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# Modeling Temperature and Photoperiod Effects on Growth and Development of Dahlia

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**Abstract.** Effects of temperature and photoperiod on growth rates and morphological development of *Dahlia pinnata* Cav. 'Royal Dahlietta Yellow' were determined by growing plants under 45 combinations of day and night temperatures (DT and NT, respectively, and photoperiod. DT and NT ranged from 10 to 30C and photoperiods from 10 to 24 hours-day<sup>-1</sup>. Photoperiod influenced vegetative development more than reproductive development as plants flowered in all photoperiods. Lateral shoot count and length decreased and tuberous root weight increased as photoperiod decreased from 16 to 10 hours. Temperature interacted with photoperiod to greatly increase tuberous root formation as temperature decreased from 25 to 15C. Increasing temperature from 20 to 30C increased the number of nodes below the first flower. Flower count and diameter decreased as average daily temperature increased. Nonlinear regression analysis was used to estimate the maximum rate and the minimum, optimum, and maximum temperatures for leaf-pair unfolding rate (0.29 leaf pair/day, 5.5, 24.6, and 34.9C, respectively), flower development rate from pinch to visible bud (0.07 flower/day, 2.4, 22.4, and 31.1C, respectively), and flower development rate from visible bud to flower (0.054 flowers/day, 5.2, 24.4, and 31.1C, respectively). The results collectively indicate a relatively narrow set of conditions for optimal 'Royal Dahlietta Yellow' dahlia flowering, with optimal defined as fast-developing plants with many large flower buds and satisfactory plant height. These conditions were a 12- to 14-hour photoperiod and ≈20C.

Dahlias propagated by tuberous roots or seed have been used as bedding plants, garden plants, and cut flowers for many years. Several cutting-propagated, dwarf dahlia cultivars have recently been introduced, making possible large-scale, commercial production of cutting-propagated dahlias as flowering pot plants. Precise knowledge of the relationships between dahlia growth and development and temperature and photoperiod is essential for optimum potted-plant production.

Previous research with tuberous and seed-propagated dahlias has shown that most cultivars are quantitative short day (SD) plants for flower initiation, with an optimum photoperiod of 12 to 14 h (Durso and De Hertogh, 1977; Konishi and Inaba, 1964, 1966; Maatsch and Rünger, 1955). Some cultivars are day neutral (Zimmerman and Hitchcock, 1929), while others are qualitative SD plants (Kumar et al., 1970; Mathur et al., 1970; Yasuda and Yokoyama, 1960). Photoperiod also affects vegetative growth and tuberous root formation, with SD inhibiting lateral shoot formation (Durso and De Hertogh, 1977) and promoting tuberous root formation (Biran et al., 1972; Kannagara and Booth, 1978; Moser and Hess, 1968). Further, flower diameter, plant height, and node counts increase with increasing daylength (Payne and Haliburton, 1976).

Increasing average daily temperature (ADT) decreases time to flower (Durso and De Hertogh, 1977; Hildrum, 1973). However, Durso and De Hertogh (1977) stated that flower diameter, plant height, and lateral shoot count were not influenced by temperature.

Morphological responses of the newly introduced, cutting-propagated dahlias to temperature and photoperiod have not been determined. Also, we found no determination of quantitative

relationships between plant development rates and temperature for any dahlia cultivar. The objectives of this study were to determine the effect of temperature and photoperiod on growth rates and morphological development of the cutting-propagated 'Royal Dahlietta Yellow' dahlia.

## Materials and Methods

**General procedures.** Rooted 'Royal Dahlietta Yellow' dahlia cuttings obtained from Yoder Brothers, Barberton, Ohio, were planted in 10-cm pots (450 cm<sup>3</sup>) filled with a commercial peat-based medium (Baccto Pro Plant Mix, Michigan Peat, Houston) and kept at 20C in a glass greenhouse for 2 weeks. Plants were then pinched to three nodes and kept in controlled-temperature chambers. Only one shoot per plant was allowed to develop during the experiments; other lateral shoots were removed.

Irradiance in the chambers was supplied by cool-white fluorescent tubes (Philips VHO F96712/CW/VHO) and incandescent bulbs (Sylvania 60-W) with an input wattage of 77%:23%, respectively. Plant temperature was measured near the shoot meristem by inserting a hypodermic-needle probe into the shoot apex (Omega Hypl-30-1/2-T-G-60-SMP-M, Omega International, Stamford, Conn.).

Plants were irrigated two to three times weekly, depending on plant size and environmental conditions. Supplemental nutrition consisted of 17.9 mM N and 6.4 mM K added through the watering system. Medium pH was adjusted to 6.0 ± 0.5 by adding 0.25 ml 75% phosphoric acid/liter water to neutralize alkalinity of the source water.

**Temperature study (Expt. 1.)** Five walk-in chambers were set at constant air temperatures of 10, 15, 20, 25, or 30C. The five constant-temperature chambers were used to create 25 factorial DT and NT treatments by moving plants from each chamber to each other chamber twice daily (0800 and 2000 HR). Plants undergoing constant-temperature treatment were moved within the chamber from one location to another to simulate stress

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Abbreviations: ADT, average daily temperature; DIF, day temperature - night temperature; DT, day temperature; DTF, days to flower; NT, night temperature; PPF, photosynthetic photon flux; SD, short day.

effects on plants that were moved between chambers. Actual measured plant temperatures during the day were 12.4, 14.2, 21.2, 24.1, and 31.3C, while those during the night were 9.3, 14.1, 17.1, 23.9, and 28.6C. Each treatment consisted of 12 plants.

The photoperiod was 12 h, with an average photosynthetic photon flux (PPF) at canopy level of  $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  ( $13 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ). Stem length, node count below the flower, and flower bud diameter were measured twice a week until plants flowered. A plant was considered in flower when the petals on the most advanced flower opened perpendicular to the pedicel. Data from plants at high temperatures that did not flower were not included in the data analysis.

**Temperature and photoperiod study (Expt. 2.)** Four walk-in chambers were set at constant temperatures of 15, 20, 25, or 30C. Twenty-four factorial temperature  $\times$  photoperiod treatments were created by placing six boxes that could be covered with black cloth in each chamber. Plants in all treatments were exposed to a PPF of  $240 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  ( $7.8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ) from 0800 to 1700 HR. Photoperiods of 10, 12, 14, 16, 20, or 24 h were established in each of the boxes by day-extension lighting for 1, 3, 5, 7, 11, and 15 h, respectively. Day-extension lighting was provided by fluorescent tubes (Philips F15 T81CW cool-white, 15-W) at an average PPF of  $7.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The boxes were uncovered at 0800 HR and covered at 1700 HR with an opaque black cloth to prevent light pollution. Each box was equipped with a constantly running exhaust fan to avoid heat accumulation. Each treatment consisted of seven plants. Stem length, node count below the flower, and flower bud diameter were measured twice a week until data on the last flowering plant were collected. Lateral shoot count, lateral shoot length, tuberous root weight, flower count, height of leaf canopy from pot edge, and leaf canopy diameter were measured on all plants at flowering. A plant was considered in flower when the petals on the most advanced flower opened perpendicular to the pedicel.

**Temperature-dependent model development.** Most biological-rate (R) responses to temperature follow an asymmetric, peak-shaped curve. Therefore, the asymmetric function (Landsberg, 1977; Reed et al., 1976):

$$R = A(T - T_{\min})(T_{\max} - T)^B \quad [1]$$

where

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

and

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

was fitted to the observed data when temperature-response curves were developed. All four parameters (Table 1),  $T_{\text{opt}}$ ,  $T_{\text{max}}$ ,  $T_{\text{min}}$ , and  $R_{\text{max}}$ , have biological meaning, and the B value defines the skew.  $T_{\text{opt}}$  is the temperature where R equals  $R_{\text{max}}$ , and  $T_{\text{min}}$  and  $T_{\text{max}}$  are the temperatures below and above  $T_{\text{opt}}$ , respectively, where R equals zero. Initial estimates for nonlinear parameters are readily made since they can be read from a graph of the observed data. It should be noted that for  $T < T_{\text{min}}$ , R will become negative and that for  $T > T_{\text{max}}$ , Eq. [1] cannot be calculated unless B is an integer (Landsberg, 1977).

Estimates for  $T_{\text{max}}$ ,  $T_{\text{min}}$ ,  $T_{\text{opt}}$ , and  $R_{\text{max}}$  based on measured plant temperature were obtained using the nonlinear regression procedure (NLIN) of the Statistical Analysis System (SAS, 1987).

**Leaf pair unfolding rate.** First-order linear regression functions relating leaf pair (dahlia leaves are opposite) count to time were calculated for each plant of all treatments in Expt. 1. The first derivative from each of the regression functions gave the

Table 1. Parameters used in modeling.

| Parameter        |  |                                  |
|------------------|--|----------------------------------|
| Symbol           | Description  | Units                            |
| $R_{\text{max}}$ | Maximum rate   | day                              |
| $T_{\text{opt}}$ | Optimum temp   | $^{\circ}\text{C}$               |
| $T_{\text{max}}$ | Maximum temp   | $^{\circ}\text{C}$               |
| $T_{\text{min}}$ | Minimum temp   | $^{\circ}\text{C}$               |
| T                | Daily avg temp                                       | $^{\circ}\text{C}$               |
| $b_1$            | Growth rate; flower development model parameter      | $\text{days}\cdot\text{mm}^{-1}$ |
| $b_0$            | DTF for 4-mm bud; flower development model parameter | days                             |
| DTF              | DTF; flower development model variable               | days                             |
| DIF              | DT-NT  | $^{\circ}\text{C}$               |

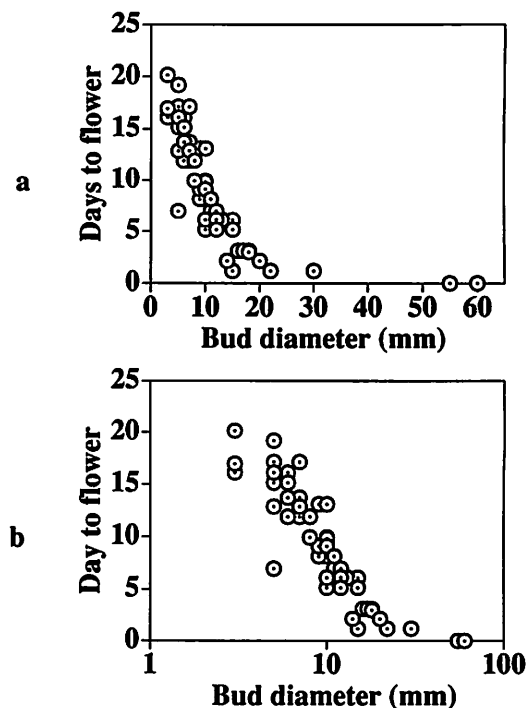


Fig. 1. Days to flower as a function of flower bud diameter (millimeters) for 'Royal Dahlia Yellow' dahlia at 20/20C (day/night) air set-point temperatures (21.2 and 17.1C plant shoot temperature). (a) Linear plot of bud diameter vs. days to flower. (b) Log-transformed bud diameter vs. days to flower.

rate of leaf pair unfolding (leaf pairs per day). The rates were then used to determine the temperature-dependent, leaf pair unfolding rate parameter values for Eq. [1].

**Days from pinch to flower.** The data of Expt. 1 on time to flower from pinch were separated into two time components describing days from pinch to visible bud and days from visible bud to flower. The average number of days from pinch to visible bud and average number of days from visible bud to flower were calculated for each treatment. To facilitate the use of Eq. [1], time periods were converted to rates by taking the reciprocals of each time period and then using these rates in the analysis.

**Flower-bud development rate.** Days to flower (DTF) were plotted against flower bud diameter for plants from each temperature treatment in Expt. 1 (Fig. 1a). Log transformation of bud diameter did not indicate exponential growth in the entire 3- to 60-mm bud range (Fig. 1b). Observations of bud devel-

opment showed that petal separation from the calyx began at a bud diameter of  $\approx 15$  mm. Since flowers were then within 2 to 3 days of open bloom (Fig. 1), DTF was modeled as a function of bud diameter in the 4- to 15-mm range using the following form:

$$DTF = b_0 + b_1 \cdot BD \quad [4]$$

where BD represented bud diameter (4 to 15 mm),  $b_0$  represented the predicted total number of days to flower when the bud diameter was zero, and  $b_1$  represented a growth rate constant at a particular temperature. No statistical advantage was observed when using log-transformed data in the 4- to 15-mm bud size range, so nontransformed data were used. Both  $b_1$  and  $b_0$  were modeled using Eq. [1]. The observed data did not provide estimates of  $T_{max}$ , so a fixed value of  $T_{max}$  equal to 33C was used based on estimates of  $T_{max}$  from the leaf pair unfolding rate, days from pinch to visible bud, and days from visible bud to flower models. To estimate Eq. [1] parameters, data points must be organized in a peak shape and must be positive. Therefore, the  $b_0$  values were transformed by taking their reciprocal, and the negative  $b_1$  values were transformed by taking the reciprocal of their absolute values before estimation, and then were back-transformed to give properly scaled values.

**Morphology data.** Means together with 95% confidence intervals were calculated for tuberous root weight, lateral shoot count, lateral shoot length, primary shoot length, flower bud count, flower diameter, and node count. Regression analysis was performed on the primary shoot length data from Expt. 1 by use of the linear regression procedure (REG) of SAS (1987) with linear terms of DIF (Erwin et al., 1989) as an independent variable.

## Results

**Leaf pair unfolding rate.** Fitting Eq. [1] to the observed leaf pair unfolding data resulted in a highly significant model fit (Fig. 2, Table 2) with an  $R^2$  of 0.87.  $T_{opt}$  was estimated at 24.6C,  $T_{min}$  at 5.5C, and  $R_{max}$  at 0.29 leaf pairs/day.  $T_{max}$  was calculated at 34.9C, but because of inadequate high-temperature data, it was not estimated precisely, as it had a large 95% confidence interval (Table 2).

**Days from pinch to flower.** Fitting Eq. [1] to the observed developmental rates from pinch to visible bud and visible bud to flower data resulted in highly significant model fits (Fig. 3, Table 2) with an  $R^2$  of 0.73 and 0.84, respectively (Table 2).

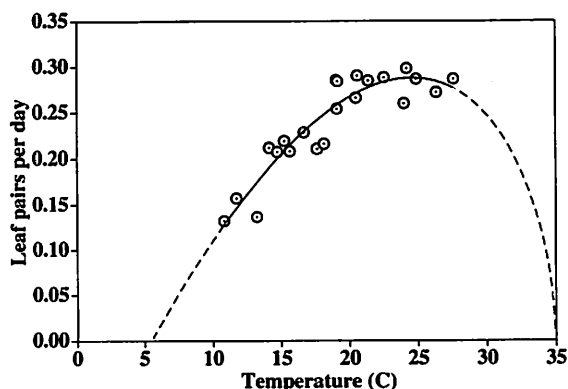


Fig. 2. Observed (symbols) and predicted (lines) leaf pair unfolding rate of 'Royal Dahlietta Yellow' dahlia in response to ADT. Dashed lines represent predictions outside the observed data range based on Eq. [1] and parameter estimates from Table 2.

$T_{opt}$  was estimated at 22.4C,  $T_{max}$  at 31.1C, and  $R_{max}$  at 0.07 flower/day for the developmental rate from pinch to visible bud model.  $T_{min}$  was calculated at 2.4C but was not estimated precisely as it had a very large 95% confidence interval (Table 2).  $T_{opt}$  was estimated at 24.4C,  $T_{min}$  at 5.2C, and  $R_{max}$  at 0.054 flower/day for the developmental rate from visible bud to flower model.  $T_{max}$  was calculated at 33.1C but was not estimated precisely because of inadequate high-temperature data (Table 2).

Days to flower from pinch decreased from 48 to 40 days as temperature increased from 15 to 20C in the 12-h photoperiod treatment of Expt. 2. These intervals compare to calculated time to flower of 47 and 35 days using Eq. [1] and parameters from Expt. 1. Photoperiod had no significant effect on time to flower in Expt. 2 except at 15C, at which flowering was delayed 15 days when photoperiod was decreased from 12 to 10 h.

**Flower bud development rate.** Fitting Eq. [1] to the observed data for  $b_1$  and  $b_0$  resulted in highly significant model fits (Fig. 4, Table 3) with an  $R^2$  of 0.67 and 0.87, respectively (Table 3).  $T_{opt}$  was estimated at 25.9C,  $T_{min}$  at 5.6C, and  $R_{max}$  at 20.8 days for the  $b_0$  model.  $T_{opt}$  was estimated at 23.3C,  $T_{min}$  at 6.1C, and  $R_{max}$  at  $-1.33$  days $\cdot$ mm $^{-1}$  for the  $b_1$  model. The 95% confidence intervals from the  $b_1$  and  $b_0$  models showed that the  $T_{opt}$  estimates were significantly different, while estimates of  $T_{min}$  were not (Table 3). For both models,  $T_{max}$  was fixed at 33C because of inadequate high-temperature data (Table 3).

Equation [1] accurately predicted ( $R^2 = 0.98$ ) DTF based on temperature and bud diameter when  $b_0$  and  $b_1$  were calculated using Eq. [1] with the parameter values in Table 3. Time to flower decreased linearly as bud diameter increased and at a decreasing rate as temperature increased (Fig. 5).

**Tuberous root weight.** Temperature and photoperiod affected tuberous root formation (Fig. 6a). Tuberous roots formed on plants in the 10- and 12-h photoperiod treatments at 15 and 20C. Only small tuberous roots formed on some plants when the photoperiod was  $\geq 14$  h at 15C, and no tuberous roots formed at 20C. No tuberous roots were formed, regardless of photoperiod, at 25 and 30C (Fig. 6a).

**Lateral shoot number.** Lateral shoot count increased with increasing photoperiod up to 14 h (Fig. 6b). When the photoperiod exceeded 14 h, plants grown at 25C generally had fewer lateral shoots than plants grown at 15 or 20C (Fig. 6b).

**Lateral shoot length.** Lateral shoot length increased as photoperiod increased from 10 to 14 h. Lateral shoot length was similar on plants exposed to photoperiods  $> 14$  h but decreased as temperature increased from 15 to 25C (Fig. 6c).

**Primary shoot length.** Primary shoot length increased from 88 to 139 mm as DIF increased from  $-16.2$  to 14.8C in Expt. 1 (Fig. 7). With the 10C NT, shoots were shorter than expected, based on the calculated DIF.

Temperature and photoperiod interacted in Expt. 2 to influence primary shoot length (Fig. 8). It decreased as temperature increased from 20 to 30C. Primary shoot length increased as photoperiod increased at 15 and 20C; at 25C, the effect of photoperiod was inconsistent, and at 30C, photoperiod had no effect as shoot elongation was minimal.

**Flower bud number.** Flower bud count decreased as temperature increased in Expt. 2 (Fig. 9). The highest number of flower buds at 15 and 20C was on plants in the 14- to 16-h and 10- to 14-h photoperiod treatments, respectively. At 25C, all flower buds on plants with photoperiods  $> 14$  h aborted. No flower buds were observed at 30C regardless of photoperiod.

Table 2. Nonlinear regression results from fitting Eq. [1] to the leaf pair unfolding and days pinch to flower developmental-rate models.

| Model                      | Parameter        | Estimate | Asymptotic 95% confidence interval |       | N <sup>z</sup> | R <sup>2y</sup> |
|----------------------------|------------------|----------|------------------------------------|-------|----------------|-----------------|
|                            |                  |          | Lower                              | Upper |                |                 |
| Leaf pair unfolding        | R <sub>max</sub> | 0.29     | 0.27                               | 0.31  | 22             | 0.87            |
|                            | T <sub>opt</sub> | 24.6     | 21.8                               | 27.4  |                |                 |
|                            | T <sub>max</sub> | 34.9     | -2.3                               | 72.2  |                |                 |
|                            | T <sub>min</sub> | 5.5      | 0.7                                | 10.3  |                |                 |
| Rate pinch to visible bud  | R <sub>max</sub> | 0.07     | 0.066                              | 0.074 | 21             | 0.73            |
|                            | T <sub>opt</sub> | 22.4     | 20.3                               | 33.8  |                |                 |
|                            | T <sub>max</sub> | 31.1     | 28.5                               | 33.8  |                |                 |
|                            | T <sub>min</sub> | 2.4      | -3.3                               | 8.2   |                |                 |
| Rate visible bud to flower | R <sub>max</sub> | 0.054    | 0.050                              | 0.058 | 21             | 0.84            |
|                            | T <sub>opt</sub> | 24.2     | 22.0                               | 26.8  |                |                 |
|                            | T <sub>max</sub> | 33.1     | 10.9                               | 55.3  |                |                 |
|                            | T <sub>min</sub> | 5.2      | 2.43                               | 10.4  |                |                 |

<sup>z</sup>No. observations in data set.

<sup>y</sup>R<sup>2</sup> was calculated as 1-SS<sub>residual</sub>/SS<sub>corrected total</sub>.

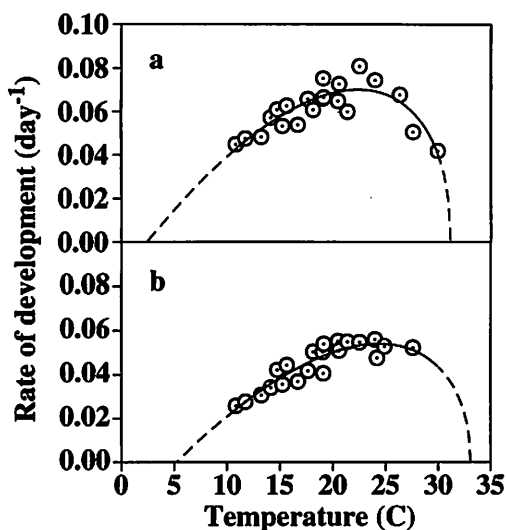


Fig. 3. Observed (symbols) and predicted (lines) developmental rate of progress from (a) pinch to visible bud and (b) visible bud to flower of 'Royal Dahlietta Yellow' dahlia in response to ADT. Dashed lines represent predictions outside the observed data range based on Eq. [1] and parameter estimates from Table 2.

**Flower diameter.** Flower diameter decreased as ADT increased (Fig. 10) but was not affected by photoperiod (data not shown).

**Node number.** Average number of nodes on lateral flowering shoots increased as ADT increased in Expts. 1 and 2 (Fig. 11). There was no statistically significant relationship between photoperiod and node count.

### Discussion

Our data on 'Royal Dahlietta Yellow' confirm earlier studies that showed a temperature and photoperiod effect on dahlia tuberous root formation, primary shoot length, lateral shoot length and count, and node count to first flower. Low temperature and SD promoted tuberous root formation (Fig. 6a), results similar to those found for other cultivars in which short (<12 h) photoperiods (Maatsch and Runger, 1955) along with low temperature (15 to 20C) (Moser and Hess, 1968) promoted tuberous root formation. When tuberous root formation was promoted as photoperiod decreased, primary shoot length (Fig. 8) and lateral

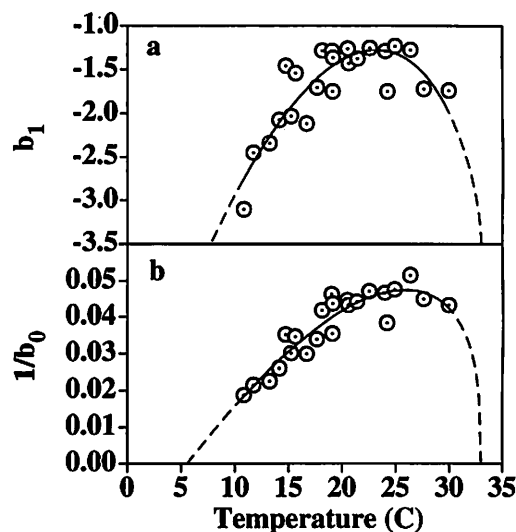


Fig. 4. Observed (symbols) and predicted (lines) (a) bud development rate (b<sub>1</sub>) and (b) 1/b<sub>0</sub> from Eq. [4] of 'Royal Dahlietta Yellow' dahlia in response to average daily temperature. Dashed lines represent predictions outside the observed data range based on Eq. [1] and parameter estimates from Table 3.

shoot length and count (Fig. 6 b and c) decreased. Similarly, others have reported primary shoot length and lateral shoot length and count to decrease as photoperiod decreased (Konishi and Inaba, 1964; Maatsch and Runger, 1955; Payne and Haliburton, 1976; Yasuda and Yokoyama, 1960). Node count below the first flower was primarily influenced by temperature, not photoperiod (Fig. 11); the temperature results were similar (Maatsch and Runger, 1955), while the photoperiod results were in contrast to those previously reported in which node count increased as photoperiod increased (Payne and Haliburton, 1976; Yasuda and Yokoyama, 1960).

Flowering in 'Royal Dahlietta Yellow' dahlia occurred under all photoperiods at 15 and 20C, but at 25C, plants only flowered under photoperiods of ≤14 h, and at 30C, no flowering occurred regardless of photoperiod (Fig. 9). Flower bud count on 'Royal Dahlietta Yellow' decreased as photoperiod increased beyond 14 h (Fig. 9). In work by others, flower bud count increased (Maatsch and Runger, 1955) or decreased (Yasuda and Yokoyama, 1960) with increasing photoperiod.

Table 3. Nonlinear regression results from fitting Eq. [1] to the flower development model.

| Model          | Parameter                     | Estimate | Asymptotic 95% confidence interval |       | N <sup>a</sup> | R <sup>2y</sup> |
|----------------|-------------------------------|----------|------------------------------------|-------|----------------|-----------------|
|                |                               |          | Lower                              | Upper |                |                 |
| b <sub>0</sub> | R <sub>max</sub>              | 20.8     | 21.7                               | 20.4  | 23             | 0.87            |
|                | T <sub>opt</sub>              | 25.9     | 24.8                               | 27.0  |                |                 |
|                | T <sub>max</sub> <sup>x</sup> | 33.0     | ---                                | ---   |                |                 |
|                | T <sub>min</sub>              | 5.6      | 3.9                                | 7.2   |                |                 |
| b <sub>1</sub> | R <sub>max</sub>              | -1.33    | -1.43                              | -1.24 | 23             | 0.67            |
|                | T <sub>opt</sub>              | 23.3     | 21.5                               | 25.1  |                |                 |
|                | T <sub>max</sub> <sup>x</sup> | 33.0     | ---                                | ---   |                |                 |
|                | T <sub>min</sub>              | 6.1      | 2.8                                | 9.4   |                |                 |

<sup>a</sup>No. observations in data set.

<sup>y</sup>R<sup>2</sup> was calculated as 1-SS<sub>residual</sub>/SS<sub>corrected total</sub>.

<sup>x</sup>The T<sub>max</sub> parameter was fixed at 33C and was not estimated.

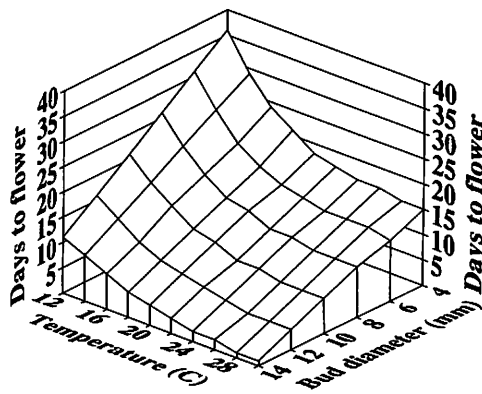


Fig. 5. Days to flower as a function of average daily temperature (°C) and bud diameter (millimeters) of 'Royal Dahlietta Yellow'.

Previous research on dahlia did not quantify leaf and flower developmental rates. Equation [1] was selected to describe temperature-dependent leaf and flower development rates (Tables 2 and 3, Figs. 2-4) because the equation readily describes typical asymmetrical peak-shaped temperature response curves and all parameters have biological significance. While a simpler model requiring only two parameters, R<sub>max</sub> and T<sub>opt</sub>, has recently been described (Volk and Bugbee, 1991), it is symmetrical around the peak and thus clearly not representative of our data or biological temperature response curves, which are typically asymmetrical.

The data collected from the experimental temperature range in these experiments generally did not allow precise estimates of T<sub>max</sub> and, to a lesser extent, T<sub>min</sub>. Further experiments at high and low temperatures are needed to estimate these parameters more precisely.

No previous values for T<sub>max</sub>, T<sub>min</sub>, and T<sub>opt</sub> have been published for dahlia; therefore, comparison of our estimated T<sub>max</sub>, T<sub>min</sub>, and T<sub>opt</sub> values with previous research is impossible. However, T<sub>opt</sub> may be compared to data from previous work in which minimum time to flowering as a function of temperature was presented. Hildrum (1973) reported that time to flowering decreased as temperature increased from 12 to 18 to 21C. Durso and De Hertogh (1977) reported an optimum ADT of 25.5C (29/20C DT/NT, 25.5C assuming 12-h day/12-h night) for time to flowering. The most rapid development from pinch to visible bud and from visible bud to flowering occurred at 22.4 and 24.2C, respectively (Table 2), temperatures similar to those reported by Durso and De Hertogh (1977).

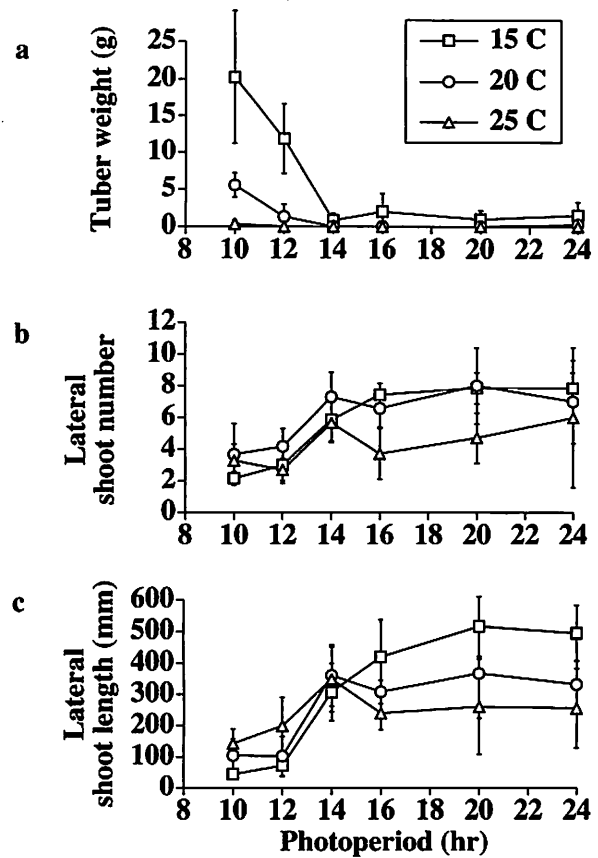


Fig. 6. (a) Tuberous root weight (grams), (b) lateral shoot number (count), and (c) lateral shoot length (millimeters) of 'Royal Dahlietta Yellow' dahlia as a function of temperature and photoperiod. Lateral shoot length is average total lateral shoot length per plant. Vertical bars represent 95% confidence intervals.

Maximum dahlia leaf pair unfolding rate was 0.29 leaf/day at 24.6C. Leaf unfolding rate in a number of species such as *Helianthus annuus* L. (Rawson and Hindmarsh, 1982), *Dendranthema grandiflora* (Ramat.) Kitamura (Karlsson et al., 1989), and *Lilium longiflorum* Thunb. (Karlsson et al., 1988) has been found to increase linearly with temperature within at least part of the 10 to 35C temperature range. However, as the temperature range widens, the relationship between leaf unfolding rate and temperature becomes nonlinear. Tollenaar et al. (1979) in *Zea mays* L. and Karlsson et al. (1991) in *Hibiscus rosa-sinensis* L. found curvilinear relationships between leaf unfolding rate

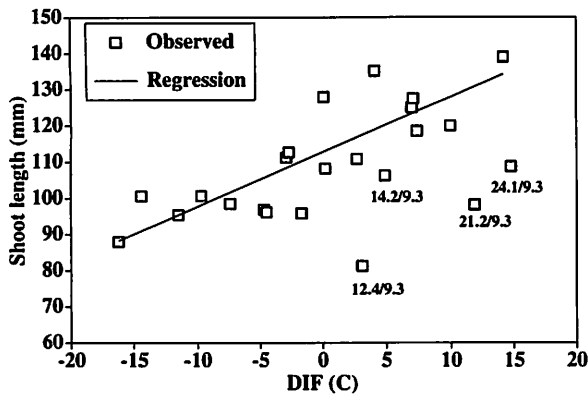


Fig. 7. Primary shoot length (millimeters) of 'Royal Dahlietta Yellow' dahlia as a function of DIF. The function was: primary shoot length (mm) = 112.77 + 1.51 \* DIF ( $r^2 = 0.71$ ). Numbers next to the symbols represent actual DT/NT for the 10C (NT) treatment.

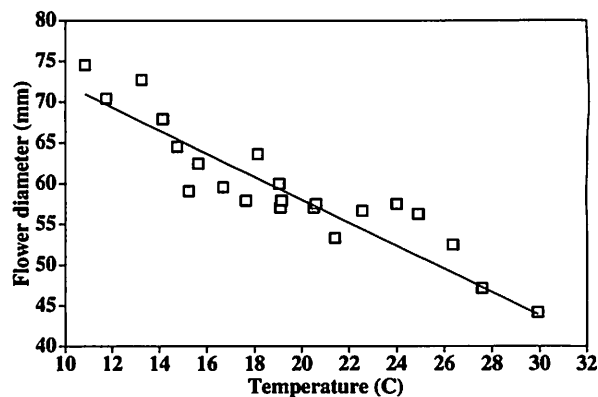


Fig. 10. Relationship between ADT and 'Royal Dahlietta Yellow' dahlia flower diameter. The function was: flower diameter = 86.32 - 1.42 \* temperature.

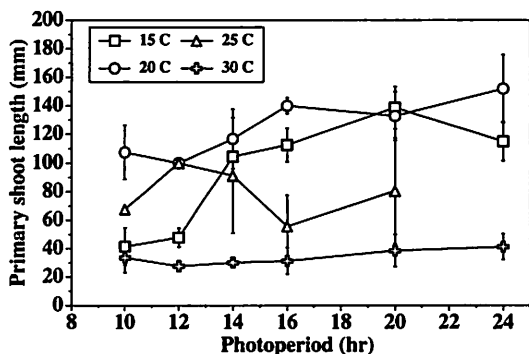


Fig. 8. Primary shoot length (millimeters) of 'Royal Dahlietta Yellow' dahlia as a function of temperature and photoperiod. Vertical bars represent 95% confidence intervals.

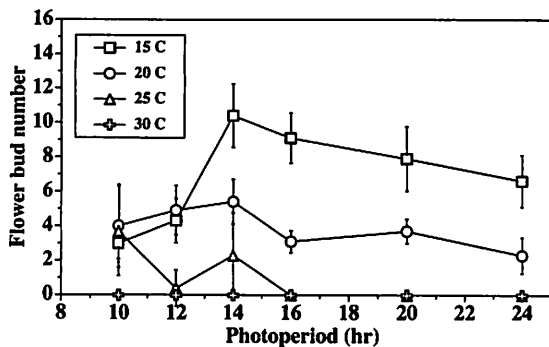


Fig. 9. Flower bud number (count) of 'Royal Dahlietta Yellow' dahlia as a function of temperature and photoperiod. Vertical bars represent 95% confidence intervals.

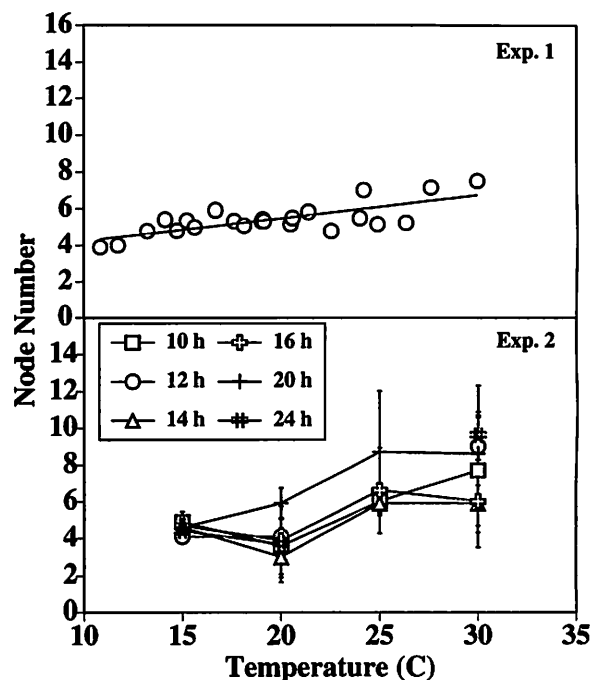


Fig. 11. Number of nodes below the flower on lateral shoots of 'Royal Dahlietta Yellow' dahlia as a function of temperature in Expt. 1 and temperature and photoperiod in Expt. 2. Plants in Expt. 1 were grown under a 12-h photoperiod and the regression line was: Node number (count) = 0.1236 \* temperature + 3.01 ( $r^2 = 0.55$ ). Vertical bars represent 95% confidence intervals.

and temperature. Cubic polynomials were used to find maximum leaf unfolding rates for *Z. mays* (0.55 to 0.60 leaf/day at 31 to 32C) and for *H. rosa-sinensis* (0.23 leaf/day at 32C). Equation [1] estimated maximum dahlia leaf pair unfolding rate at 0.29 leaf pair/day (Fig. 2, Table 2). The base temperature under which no leaf unfolding is expected was estimated at 5.5C in dahlia (Table 2) and at 9.8 and 6C for *H. rosa-sinensis* and *Z. mays*, respectively.

Days to flower was found to be a function of bud size and ADT, given the proper photoperiod (Fig. 5). The developed relationship allowed prediction of days to flower given a certain bud size and ADT, or ADT needed given a certain bud size and

desired days to flower. This model allows determination of the optimum temperature for shortest time to flowering given a bud size (4 to 15 mm).

Payne and Haliburton (1976) reported that flower diameter increased with increasing photoperiod, while Durso and De Hertogh (1977) found no effect of temperature on flower diameter. 'Royal Dahlietta Yellow' flower diameter was not affected by photoperiod but decreased with increasing temperature (Fig. 10).

DIF describes stem elongation better than actual DT or NT between 10 and 30C in many species. Stem elongation in *Streptocarpus nobilis* C.B. Clarke, *Xanthium strumarium* L., *Lycopersicon esculentum* L., *Z. mays*, *Salvia splendens* F., *Impatiens wallerana* Hook, *Nephrolepis exaltata* L., *Fuchsia × hybrida* Vilm. (Erwin et al., 1991), *Dendranthema × grandiflora* Tzvelev, (Karlsson et al., 1989), *Campanula isophylla* Moretti (Moe and

Heins, 1990; Moe et al., 1991), *Euphorbia pulcherrima* Klotz (Berghage and Heins, 1991), and *L. longiflorum* (Erwin et al., 1989) was best described by DIF, and increased as DIF increased. Likewise, dahlia was responsive to DIF, with primary shoot length linearly and positively related to DIF, except at and perhaps below NT of 10C (Fig. 7). While no data were collected on tuberous root size in Expt. 1, the unusually short shoots at 10C might be related to increased tuberous root formation in the 12-h photoperiod, thereby decreasing vegetative growth as seen in Expt. 2.

The results collectively indicate a relatively narrow set of conditions for optimal 'Royal Dahlietta Yellow' flowering, with optimal defined as fast-developing plants with many flower buds and satisfactory plant height. These conditions are met by 12- to 14-h photoperiods at  $\approx$ 20C. Photoperiods <12 h promote tuberous root formation and inhibit vegetative and reproductive shoot growth and should be avoided. Similarly, 15C promotes tuberous root formation, while temperatures of 25C or higher reduce or prevent flowering entirely.

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