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# Prolonged High Temperature Exposure and Daily Light Integral Impact Growth and Flowering of Five Herbaceous Ornamental Species

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**Additional index words.** heat stress, flower initiation, flower development, flower size, *Antirrhinum majus*, *Calendula officinalis*, *Impatiens wallerana*, *Mimulus ×hybridus*, *Torenia fournieri*

**Abstract. Flowering of many herbaceous ornamentals is reduced or eliminated under high temperatures. On warm, sunny days, greenhouse growers often cover crops with light-reducing screening materials to reduce air and plant temperature. However, low irradiance can also reduce flowering on many species. To examine the impacts of temperature and irradiance on herbaceous ornamental flowering and to select a model to study high temperature-reduced flowering, *Antirrhinum majus* L. (snapdragon) 'Rocket Rose', *Calendula officinalis* L. (calendula) 'Calypso Orange', *Impatiens wallerana* Hook.f. (impatiens) 'Super Elfin White', *Mimulus ×hybridus* Hort. ex Siebert & Voss (mimulus) 'Mystic Yellow', and *Torenia fournieri* Linden ex E. Fourn (torenia) 'Clown Burgundy' were grown at constant 32 ± 1 °C or 20 ± 1.5 °C under a 16-hour photoperiod with daily light integrals (DLI) of 10.5, 17.5, or 21.8 mol·m$^{-2}$·d$^{-1}$. Flower bud number per plant (all flower buds ≥1 mm in length when the first flower opened) of all species was lower at 32 than 20 °C. Reduction in flower bud number per plant at 32 compared to 20 °C varied from 30% (impatiens) to 95% (torenia) under a DLI of 10.5 mol·m$^{-2}$·d$^{-1}$. Flower diameter of all species except snapdragon was less at 32 than 20 °C. Decreasing DLI from 21.8 to 10.5 mol·m$^{-2}$·d$^{-1}$ decreased flower diameter of all species except snapdragon. Calendula, impatiens, and torenia leaf number below the first flower was greater at 32 than 20 °C, regardless of DLI. Increasing DLI from 10.5 to 17.5 mol·m$^{-2}$·d$^{-1}$ increased shoot dry mass gain rate of all species, regardless of temperature. Further increasing DLI from 17.5 to 21.8 mol·m$^{-2}$·d$^{-1}$ at 20 °C increased shoot dry mass gain rate of all species except snapdragon and mimulus, indicating that these species may be light saturated below 21.8 mol·m$^{-2}$·d$^{-1}$. Under DLIs of 17.5 and 21.8 mol·m$^{-2}$·d$^{-1}$ shoot dry mass gain rate was lower at 32 than 20 °C for all species except torenia. Torenia shoot dry mass gain rate was 129 mg·d$^{-1}$ at 20 °C compared to 252 mg·d$^{-1}$ at 32 °C under a DLI of 17.5 mol·m$^{-2}$·d$^{-1}$. We suggest torenia may be a good model to study the basis for inhibition of flowering under high temperatures as flowering, but not dry mass gain, was reduced at 32 °C.**

High temperatures negatively impact flower induction (Schwabe, 1985), flower development (Abdul-Baki, 1991) and flower size (Niu et al., 2000). For example, night temperatures above 30 °C reduce flower number per inflorescence of *Kalanchoe blossfeldiana* Poelln. (kalanchoe) (Schwabe, 1985). Similarly, increasing the duration of a high temperature (30/26 °C day/night) exposure reduced floret number formed on *Chrysanthemum ×moriflorum* Ramat. (chrysanthemum) 'Orange Bowl' flowers (Whealy et al., 1987). Differences in high temperature sensitivity among cultivars or genotypes have been noted for many species. For example, high temperature-induced (32/28 °C compared to 22/18 °C day/night) reduction in *Lycopersicon esculentum* Mill. (tomato) flower number per inflorescence varied across genotypes (Warner and Erwin, 2001a).

The widely observed physiological disorder termed "heat delay" results from high temperatures delaying flower initiation (Whealy et al., 1987). Temperatures that result in "heat delay" vary across species. Night temperatures ≥25 °C delay chrysanthemum flower initiation (de Lint and Heij, 1987; Whealy et al., 1987; Wilkins et al., 1990). This response occurred irrespective of day temperatures up to 25 °C (the highest day temperature studied; de Lint and Heij, 1987). *Schlumbergera truncata* (Haw.) Moran (thanksgiving cactus) flower initiation was inhibited when day or night temperature was 30 °C (9-h photoperiod), or when average daily temperature was ≥25 °C (Erwin et al., 1990). In contrast, increasing night temperature from 12 to 30 °C increased the percentage of *Pharbitis nil* Chois. (japanese morning glory) plants flowering from 0 to 100% (24 °C day temperature) (Reese and Erwin, 1997).

High temperatures can also inhibit flower development (Abdul-Baki, 1991), including pollen development (Pressman et al., 2002). Temperatures that negatively impact floral development vary across species. *Capsicum annuum* L. (pepper) flower abscission (associated with floral developmental arrest) is high when day temperature is 32 to 38 °C or when night temperature is >21 °C (Rylski, 1986). Aloni et al. (1991) reported that increasing day/night temperatures from 25/18 °C to 35/25 °C did not affect pepper flower bud growth after 6 h of heat stress. However, flower bud growth ceased after 24 h at 35/25 °C and flower diameter decreased from 24 to 48 h at 35/25 °C. After a 5-d 35/25 °C exposure, ~35% of flower buds abscised from plants with developing fruit, while no flower buds abscised if plants did not have developing fruit, suggesting competition for photoassimilates between developing flowers and developing fruits. High night temperature increased

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flower abscission, as a 5-d 25/35 °C exposure resulted in 100% and 50% flower bud abscission on plants with and without developing fruits, respectively. Similarly, *Brassica oleracea* L. var. *botrytis* L. (broccoli) inflorescence development is disrupted by temperatures above 30 °C (Bjorkman and Pearson, 1998; Carr and Irish, 1997). Bjorkman and Pearson (1998) reported that exposure to 35 °C for 7–10 d when the inflorescence was less than 5 mm in diameter disrupted inflorescence development; the inflorescence was not sensitive to the same high temperature exposures when 5–10 mm in diameter or larger. In contrast to the heat sensitivity of young flower buds in broccoli, *Phaseolus vulgaris* L. (bean) flower buds <6 d before anthesis were more heat sensitive than younger reproductive organs, averaging 79% abscission following a 1–3 d exposure to 35 °C compared to 53% abscission of buds >8 d before anthesis (Monterosso and Wien, 1990).

High temperatures also reduce flower size. For example, *Viola* ×*wittrockiana* Gams. (pansy) flower size decreased linearly as temperature increased from 9 to 31 °C (Pearson et al., 1995) or from 16 to 26 °C (Niu et al. 2000). Similarly, *Pelargonium* ×*hortorum* Bailey (geranium) flower diameter decreased as temperature increased from 15 to 32 °C (Armitage et al., 1981).

In addition to high temperatures, the total amount of light received by a plant in a day, the DLI, can also impact flower initiation (Warner and Erwin, 2003), flower development (Calvert, 1969), and dry mass gain (Karlsson and Heins, 1992). In general, plant dry mass increases as DLI increases (Fierro et al., 1994; Kitaya et al., 1998) up to a light saturation point. For example, *Lactuca sativa* L. (lettuce) 'Summer-green' dry mass increased linearly as DLI increased from 5.8 to 17.3 mol·m$^{-2}$·d$^{-1}$ (the highest DLI examined; Kitaya et al., 1998).

Increasing DLI can increase flower bud number per plant (Mortensen and Moe, 1995; Serek, 1991; Warner and Erwin, 2003). For example, increasing DLI from 6.7 to 8.9 mol·m$^{-2}$·d$^{-1}$ increased *Hibiscus radiatus* Cav. flower bud number at first flower from 7 to 10 buds (Warner and Erwin, 2003). Further increasing DLI did not impact flower bud number. Similarly, increasing DLI from 5.5 to 8.4 mol·m$^{-2}$·d$^{-1}$ increased *Rosa* L. (miniature rose) 'Rubino' flower number from 10 to 18 flowers and buds per plant (Mortensen and Moe, 1995).

Increasing DLI can also hasten flowering developmentally (i.e., reduce leaf number below the first flower) in some species. For example, increasing DLI from 8.3 to 25.5 mol·m$^{-2}$·d$^{-1}$ decreased *Hibiscus cisplatinus* St-Hil. leaf number below the first flower from 26 to 18 leaves (Warner and Erwin, 2003). Increasing DLI also reduced leaf number below the first flower of several annual herbaceous ornamental species, including *Cosmos bipinnatus* Cav. Ann. (cosmos) 'White Sensation', *Nicotiana alata* Link & Otto (flowering tobacco) 'Domino White', and *Silene armeria* L. (catchfly) (Erwin and Warner, 2002).

As described above, high temperature and/or low irradiance can reduce crop quality by reducing plant mass at flowering, flower size, and flower number. The objectives of this study were to 1) characterize the impact of high temperature exposure and DLI on growth and flowering characteristics of five herbaceous ornamental species; 2) determine whether reductions in flowering of these species were associated with high temperature, DLI, or interaction between temperature and DLI; and 3) determine whether there is an association between flowering reduction and dry mass gain rate. A further objective was to identify a species as a potential model for studying high temperature-induced flowering inhibition.

## Materials and Methods

*Antirrhinum majus* 'Rocket Rose', *Calendula officinalis* 'Calypso Orange', *Impatiens wallerana* 'Super Elfin White', *Mimulus* ×*hybridus* 'Mystic Yellow', and *Torenia fournieri* 'Clown Burgundy' seeds were sown on 26 Feb. in 25-mL cells in a soilless medium (Germination Mix; Strong-Lite Horticultural Products, Pine Bluff, Ark.) and placed under intermittent mist (6-s mist every 10 min from 0800–2000 HR) at 23 ± 1 °C (24-h mean ± SE) air temperature until the cotyledons were parallel to the media surface. Seedlings were then transplanted into 450-mL pots in a soilless medium (Universal Mix; Strong-Lite Horticultural Products) and placed in a greenhouse at 18 ± 1.5 °C air temperature under a 14-h photoperiod provided by ambient irradiance and high-pressure sodium lamps (0600–2000 HR; Lucolux LU400; General Electric, Cleveland), until treatments were initiated (when seedlings had unfolded two true leaves).

On 22 Mar. plants were placed under one of two temperatures (constant 20 ± 1.5 °C or 32 ± 1 °C) and under one of three irradiance levels within each temperature treatment: 60% ambient (St. Paul, Minn.; 45°N) irradiance (using a 40% light reduction material), ambient irradiance, or ambient plus 75 $\mu$mol·m$^{-2}$·s$^{-1}$ [all supplemental irradiance provided from 0600–2200 HR by high-pressure sodium lamps (Lucolux LU400). To prevent confounding effects of photoperiod and light quality on flower induction, a low supplemental irradiance level (10 $\mu$mol·m$^{-2}$·s$^{-1}$) was provided to the 60% ambient and ambient irradiance treatments to maintain the same photoperiod and similar light spectra. The irradiance treatments resulted in average DLIs of 10.5 ± 0.7, 17.5 ± 1.8, and 21.8 ± 1.8 mol·m$^{-2}$·d$^{-1}$. Ambient irradiance and temperature were measured every 60 s with a quantum sensor (QSO-SUN; Apogee Instruments, Logan, Utah) and a thermocouple (Type E Wire chromega/constantan; Omega Engineering, Stamford, Conn.), respectively, connected to a datalogger (CR10; Campbell Scientific, Logan, Utah) and averaged every hour. Hourly averages were used to calculate ambient DLI. DLIs for the 60% ambient and ambient plus 75 $\mu$mol·m$^{-2}$·s$^{-1}$ were calculated from the ambient DLI. Plants were fertilized at each watering with 14.3 mM N, 0.72 mM P, 6.5 mM K, 1.67 mM Ca, 1.1 mM Mg, plus trace amounts of micronutrients (Miracle-Gro Excel 15–2.2–12.5 Cal-Mag; Scott's Co., Marysville, Ohio). Plants were watered/fertilized until the solution ran out the bottom of the pot to eliminate fertility differences due to differences in watering practices between temperature/lighting treatments.

The experiment employed a split-plot statistical design with temperature as the main plot and irradiance as the subplot with species completely randomized within each subplot. Irradiance subplots were replicated twice within each temperature. Ten plants of each species were used in each subplot. Date of first open flower [from which days to first open flower (DTF) was calculated (from germination)], flower bud number (all buds >1 mm long), first flower diameter, and leaf number below the first flower were determined when the first flower opened. Aboveground (shoot) biomass was harvested when the first flower opened and dry mass was determined after drying the tissue for 3 d at 70 °C. Shoot dry mass gain rate was determined by dividing total shoot dry mass by DTF.

## Results

Temperature and DLI each interacted with species to impact flower bud number per plant, first flower diameter, leaf number

Table 1. Analysis of variance of the impact of species, temperature, and average daily light integral (DLI) on flower bud number at first flower opening (flower bud number), first flower diameter, leaf number below the first flower (leaf number), days to first flower opening (days to first flower) and shoot dry mass gain rate (dry mass gain rate).

| Source of variation | Flower bud no. | First flower diam | Leaf no. | Days to first flower | Dry mass gain rate |
|---|---|---|---|---|---|
| Species (S) | *** | *** | *** | *** | *** |
| Temp (T) | *** | *** | * | *** | *** |
| DLI | *** | *** | *** | *** | *** |
| S × T | *** | *** | *** | *** | *** |
| S × DLI | *** | *** | *** | *** | *** |
| T × DLI | * | NS | NS | * | *** |
| S × T × DLI | NS | NS | NS | NS | *** |

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

below the first open flower, DTF, and shoot dry mass gain per day (Table 1). Species, temperature and DLI all interacted to impact shoot dry mass gain rate per day only (Table 1).

**Flower bud number per plant.** High temperature (32 °C) reduced flower bud number per plant of all species (Fig. 1). For example, increasing temperature from 20 to 32 °C decreased calendula flower bud number per plant, which was 14 at 20 °C compared to 7 at 32 °C (10.5 mol·m$^{-2}$·d$^{-1}$ DLI; Fig. 1). The percent reduction in flower bud number per plant at 32 compared to 20 °C (10.5 mol·m$^{-2}$·d$^{-1}$ DLI) varied from 30% (impatiens) to 95% (torenia; Fig. 1).

Increasing DLI from 10.5 to 17.5 mol·m$^{-2}$·d$^{-1}$ within a temperature treatment increased flower bud number per plant on all species except calendula (Fig. 1). For example, mimulus flower bud number per plant increased from 19 to 32 buds as DLI increased from 10.5 to 17.5 mol·m$^{-2}$·d$^{-1}$ at 20 °C (Fig. 1). Further increasing DLI from 17.5 to 21.8 mol·m$^{-2}$·d$^{-1}$ did not increase flower bud number of any species at either temperature.

**First flower diameter.** Temperature and DLI affected first flower diameter of all species (Fig. 2) except snapdragon. Snapdragon first flower diameter was 37 mm, regardless of temperature or DLI (data not shown). Calendula first flower diameter was unaffected by DLI at 20 °C, but declined from 41 to 37 mm as DLI increased from 10.5 to 21.8 mol·m$^{-2}$·d$^{-1}$ at 32 °C (Fig. 2). In contrast, impatiens, mimulus, and torenia first flower diameter increased as DLI increased, regardless of temperature (Fig. 2).

**Leaf number below the first flower.** Leaf number below the first flower was greater at 32 than 20 °C for calendula, impatiens, and torenia, regardless of DLI, and for snapdragon under a DLI of 10.5 mol·m$^{-2}$·d$^{-1}$ only (Fig. 3). Mimulus leaf number below the first flower was three leaves, regardless of temperature or DLI (data not shown). Increasing DLI decreased leaf number below the first flower of snapdragon and calendula only (Fig. 3).

**Days to first open flower.** The impact of DLI and temperature on DTF varied across species. Increasing DLI from 10.5 to 17.5 mol·m$^{-2}$·d$^{-1}$ reduced DTF for snapdragon, calendula, mimulus and torenia, regardless of temperature, and reduced impatiens DTF at 32 °C only (Table 2). Further increasing DLI from 17.5

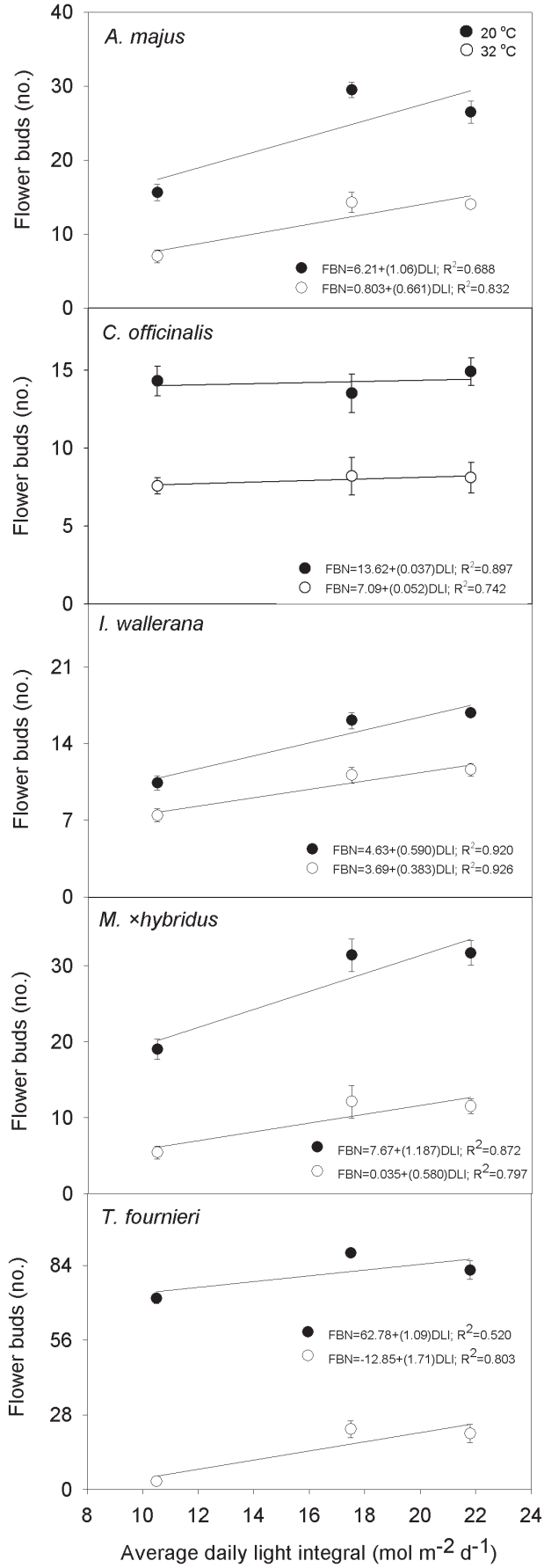


Fig. 1. Impact of temperature and daily light integral on flower bud number per plant (visible buds ≥1 mm in length) when the first flower opened [flower bud number (FBN)] of *Antirrhinum majus* 'Rocket Rose', *Calendula officinalis* 'Calypso Orange', *Impatiens wallerana* 'Super Elfin White', *Mimulus ×hybridus* 'Mystic Yellow', and *Torenia fournieri* 'Clown Burgundy'. Data points are means ±SE. Lines represent linear regression analysis of the means.

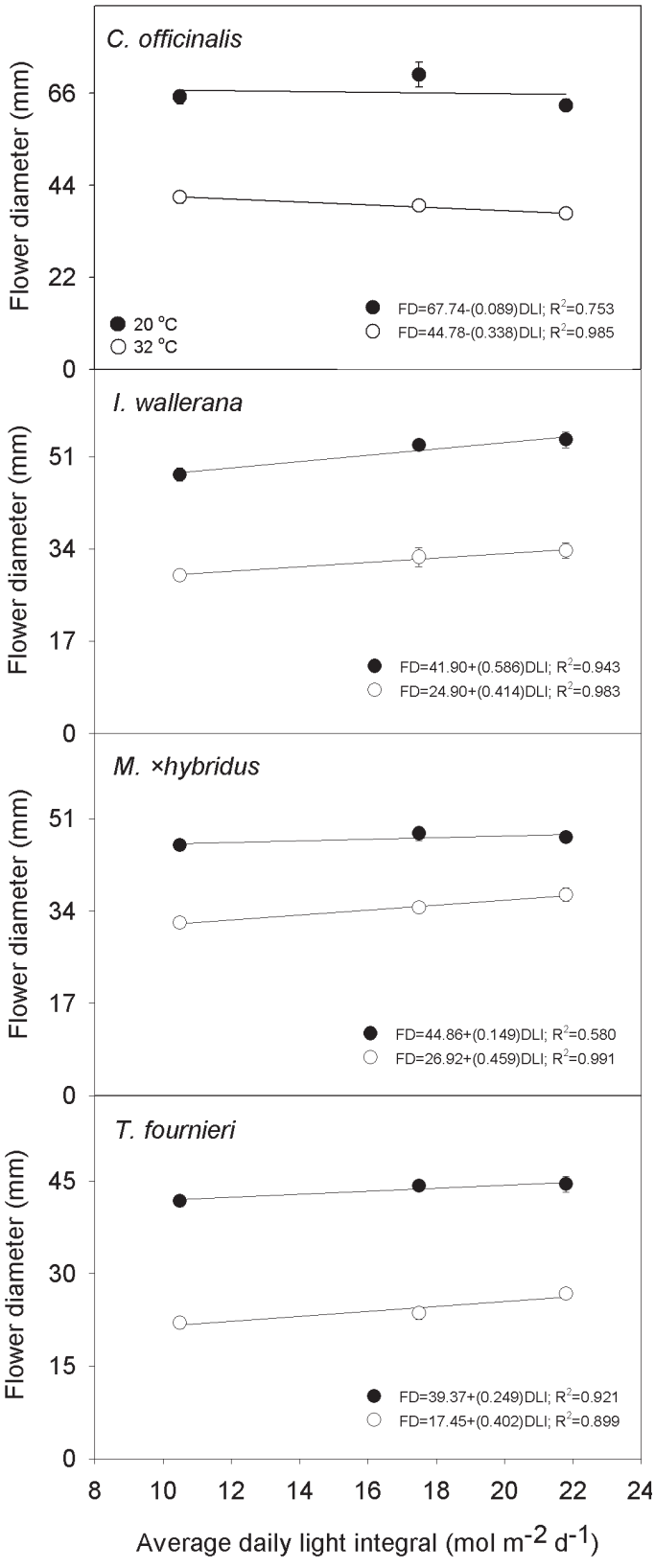


Fig. 2. Impact of temperature and daily light integral on first flower diameter [flower diameter (FD)] of *Calendula officinalis* 'Calypso Orange', *Impatiens wallerana* 'Super Elfin White', *Mimulus ×hybridus* 'Mystic Yellow', and *Torenia fournieri* 'Clown Burgundy'. Data points are means ±SE. Lines represent linear regression analysis of the means.

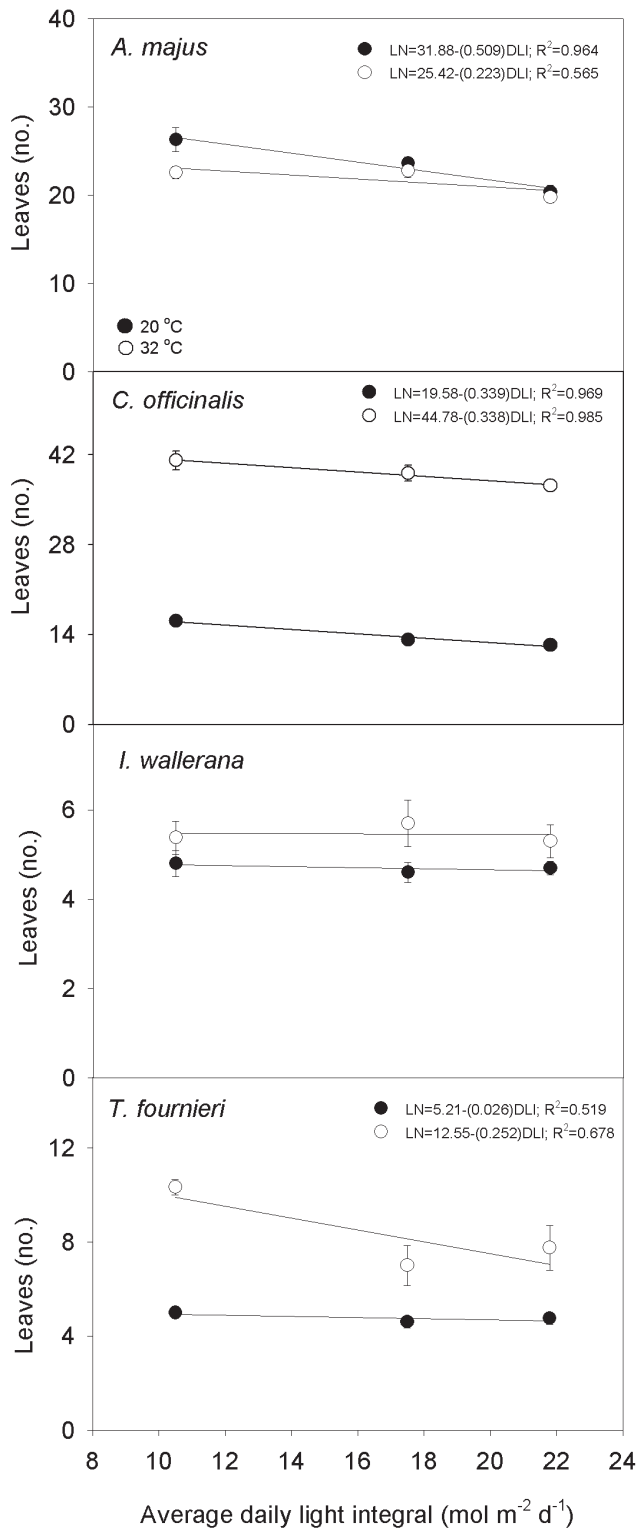


Fig. 3. Impact of temperature and daily light integral on leaf number below the first open flower [leaf number (LN)] of *Antirrhinum majus* 'Rocket Rose', *Calendula officinalis* 'Calypso Orange', *Impatiens wallerana* 'Super Elfin White', and *Torenia fournieri* 'Clown Burgundy'. Data points are means ±SE. Lines represent linear regression analysis of the means.

Table 2. Impact of temperature and average daily light integral on days to first flower and shoot dry mass gain rate of five herbaceous ornamental species. Capital letters represent mean separation across temperature within daily light integral and species. Lowercase letters represent mean separation across daily light integral, within temperature and species. Mean separation was conducted using Tukey's honestly significant difference at $P \leq 0.05$.

| Species | Temp (°C) | Avg daily light integral (mol·m$^{-2}$·d$^{-1}$) 10.5 | 17.5 | 21.8 | Avg daily light integral (mol·m$^{-2}$·d$^{-1}$) 10.5 | 17.5 | 21.8 |
|---|---|---|---|---|---|---|---|
| | | *Days to first flower* | | | *Shoot dry mass gain rate (mg·d$^{-1}$)* | | |
| *Antirrhinum majus* 'Rocket Rose' | 20 | 62[z] Ac | 49 Bb | 41 Aa | 77 Ba | 188 Bb | 213 Bb |
| | 32 | 59 Ab | 40 Aa | 38 Aa | 29 Aa | 73 Ab | 97 Ac |
| *Calendula officinalis* 'Calypso Orange' | 20 | 42 Ab | 29 Ba | 26 Ba | 97 Ba | 171 Bb | 196 Bc |
| | 32 | 40 Ab | 25 Aa | 20 Aa | 49 Aa | 98 Ab | 97 Ab |
| *Impatiens wallerana* 'Super Elfin White' | 20 | 33 Aa | 31 Aa | 30 Aa | 30 Aa | 64 Ab | 102 Bc |
| | 32 | 35 Ab | 32 Aa | 31 Aa | 25 Aa | 68 Ab | 59 Ab |
| *Mimulus* ×*hybridus* 'Mystic Yellow' | 20 | 21 Ab | 19 Aa | 17 Aa | 19 Ba | 49 Bb | 50 Bb |
| | 32 | 23 Ab | 16 Aa | 16 Aa | 7 Aa | 16 Ab | 14 Ab |
| *Torenia fournieri* 'Clown Burgundy' | 20 | 58 Ab | 51 Aa | 46 Aa | 89 Aa | 129 Ab | 181 Ac |
| | 32 | 71 Bb | 50 Aa | 47 Aa | 94 Aa | 252 Bb | 290 Bc |

[z]Numeral represents treatment mean.

to 21.8 mol·m$^{-2}$·d$^{-1}$ reduced DTF for snapdragon at 20 °C only. Calendula DTF was lower at 32 than 20 °C under DLIs of 17.5 and 21.8 mol·m$^{-2}$·d$^{-1}$ only, while snapdragon DTF was lower at 32 than 20 °C under a DLI of 17.5 mol·m$^{-2}$·d$^{-1}$ only (Table 2). In contrast, torenia DTF was greater at 32 compared to 20 °C under a DLI of 10.5 mol·m$^{-2}$·d$^{-1}$. Temperature did not impact impatiens or mimulus DTF, regardless of DLI (Table 2).

**Shoot dry mass gain rate**. Temperature, DLI, and species interacted to impact shoot dry mass gain rate (Table 2). Snapdragon, calendula, and mimulus shoot dry mass gain rate was greater at 20 than 32 °C, regardless of DLI (Table 2). Shoot dry mass gain rate for impatiens was similar across temperature at 10.5 and 17.5 mol·m$^{-2}$·d$^{-1}$, but lower at 32 than 20 °C (59 compared to 102 mg·d$^{-1}$) at a DLI of 21.8 mol·m$^{-2}$·d$^{-1}$ (Table 2). In contrast, shoot dry mass gain rate of torenia was greater at 32 than 20 °C at DLIs of 17.5 and 21.8 mol·m$^{-2}$·d$^{-1}$ (Table 2). Torenia shoot dry mass gain rate increased 95% (from 129 to 252 mg·d$^{-1}$) at a DLI of 17.5 mol·m$^{-2}$·d$^{-1}$ and 60% (from 181 to 290 mg·d$^{-1}$) at a DLI of 21.8 mol·m$^{-2}$·d$^{-1}$ at 32 compared to 20 °C.

## Discussion

Under field conditions, it is difficult to determine whether observed reductions in flowering are due to high temperatures and/or water stress. This experiment examined the responses of five annual herbaceous ornamentals to prolonged elevated temperatures under conditions of adequate water availability with varying DLI. Our results indicate that high temperatures alone reduce flowering (reductions in flower number and diameter) in these five species. Increasing temperature reduced flower bud number of all species, regardless of DLI. Similar reductions in flower bud number as temperature increases occur on *Brassica napus* L. (canola), *B. rapa* L. (oilseed rape), and *B. juncea* (L.) Czernj. & Cosson (mustard) (Morrison and Stewart, 2002); *Campanula carpatica* Jacq. (tussock bellflower) 'Deep Blue Clips' and *Campanula* L. 'Birch Hybrid' (Niu et al., 2001); and *Rudbeckia fulgida* Ait. (coneflower) 'Goldsturm' (Yuan et al., 1998). For example, *Oenothera fruiticosa* L. (sundrops) 'Youngii-lapsley' flower bud number decreased from about 170 to fewer than 30 as temperature increased from 15 to 30 °C (Clough et al., 2001).

Increasing DLI within a temperature treatment increased flower bud number of snapdragon, impatiens, mimulus, and torenia (Fig. 1). Increasing DLI increased flower bud number of several other species, including *Hibiscus radiatus* (Warner and Erwin, 2003), chrysanthemum 'Resiliance' (Warrington and Norton, 1991), tussock bellflower 'Karl Foerster' (Serek, 1991), and miniature rose 'Rubino' (Mortensen and Moe, 1995). For example, increasing DLI from 9.8 to 19.4 mol·m$^{-2}$·d$^{-1}$ increased chrysanthemum 'Resiliance' flower number per plant from 3 to 11 flowers (Warrington and Norton, 1991).

The reduced flower diameter under elevated temperatures observed here for several species is consistent with results for other species, including sundrops (Clough et al., 2001), pansy (Niu et al., 2000), *Leucanthemum* ×*superbum* Bergman ex. J. Ingram (shasta daisy) (Yuan et al., 1998), and *Campanula carpatica* (Niu et al., 2001). Pansy 'Universal Violet' flower area decreased from 25.8 to 10.1 cm$^2$ as average daily temperature increased from 15 to 25 °C (Pearson et al., 1995).

Flowering of snapdragon, calendula, and torenia was delayed developmentally (as evidenced by increased leaf number below the first flower) at 32 compared to 20 °C. The increase in leaf number below the first flower observed for these species is consistent with results for other species. For example, increasing day/night temperature (9-h day/15-h night) from 22/18 °C to 30/26 °C increased chrysanthemum 'Orange Bowl' leaf number below the first flower from 16 to 20 leaves (Whealy et al., 1987). Similarly, increasing temperature from 20 to 25 °C increased leaf number below the first flower of *Hibiscus asper* Hook f. from 7 to 23 leaves and of *Hibiscus physaloides* Guill. from 15 to 24 leaves (Warner and Erwin, 2001b). Increasing temperature from 20 to 30 °C increased chrysanthemum 'Bright Golden Anne' days to visible flower bud from 33 to 48 d and increased total DTF from 78 to 137 d (Karlsson et al., 1989). Yeh and Lin (2003) found that the degree of heat-induced delay in flowering across chrysanthemum cultivars correlated with thermostability of cell membranes of young vegetative plants, as determined by measuring electrolyte leakage. Electrolyte leakage may be a useful assay for breeders to screen large populations for heat tolerance of flowering early in development.

Shoot dry mass gain rate of all species presented here increased

as DLI increased from 10.5 to 17.5 mol·m$^{-2}$·d$^{-1}$, consistent with results for other species, including lettuce (Kitaya et al., 1998) and chrysanthemum (Karlsson and Heins, 1992). For example, chrysanthemum 'Bright Golden Anne' dry mass at flowering increased from 3.6 to 15.3 g as DLI increased from 1.8 to 21.6 mol·m$^{-2}$·d$^{-1}$ at 20 °C (Karlsson and Heins, 1992).

Increasing temperature reduced flowering of all species, but differentially impacted shoot dry mass gain across species. Increasing temperature from 20 to 32 °C under a DLI of 21.8 mol·m$^{-2}$·d$^{-1}$ reduced shoot dry mass gain rate for all species except torenia (Table 2). Reductions in plant dry mass at elevated temperatures were observed previously for a number of species. For example, *Platycodon grandiflorus* (Jacq.) A. DC. (balloon flower) 'Astra Blue' dry mass at flowering decreased from 5.1 to 1.1 g as temperature increased from 13.7 to 28.9 °C (Park et al., 1998). Pansy 'Delta Yellow Blotch' flower bud and shoot dry mass at flowering decreased as average daily temperature increased from 15 to 25 °C under DLIs of 10.6 or 15.6 mol·m$^{-2}$·d$^{-1}$ (Niu et al., 2000). The reductions in dry mass gain rate observed herein are consistent with observed reductions in net photosynthetic rate following high temperature exposures. For example, photosynthetic rates of five *Betula* L. species declined as temperature increased above 25 °C (Ranney and Peet, 1994). Similarly, photosynthetic rates of four herbaceous ornamentals [pansy 'Scarlet Bronze', geranium 'Pinto Violet', *Tagetes patula* L. (french marigold) 'Antigua Orange', and *Petunia* ×*hybrida* Hort. Vilm.-Andr. (petunia) 'Dreams Red'] decreased as temperature increased from 15 to 38 °C (van Iersel, 2003).

Torenia may serve as a useful model for studying reduced flowering associated with high temperatures without the confounding effects of reduced growth rate under high temperature. In contrast to other species studied here, high temperature-induced flowering reductions in torenia were not correlated with dry mass gain reductions. More torenia cultivars must be screened to determine the range of variation that exists for high temperature effects on growth and flowering. Torenia may also be useful to study interactions between temperature and DLI on flower initiation, as torenia leaf number below the first flower was unaffected by DLI at 20 °C, but decreasing DLI from 21.8 to 10.5 mol·m$^{-2}$·d$^{-1}$ increased leaf number below the first flower at 32 °C (Fig. 3). In contrast, calendula may be useful for studying temperature effects on flower initiation independent of DLI, as increasing temperature from 20 to 32 °C nearly tripled the number of leaves formed below the first flower, regardless of DLI.

It is common for greenhouse growers to cover crops with screening materials that reduce irradiance from 33% to 80% during hot days to help reduce greenhouse air and plant temperature. In the present study, we observed that snapdragon, calendula, and mimulus shoot dry mass gain rates were dramatically reduced under high temperature (32 °C), low light (10.5 mol·m$^{-2}$·d$^{-1}$; Table 2) conditions, and torenia flowering was almost completely inhibited under these conditions. Decreasing DLI from 21.8 to 10.5 mol·m$^{-2}$·d$^{-1}$ at 32 °C also delayed flowering (i.e., increased leaf number below the first flower) in snapdragon, calendula, and torenia (Fig. 3) and decreased flower bud number of all species except calendula (Fig. 2). Instead of covering crops with light-reduction materials, growers may be better served by investing in greater greenhouse cooling capacity through vents, fans, and/or evaporative cooling pads to increase plant quality during high irradiance and temperature periods of the year.

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