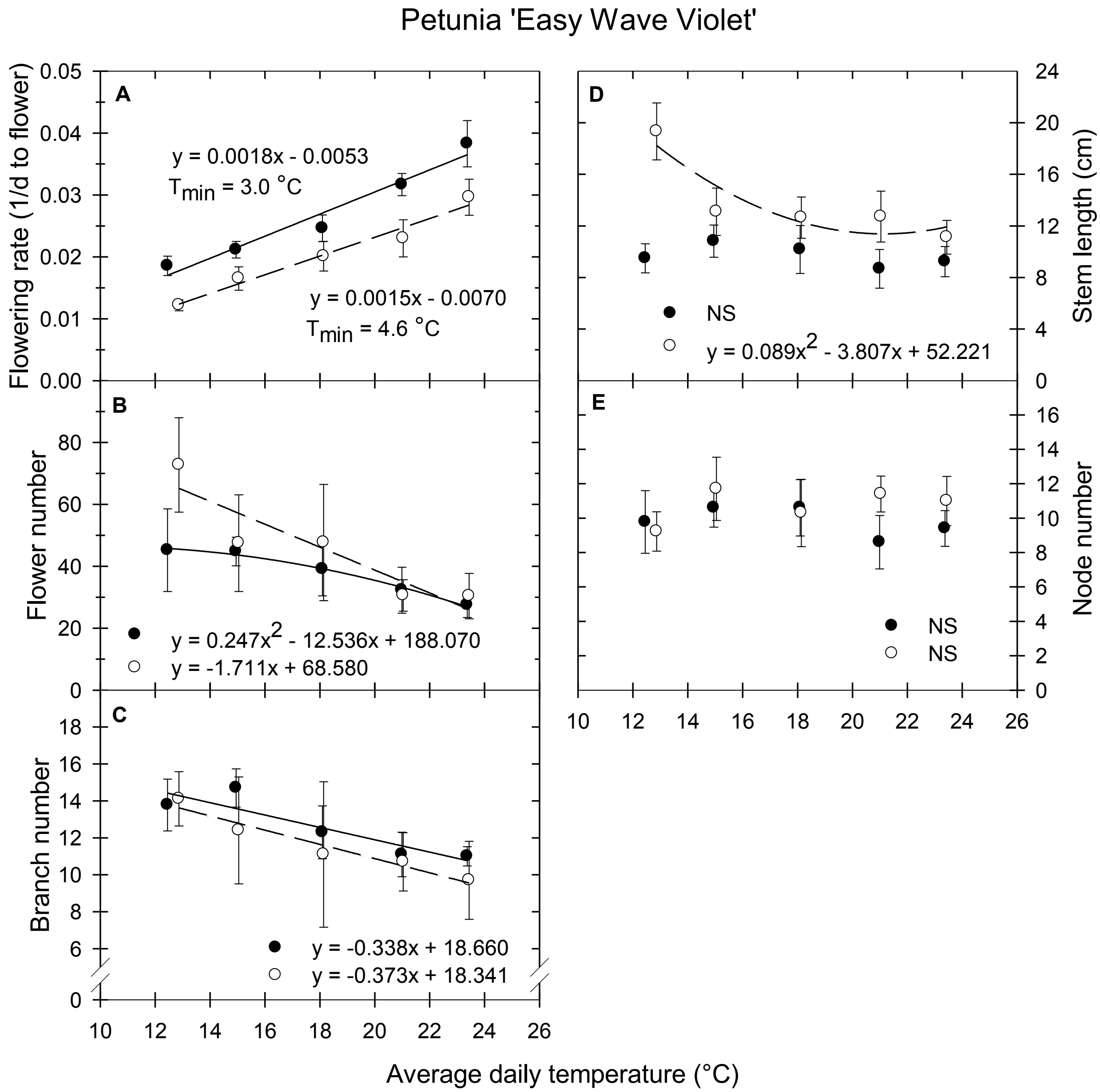

Figure 5.7. The effect of average daily temperature on flowering characteristics of petunia 'Easy Wave Violet' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at $P > 0$ .05.

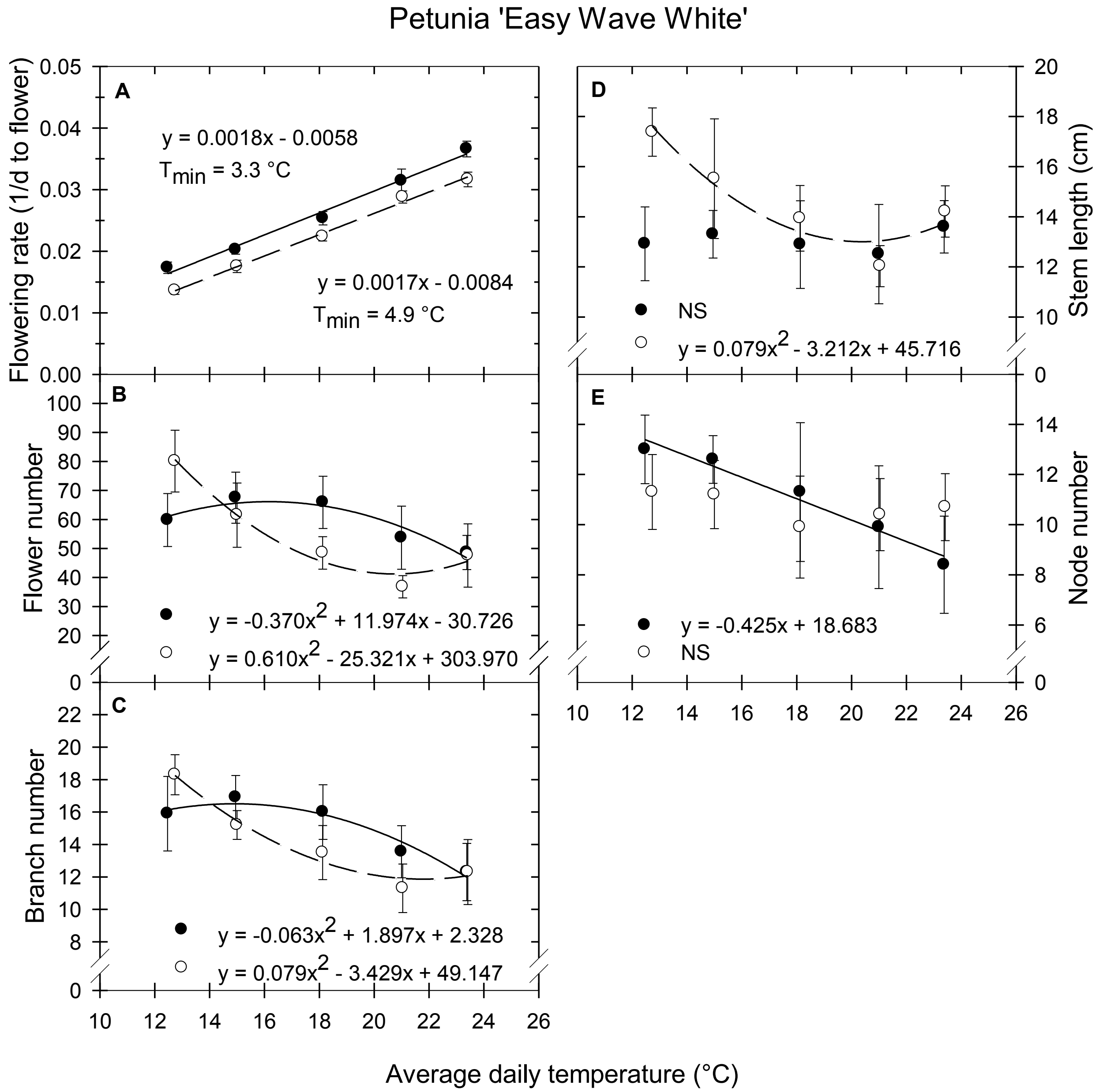

Figure 5.8. The effect of average daily temperature on flowering characteristics of petunia 'Easy Wave White' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at P > 0 .05.

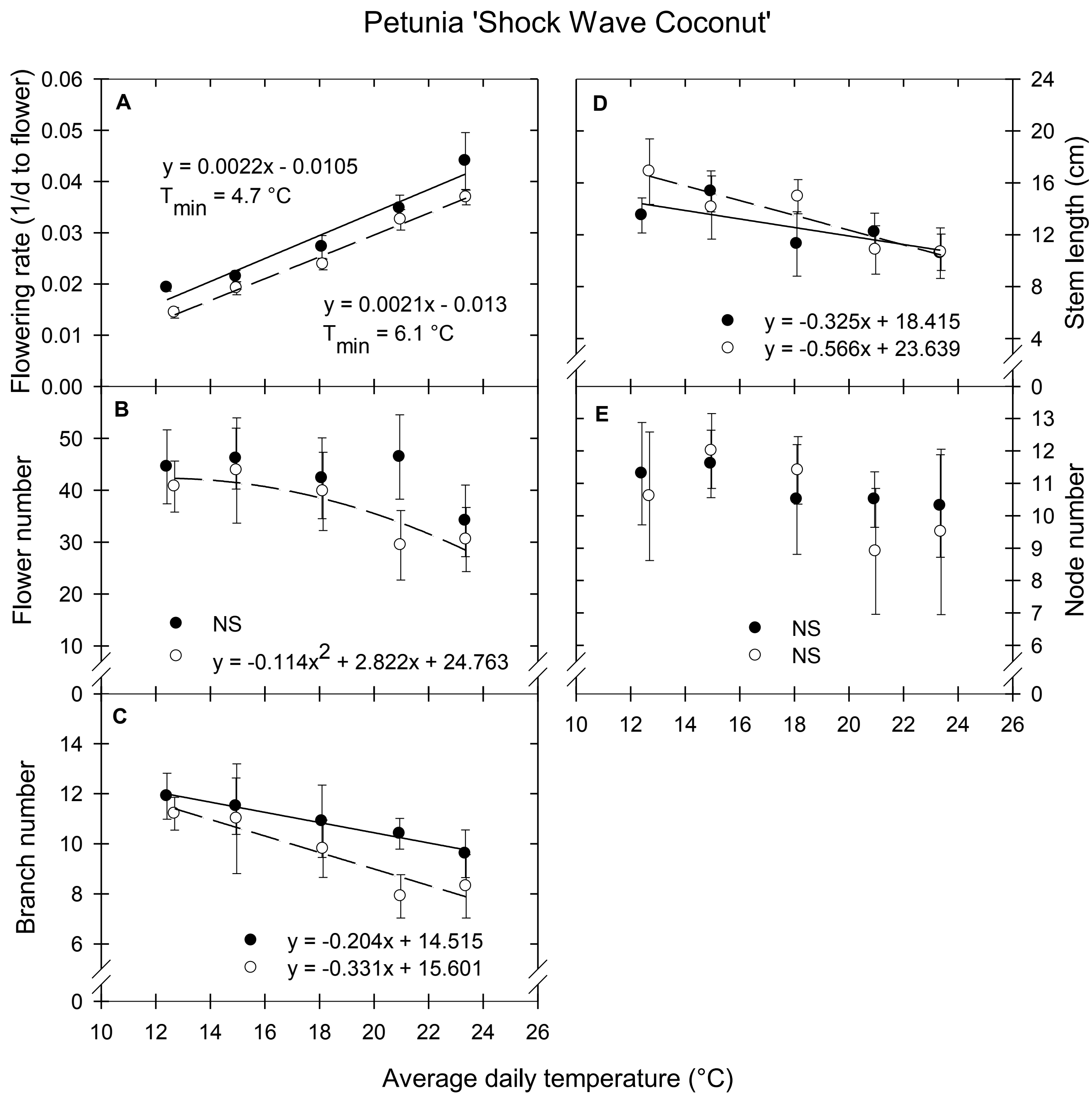

Figure 5.9. The effect of average daily temperature on flowering characteristics of petunia 'Shock Wave Coconut' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at $P > 0\ .05$.

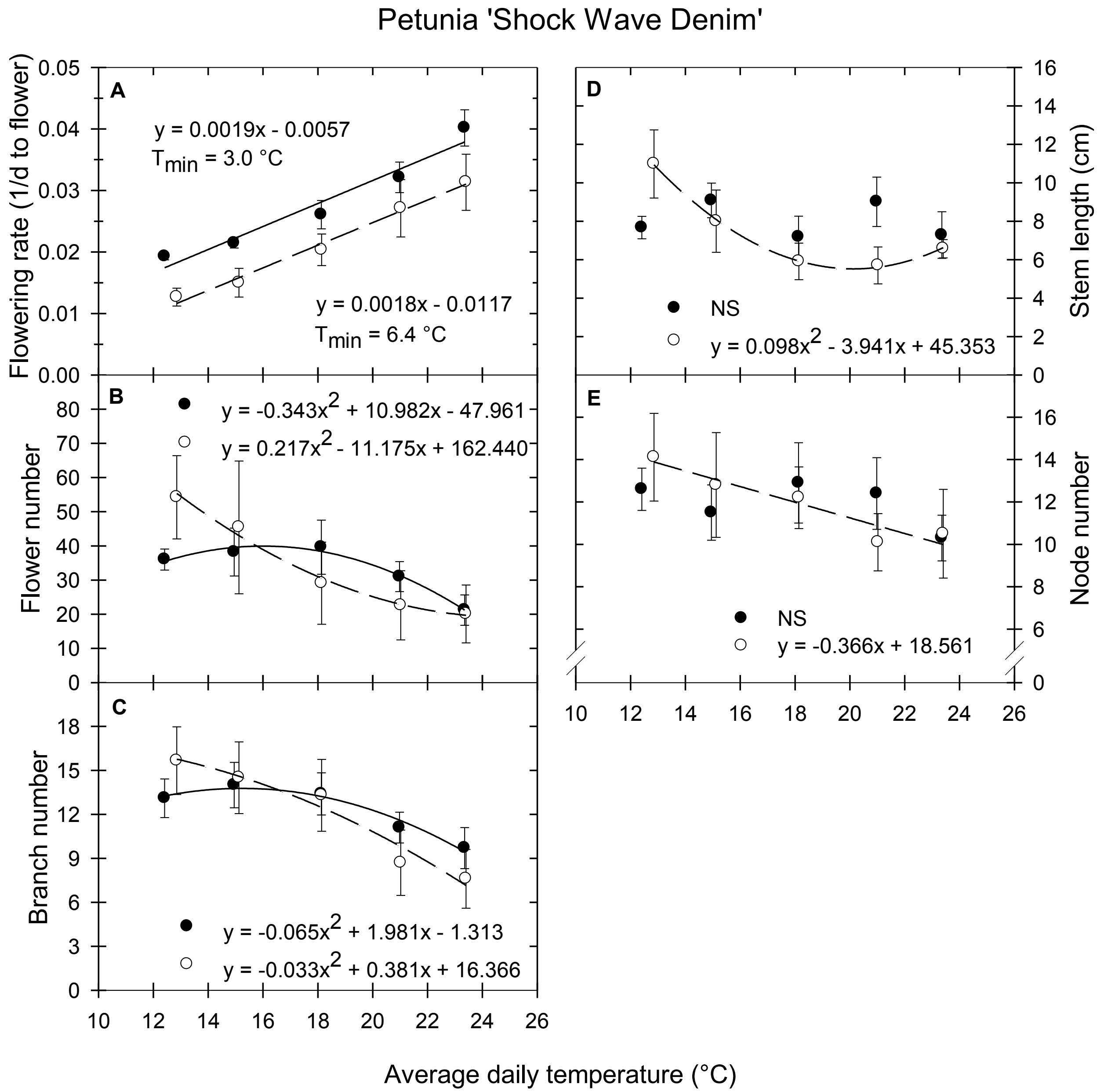

Figure 5.10. The effect of average daily temperature on flowering characteristics of petunia 'Shock Wave Denim' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at *P* > 0 .05.

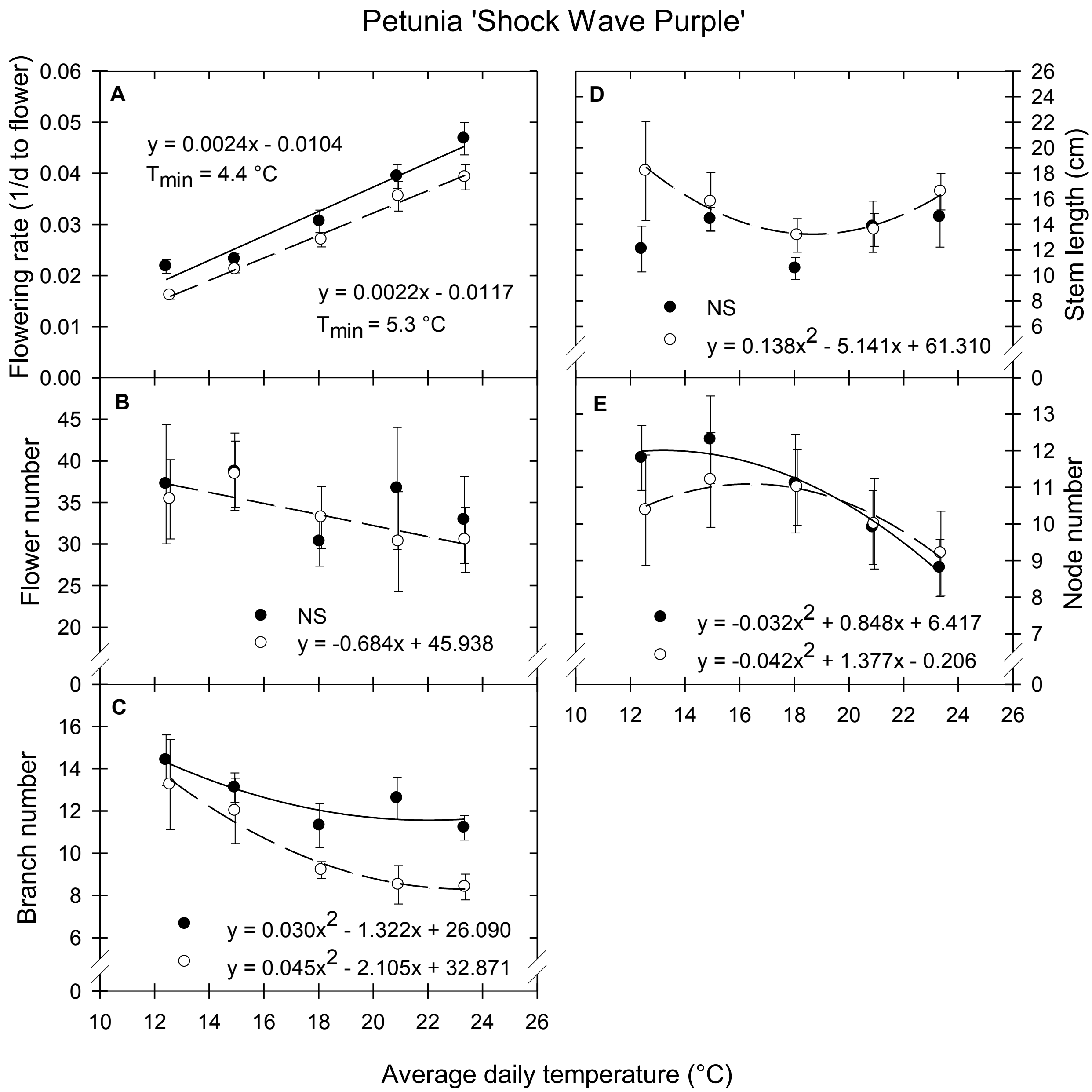

Figure 5.11. The effect of average daily temperature on flowering characteristics of petunia 'Shock Wave Purple' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at $P > 0$ .05.

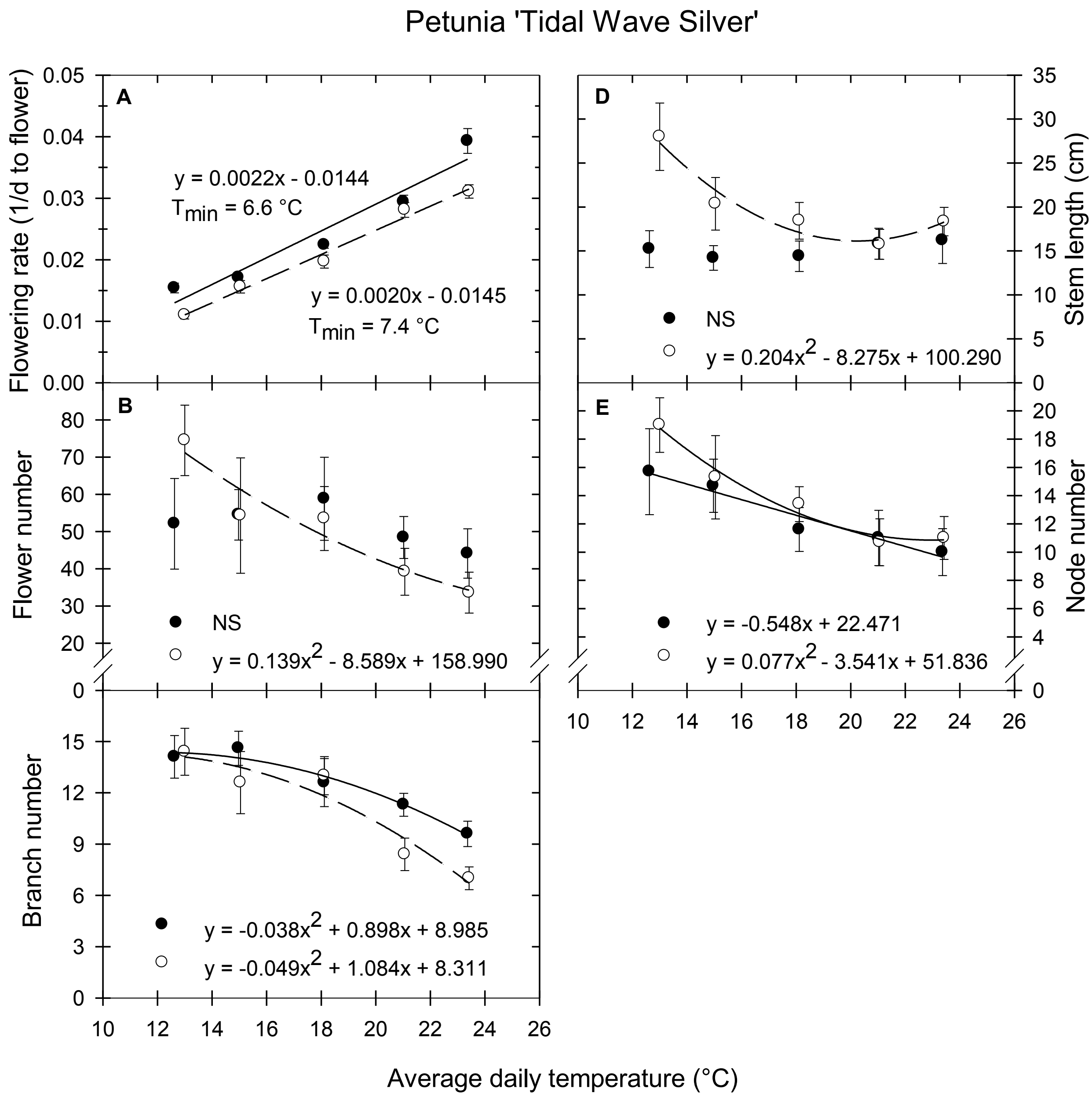

Figure 5.12. The effect of average daily temperature on flowering characteristics of petunia 'Tidal Wave Silver' grown under an average daily light integral of 7 $mol·m^{-2}·d^{-1}$ (open symbols) or 14 $mol·m^{-2}·d^{-1}$ (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 $mol·m^{-2}·d^{-1}$ DLI treatments, respectively. NS = nonsignificant at P > 0 .05.

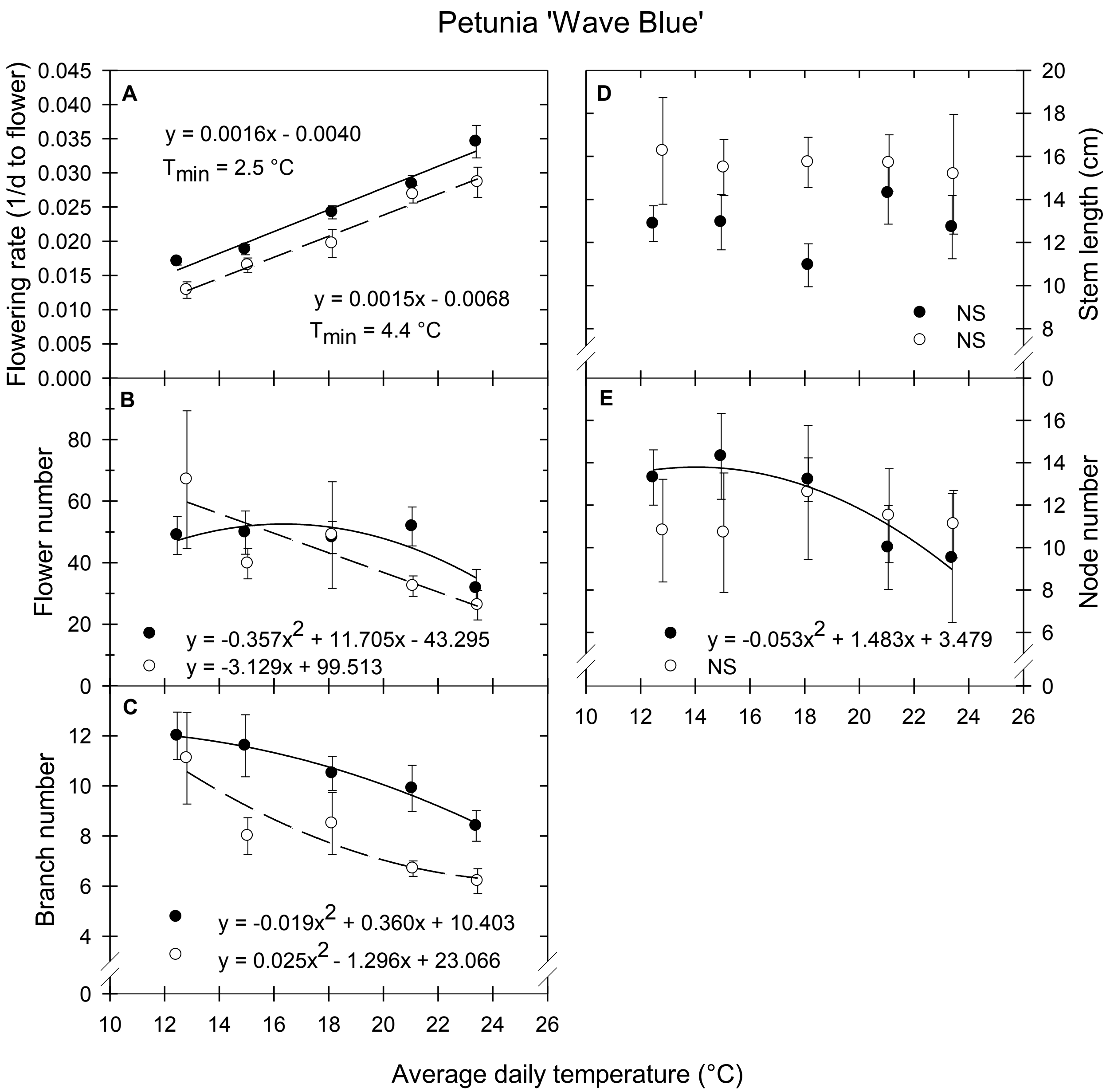

Figure 5.13. The effect of average daily temperature on flowering characteristics of petunia 'Wave Blue' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at *P* > 0 .05.

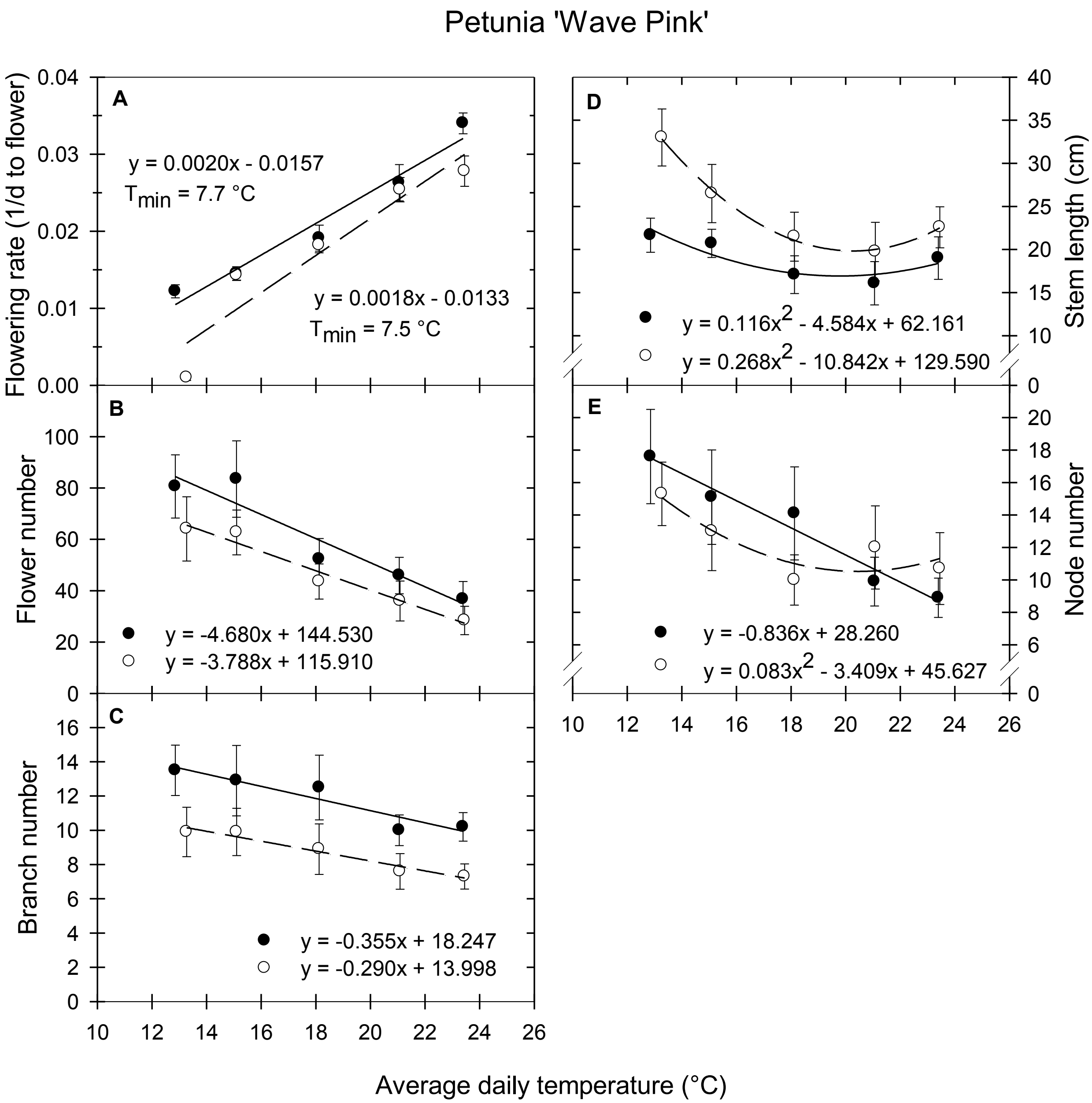

Figure 5.14. The effect of average daily temperature on flowering characteristics of petunia 'Wave Pink' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at $P > 0.05$.

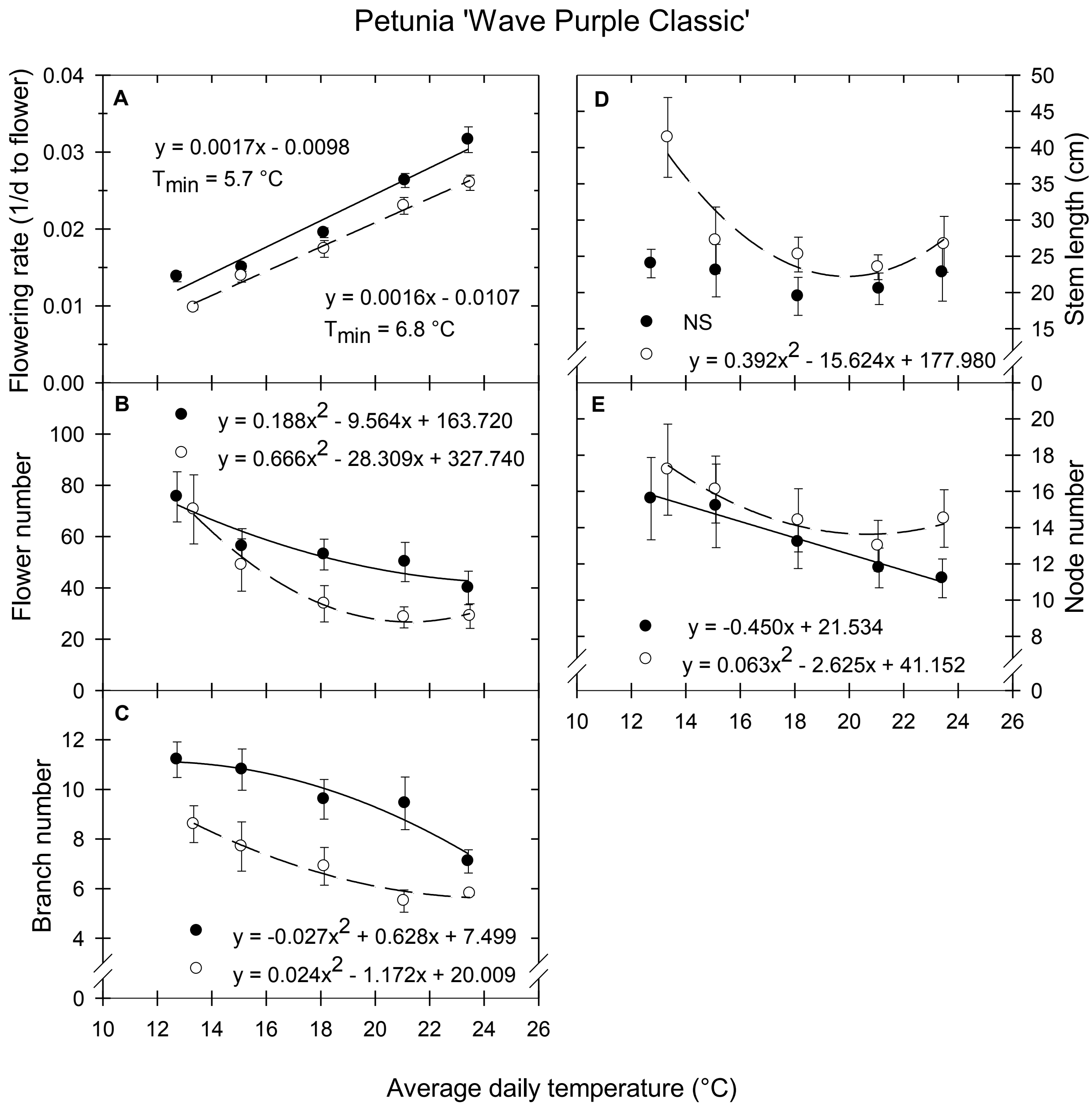

Figure 5.15. The effect of average daily temperature on flowering characteristics of petunia 'Wave Purple Classic' grown under an average daily light integral of 7 mol·m^{-2}·d^{-1} (open symbols) or 14 mol·m^{-2}·d^{-1} (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 mol·m^{-2}·d^{-1} DLI treatments, respectively. NS = nonsignificant at P > 0 .05.

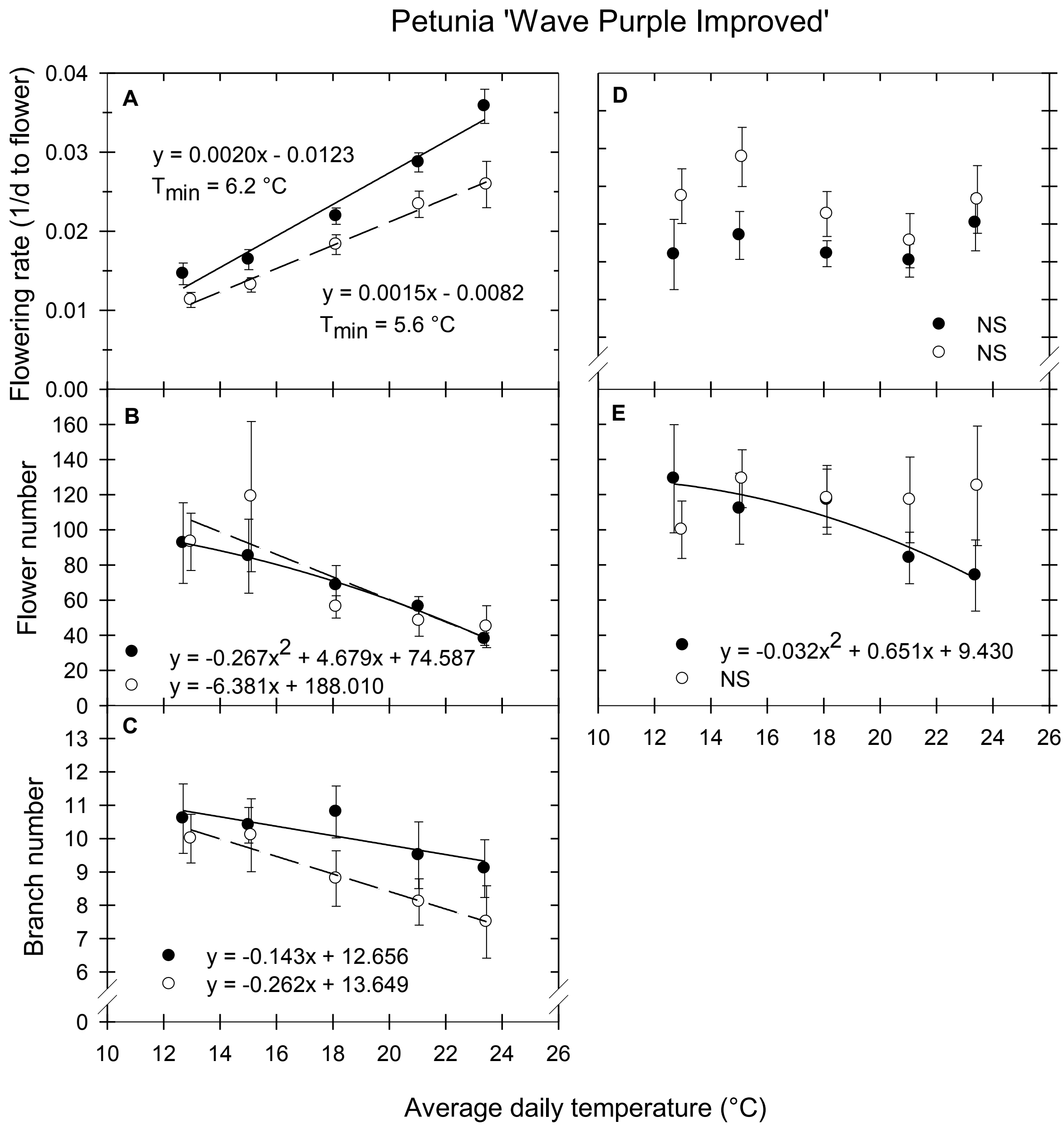

Figure 5.16. The effect of average daily temperature on flowering characteristics of petunia 'Wave Purple Improved' grown under an average daily light integral of 7 $mol \cdot m^{-2} \cdot d^{-1}$ (open symbols) or 14 $mol \cdot m^{-2} \cdot d^{-1}$ (solid symbols) Flowering rate was calculated as the reciprocal of days to flower. T_{min} is the estimated temperature at or below which the rate of progress towards flowering is zero. Each symbol represents the treatment means, and error bars represent 95% confidence intervals. Dashed and solid lines represent regression equations for the 7 and 14 $mol \cdot m^{-2} \cdot d^{-1}$ DLI treatments, respectively. NS = nonsignificant at $P > 0 .05$.

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