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Temperature and Photosynthetic Photon Flux Influence Chrysanthemum Shoot Development and Flower Initiation under Short-day Conditions

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Abstract. **The effects of photosynthetic photon flux (PPF), day temperature (DT) and night temperature (NT) on leaf number, leaf unfolding rate and shoot length were determined for chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') grown under short day (SD) conditions. A functional relationship was first developed to predict if flower bud appearance would occur within 100 SD under a given set of environmental conditions. All combinations of DT and NT in the range from 10° to 30°C were predicted to result in flower bud appearance at higher PPF than 10.8 mol·day^{-1}·m^{-2}. The number of leaves formed below the flower increased quadratically as DT and/or NT increased from 10° to 30°. As PPF increased from 1.8 to 21.6 mol·day^{-1}·m^{-2}, one to two fewer leaves were formed per shoot. Rate of leaf unfolding increased linearly with increasing average daily temperature from 0.2 leaves/day at 10° to 0.5 leaves/day at 30°. Internode length was highly correlated with the difference between DT and NT (DIF = DT − NT) such that increasing DIF from −12° to 12° resulted in progressively longer internodes.**

Functional relationships between plant processes and environmental conditions are required for modeling plant growth and development. In commercial production of chrysanthemum [*Dendranthema grandiflora* Tzvelev., (Anderson, 1987)], plants are flowered by exposure to short-day (SD) conditions. Most plants are pinched before, or at the start, of SD (Crater, 1980). Plant development of pinched plants under SD starts with the formation of lateral shoots, appearance of leaves, and transition of the apical meristem from vegetative to reproductive. The time required from pinch to visible flower bud is determined by the number of leaves initiated before meristem transition and subsequent leaf unfolding rate (Cockshull et al., 1981).

Many plants adapt to a wide range of environmental conditions by changes in morphological characteristics and dry weight partitioning patterns (Hickman, 1975; Thompson and Stewart, 1981). Plant height, an important quality factor in chrysanthe-

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mum pot plant production, is a plant characteristic that demonstrates large adaptability to the environment (Karlsson et al., 1983; Karlsson, 1984; Erwin 1986). An understanding of how the environment influences final height is necessary to produce plants with desirable height.

To model leaf number, leaf unfolding rate, and plant height for a flowering chrysanthemum, it is necessary to first establish whether flower initiation and continued development to a flower will occur in a reasonable number of SD under a given set of environmental conditions. Models for the transition from vegetative to reproductive meristem have previously been developed for chrysanthemum. These models (Charles-Edwards et al., 1979; Thornley and Cockshull, 1980) are based on relationships between apex size and stage of development, but ignore environmental effects.

This study was initiated to quantitatively describe the effects of photosynthetic photon flux (PPF), day temperature (DT), and night temperature (NT) on flower bud appearance, leaf number, leaf unfolding rate, and plant height in reproductive chrysanthemum.

Materials and Methods

Rooted cuttings of 'Bright Golden Anne' were potted individually in 10-cm pots and placed in growth chambers for 7 days under a PPF of 18.7 $mol \cdot day^{-1} \cdot m^{-2}$ (325 $\mu mol \cdot s^{-1} \cdot m^{-2}$, 16 hr/day) and at a constant 20°C. On the 7th day, plants were pinched to six nodes and SD (10 hr of light/day) were initiated. The PPF, DT, and NT were then altered in the chamber to provide one of the treatment combinations given in Table 1. The DT and NT paralleled the photoperiod and skotoperiod. A 15.6-mM butanedioic acid mono(2,2-dimethylhydrazide) (daminozide) solution was applied as a foliar spray 7 and 14 days after the start of SD (Crater, 1980). The number of lateral shoots was reduced to three per plant 10 days after the start of SD. Lateral flower buds were removed when the terminal flower bud was 10 mm in diameter.

The PPF was provided by cool-white fluorescent (GE, F48T12, CW 1500) and incandescent lamps (GE, 40-W, 120-V) with an input wattage of 80:20, respectively. PPF was measured with a LI-COR LI-185B meter and LI-190SB quantum sensor. Plants were lowered as necessary to maintain the desired PPF at canopy level. Average daily temperature fluctuated ±1°C from the setpoints and PPF varied ±10% over the canopy.

Plants were grown in a commercial peat-lite medium (Michigan Peat Co.) and irrigated as necessary. The nutritional program consisted of 9.7 $mol \cdot m^{-3}$ NO_3^-, 4.6 $mol \cdot m^{-3}$ NH_4^-, and 5.1 $mol \cdot m^{-3}$ K from ammonium nitrate and potassium nitrate at each watering. Medium pH was maintained at 6.0 ± 0.2 by adjusting nutrient solution pH with nitric acid.

A central composite statistical design was used to select treatment combinations (Gardiner et al., 1967; Karlsson and Heins, 1986). PPF ranged from 1.8 to 21.6 $mol \cdot day^{-1} \cdot m^{-2}$ (50 to 600 $\mu mol \cdot s^{-1} \cdot m^{-2}$, 10 hr/day) and both DT and NT ranged from 10° to 30°C. To strengthen the data base, the 15 treatment combinations required in the statistical design were supplemented with 10 additional treatments at the endpoints of the PPF and temperature ranges (Table 1).

Five plants from each treatment were randomly selected at the start of SD and every 10 days thereafter to determine leaf number and shoot length of the main shoot and the three lateral shoots. A leaf was recorded as unfolded when it was $\geq$ 10 mm. The experiment was terminated at flowering or after 100 SD if flower buds (2 mm in diameter) were not apparent at that time.

Models of leaf number and internode length were developed on combined data from the first and second lateral shoot, as no significant differences ($P < 0.05$) in leaf number or shoot length existed between the two uppermost lateral shoots on plants within a treatment. Models of leaf number and shoot length for the third shoot were not developed. Leaf number and shoot length of shoot 3 were significantly different from shoot 1 and/or shoot 2 in certain treatments (Tables 1 and 2).

Multiple linear regression analyses were performed using the Statistical Package for the Social Sciences "New Regression" (Nie et al., 1975) and the Systat statistical package (Wilkenson, 1986). Leaf number was correlated with time by linear regression analysis to obtain estimates of average leaf unfolding rate for each treatment. Surface and isopleth graphs were created using the selected functions with the Surfer graphing program (Golden Software, Inc., 1987).

Stepwise regression analyses with linear, quadratic, and interaction terms of DT, NT, PPF, and average daily temperature (ADT) were initially used to select a functional relationship for each developmental or growth process. In the analysis of internode length, the difference between DT and NT (DIF = DT − NT) was also added to the independent variables. Efforts were made to improve the resulting equations by addition and deletion of independent variables using both the terms available in the stepwise regression analyses and higher-order terms. Final equations were selected based on the statistical significance of included variables, r^2, and F values of the equations and the adequacy of prediction. All independent variables included in the final equations were significant at the 5% level as indicated by a two-tailed t test.

Results and Discussion

Plants that did not develop 2-mm flower buds within 100 SD had a minimum of 20 leaves on both the first and second lateral shoot (Table 1). This leaf number information was used in model development as plants with more than 20 leaves were not considered reproductive. The selected regression function predicting leaf number for the purpose of determining the event of flower initiation was mathematically manipulated by dividing the function by 20 and then inverting it to yield its reciprocal. The resulting "visible flower bud index" indicated that flower bud appearance would occur within 100 SD at values >1.0 and that flower bud appearance would not occur if the index was $\leq$1.0.

Fig. 1 shows the combinations of DT and NT at 1.8 $mol \cdot day^{-1} \cdot m^{-2}$ where visible flower buds were not predicted to occur after 100 SD. Visible flower buds were not predicted at 30°C DT with any NT. At 30° NT, flower buds were not predicted to appear when the DT was 10° or between 23° and 30°. The number of DT and NT combinations resulting in visible flower buds were predicted to increase as PPF increased from 1.8 to 10.8 $mol \cdot day^{-1} \cdot m^{-2}$. Flowering was predicted to occur under all DT and NT combinations in the range from 10° to 30° at more than 10.8 $mol \cdot day^{-1} \cdot m^{-2}$. These predictions are consistent with the observed results (Table 1).

The functional relationships for leaf number, leaf unfolding rate, and internode length were developed under the assumption that flowers would develop. Data from plants in treatments that did not have visible flower buds within 100 SD were therefore excluded in the continued analyses. Consequently, the functional relationships discussed below can only be used for prediction when flower bud appearance first has been established.

The SD environmental conditions modified leaf number be-

Table 1. Influence of photosynthetic photon flux (PPF) and of day and night temperatures on number of leaves in 'Bright Golden Anne' chrysanthemum.

Environment			Average daily temp (°C)	No. leaves^{y}		
PPF^{z} (mol·day^{-1}·m^{-2})	Temp (°C) Day	Night		Shoot 1	Shoot 2	Shoot 3
1.8	10	10^{x}	10.0	9 ± 0.6	10 ± 0.5	10 ± 0.5^{NS}
1.8	30	10^{xv}	18.3	24 ± 0.6	22 ± 1.0	12 ± 1.4^{*}
1.8	20	20	20.0	10 ± 0.4	11 ± 0.6	13 ± 1.0^{*}
1.8	10	30^{xv}	21.7	21 ± 1.0	20 ± 0.4	14 ± 0.5^{*}
1.8	30	30^{xv}	30.0	25 ± 0.8	24 ± 0.7	21 ± 0.4^{*}
5.8	14	14	14.0	9 ± 0.5	10 ± 0.6	10 ± 0.6^{NS}
5.8	26	14	19.0	10 ± 0.2	11 ± 0.5	12 ± 0.6^{*}
5.8	20	20^{x}	20.0	9 ± 0.4	10 ± 0.5	11 ± 0.3^{*}
5.8	14	26	21.0	11 ± 0.2	11 ± 0.3	12 ± 0.6^{NS}
5.8	26	26	26.0	15 ± 0.6	15 ± 0.7	16 ± 0.5^{NS}
11.7	20	10	14.2	10 ± 0.4	10 ± 0.2	10 ± 0.2^{NS}
11.7	10	20	15.8	9 ± 0.5	9 ± 0.4	9 ± 0.4^{NS}
11.7	20	20	20.0	10 ± 0.2	10 ± 0.2	11 ± 0.5^{NS}
11.7	30	20	24.2	14 ± 0.5	14 ± 0.4	14 ± 0.6^{NS}
11.7	20	30	25.8	11 ± 0.2	11 ± 0.3	11 ± 0.5^{NS}
17.6	14	14	14.0	9 ± 0.3	11 ± 0.2	11 ± 0.2^{NS}
17.6	26	14	19.0	10 ± 0.4	11 ± 0.2	10 ± 0.2^{NS}
17.6	20	20^{x}	20.0	9 ± 0.5	10 ± 0.5	10 ± 0.5^{NS}
17.6	14	26	21.0	11 ± 0.6	12 ± 0.7	13 ± 0.2^{*}
17.6	26	26	26.0	14 ± 0.6	14 ± 1.2	14 ± 0.8^{NS}
21.6	10	10^{x}	10.0	8 ± 0.5	9 ± 0.6	10 ± 0.4^{*}
21.6	30	10^{x}	18.3	14 ± 0.7	16 ± 0.9	18 ± 1.4^{NS}
21.6	20	20	20.0	9 ± 0.2	10 ± 0.4	11 ± 0.3^{*}
21.6	10	30^{x}	21.7	11 ± 0.4	12 ± 0.5	12 ± 0.3^{NS}
21.6	30	30^{x}	30.0	13 ± 0.5	14 ± 0.3	13 ± 0.9^{NS}

^{z}Ten hours of irradiation per day.

^{y} ± SE

^{x}Treatments added to the basic central composite design.

^{v}No flower initiation after 100 short days.

^{*,NS}Leaf number of shoot 3 significantly ($P < 0.05$) or nonsignificantly different from shoot 1 and/or shoot 2, respectively. Differences between shoot 1 and shoot 2 were all nonsignificant.

low the flower (Table 1). The effects of DT and NT on predicted average leaf number in chrysanthemum at 11.7 mol·day^{-1}·m^{-2} are shown in Fig. 2. Leaf number increased in response to either high DT or high NT with a larger increase in response to DT. Plants grown under a PPF of 11.7 mol·day^{-1}·m^{-2} had 11 leaves per shoot at 20°C DT and 30° NT but 14 leaves per shoot at 30° DT and 20° NT (Table 1). Only small changes in leaf number were predicted for DT and NT between 10° and 20°.

Higher temperatures during SD result in more leaves below the flower, leading to delayed morphological flower initiation (Cathey, 1955; Whealy et al., 1987) and heat delay (Post and Lacey, 1951). For example, a heat-sensitive cultivar ('Orange Bowl') formed four more leaves per shoot when the temperature under SD increased from 22°C DT/18° NT to 30° DT/26° NT (Whealy et al., 1987). Our model predicts a five-leaf increase for 'Bright Golden Anne' under comparable irradiance and temperature conditions.

Many studies (Vince, 1960; Cockshull and Hughes, 1971; Cockshull and Hughes, 1972; Cockshull, 1979) have shown an increased leaf number on plants grown under low PPF. Our study indicated that the number of leaves only increased by one or two as PPF decreased from 21.6 to 1.8 mol·day^{-1}·m^{-2} (Table 1). The plants in the other cited studies (Vince, 1960; Cockshull and Hughes, 1971; Cockshull and Hughes, 1972; Cockshull, 1979) were grown at the same PPF during both LD and SD. In contrast, plants in our experiment were placed under a relatively high PPF of 18.7 mol·day^{-1}·m^{-2} for 1 week before start of SD. The high PPF provided during LD may have prevented the expected increase in leaf number at low PPF during SD.

Rate of leaf appearance in several species has been found to increase linearly to a maximum rate as temperature increases (Friend et al., 1962; Balvoll and Bremer, 1965; Tollenaar et al., 1979; Rawson and Hindmarsh, 1982; Karlsson et al., 1988). Cockshull et al. (1981) reported that leaf appearance in chrysanthemum was also an average daily temperature (ADT) response. Stepwise regression analysis on leaf unfolding in this study with linear, quadratic, and interaction terms of PPF, DT, NT, and ADT resulted in a regression function with only ADT as the independent variable (Fig. 3). Efforts to improve this relationship by adding higher-order terms were ineffective.

Cockshull et al. (1981) did not present a functional relationship for leaf unfolding in chrysanthemum. Their reported leaf unfolding rate at 10°C was similar to the rate observed in this study at 10°, but their rate at 20° was 39% higher than we observed. The deviation may be due to differences in cultivars or cultural practices. A 1° increase in ADT was predicted to

Table 2. Influence of photosynthetic photon flux (PPF) and of day and night temperatures on shoot and internode length in 'Bright Golden Anne' chrysanthemum.

Environment			Day temp minus night temp (°C)	Shoot length (cm)[y]			Internode length (cm)		
PPF[z] ($mol \cdot day^{-1} \cdot m^{-2}$)	Temp (°C) Day	Temp (°C) Night		Shoot 1	Shoot 2	Shoot 3	Shoot 1	Shoot 2	Shoot 3
1.8	10	10[x]	0	15 ± 5.0	15 ± 3.7	15 ± 6.3[NS]	1.4	1.5	1.5
1.8	30	10[xv]	20	26 ± 3.9	24 ± 5.3	13 ± 7.4[**]	1.1	0.9	1.2
1.8	20	20	0	18 ± 1.7	19 ± 1.2	14 ± 5.7[NS]	1.8	1.7	0.9
1.8	10	30[xv]	−20	14 ± 3.9	13 ± 2.8	9 ± 1.0[*]	0.7	0.7	0.6
1.8	30	30[xv]	0	39 ± 2.8	38 ± 4.0	30 ± 1.0[**]	1.6	1.6	1.4
5.8	14	14	0	16 ± 2.4	17 ± 0.5	16 ± 1.1[NS]	1.9	1.6	1.6
5.8	26	14	12	33 ± 3.2	34 ± 2.1	27 ± 11.7[NS]	3.3	3.1	2.3
5.8	20	20[x]	0	16 ± 0.7	17 ± 0.5	16 ± 1.1[NS]	1.8	1.7	1.4
5.8	14	26	−12	17 ± 0.7	17 ± 1.1	18 ± 1.4[NS]	1.5	1.5	1.5
5.8	26	26	0	29 ± 2.4	29 ± 3.3	29 ± 5.3[NS]	1.9	1.9	1.8
11.7	20	10	10	30 ± 0.4	31 ± 2.6	29 ± 3.0[NS]	3.0	3.1	2.9
11.7	10	20	−10	10 ± 0.8	9 ± 1.0	10 ± 1.2[NS]	1.1	1.0	1.1
11.7	20	20	0	22 ± 1.3	24 ± 2.2	22 ± 1.2[NS]	2.2	2.4	2.0
11.7	30	20	10	28 ± 1.5	28 ± 1.5	29 ± 1.8[NS]	2.0	2.0	2.1
11.7	20	30	−10	18 ± 1.0	18 ± 0.7	20 ± 1.4[NS]	1.6	1.6	1.8
17.6	14	14	0	15 ± 1.7	16 ± 0.4	18 ± 1.7[*]	1.7	1.5	1.6
17.6	26	14	12	28 ± 2.2	31 ± 3.2	31 ± 2.5[NS]	2.8	2.8	3.1
17.6	20	20[x]	0	15 ± 1.5	16 ± 1.4	15 ± 1.5[NS]	1.6	1.5	1.5
17.6	14	26	−12	15 ± 2.0	16 ± 2.3	17 ± 2.4[NS]	1.4	1.3	1.3
17.6	26	26	0	31 ± 3.2	31 ± 4.1	31 ± 2.2[NS]	2.2	2.2	2.2
21.6	10	10[x]	0	11 ± 2.2	12 ± 3.6	11 ± 2.2[NS]	1.4	1.3	1.1
21.6	30	10[x]	20	30 ± 2.8	31 ± 2.3	34 ± 1.8[NS]	2.1	1.9	1.9
21.6	20	20	0	16 ± 0.6	17 ± 1.4	17 ± 0.6[NS]	1.8	1.7	1.5
21.6	10	30[x]	−20	17 ± 0.6	18 ± 1.7	20 ± 1.6[*]	1.5	1.5	1.7
21.6	30	30[x]	0	23 ± 3.3	23 ± 2.8	22 ± 1.6[NS]	1.8	1.6	1.7

[z] Ten hours of irradiation per day.

[y] ± SE.

[x] Treatments added to the basic central composite design.

[v] No flower initiation after 100 short days.

[**,*,NS] Length of shoot 3 significantly ($P < 0.01$ or 0.05) or nonsignificantly different from shoot 1 and/or shoot 2, respectively. Differences between shoot 1 and shoot 2 were all nonsignificant.

increase chrysanthemum leaf unfolding by 0.017 leaves/°C per day. This rate of increase in leaf unfolding per 1° increase in ADT is comparable to pea with 0.020 leaves/°C per day (Balvoll and Bremer, 1965) and to sunflower with 0.022 leaves/°C per day (Rawson and Hindmarsh, 1982). However, the rate of leaf unfolding was five times slower than Easter lily at 0.094 leaves/°C per day (Karlsson et al., 1988) and four times slower than maize at 0.067 leaves/°C per day (Tollenaar et al., 1979).

Temperature was the determining factor influencing chrysanthemum shoot length. PPF between 1.8 and 21.6 $mol \cdot day^{-1} \cdot m^{-2}$ had no significant effect on elongation. High DT in combinations with low or high NT in this study resulted in tall plants (Table 2). Plants grown at constant 14°C averaged 16-cm-long shoots compared to 29- or 31-cm-long shoots at constant 26°. When DT increased from 14° to 26° with a NT of 14°, shoot length increased 16 cm. Shoot length did not increase when NT increased from 14° to 26° with the DT at 14°.

The number of leaves formed below the flower increased with increasing temperatures (Table 1, Fig. 2). Plants with many leaves were always tall, but two groups of tall plants could be distinguished (Table 2). The first group of tall plants were grown at high DT and NT and had internode lengths similar to that of the shorter plants, but had more internodes. The second group of taller plants were grown at high DT and low NT and had a similar number of internodes as the shorter plants, but of greater length. The difference in shoot length among plants exhibiting 10 or 11 leaves were determined by the length of the internodes.

A functional relationship between environment and internode length was developed rather than a functional relationship for total shoot length. The difference between DT and NT (DIF) was a determining factor for internode length in *Lilium longiflorum* (Erwin et al., 1988). A large positive DIF resulted in longer internodes. The selected environmental conditions in this study did not provide an equal distribution of DIF values, since the importance of DIF was not anticipated at the initiation of the experiment. An examination of observed internode lengths in relation to DIF (Table 2) and earlier studies with chrysanthemum (Karlsson et al., 1983; Karlsson, 1984; Erwin, 1986; Karlsson and Heins, 1986) suggested, however, the importance of DIF for chrysanthemum internode length. The regression analysis confirmed the expected significance of DIF (Fig. 4).

Extreme differences between DT and NT may result in slower and abnormal plant development and growth (Mastalerz, 1977). The relationship between environmental conditions and internode length may change when DIF approaches values of −20° or 20°C. Due to the small number of available data points with large values of DIF, predicted internode lengths were limited to DIF values between −12° and 12° and ADT values between

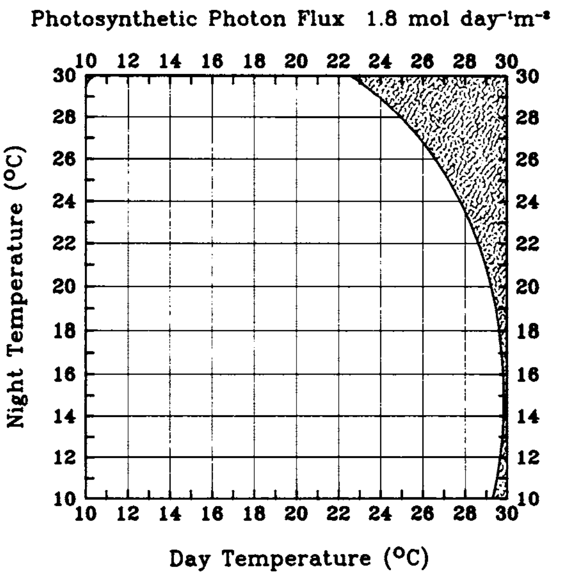

Fig. 1. Predicted flower bud appearance or continued vegetative growth after 100 short days in 'Bright Golden Anne' chrysanthemum as affected by day temperature (DT) and night temperature (NT) at a photosynthetic photon flux of 1.8 mol·day^{-1}·m^{-2}. Visible flower buds were predicted not to occur within the shaded area. The functional relationship used to create the graph was: Visible flower bud index = 1.0/[1.4815 − (7.9576 ∗ 10^{-2} ∗ DT) + (2.5316 ∗ 10^{-3} ∗ DT^2) − (4.6486 ∗ 10^{-2} ∗ NT) + (1.6303 ∗ 10^{-3} ∗ NT^2) − (4.6000 ∗ 10^{-5} ∗ PPF ∗ DT ∗ NT)]; r^2 = 0.76.

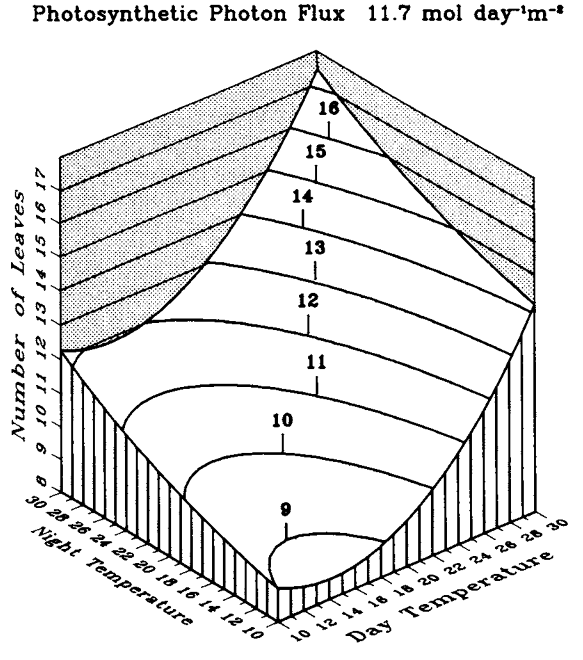

Fig. 2. The effect of day (DT) and night temperature (NT) on number of leaves formed per shoot before flower initiation in 'Bright Golden Anne' chrysanthemum at a PPF of 11.7 mol·day^{-1}m^{-2}. The functional relationship used to create the graph was: Leaf number = 12.635 − 6.2785 ∗ 10^{-1} ∗ DT + 2.2224 ∗ 10^{-2} ∗ DT^2 + 4.0529 ∗ 10^{-3} ∗ NT^2 − 7.0000 ∗ 10^{-9} ∗ PPF ∗ DT^2 ∗ NT^2; r^2 = 0.79.

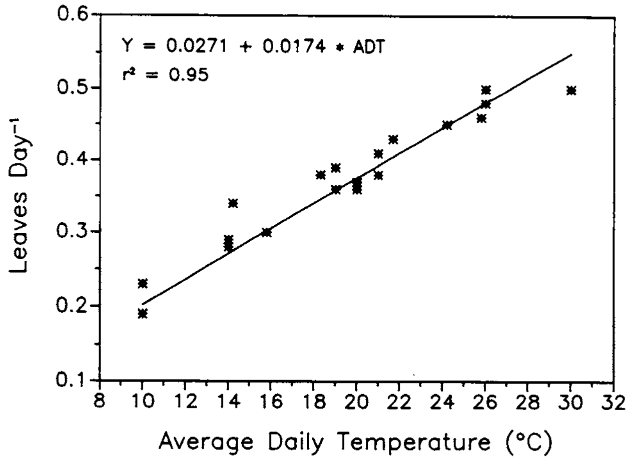

Fig. 3. Number of 'Bright Golden Anne' chrysanthemum leaves unfolded per day as a function of average daily temperature (ADT). Asterisks indicate observed leaf unfolding rates. The functional relationship for leaf unfolding rate was: Leaves/day = 2.7064 ∗ 10^{-2} + (1.7447 ∗ 10^{-2} ∗ ADT); r^2 = 0.95.

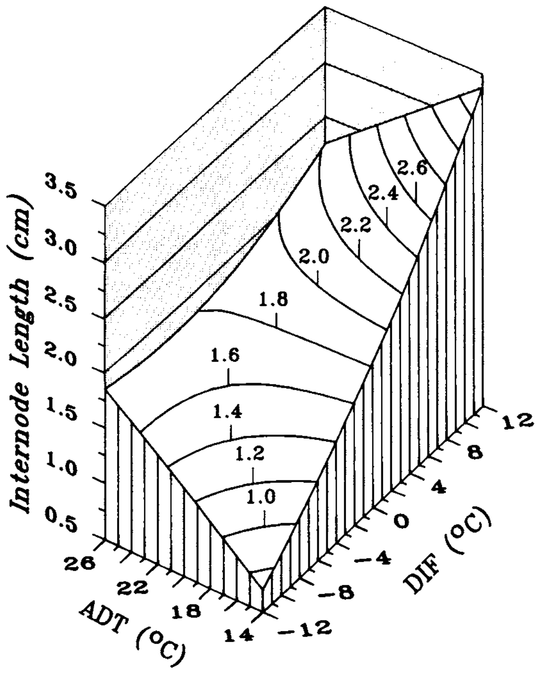

Fig. 4. The effect of the difference between day and night temperature (DIF) and average daily temperature (ADT) on internode length in 'Bright Golden Anne' chrysanthemum. The functional relationship used to create the graph was: Internode length = 1.8237 + 2.2362 ∗ 10^{-1} ∗ DIF + 1.4921 ∗ 10^{-3} ∗ DIF^2 − 8.0149 ∗ 10^{-3} ∗ DIF ∗ ADT; r = 0.86.

14° and 26° (Fig. 4). Internode length was predicted to increase from 1.2 to 2.8 cm as DIF increased from −12° to 12° at an ADT of 20°. As ADT increased, the internode length was predicted to increase at a negative DIF (higher NT than DT), while, at a positive DIF (higher DT than NT), the internode length was predicted to decrease (Fig. 4). Prediction of total shoot length using the functions for leaf number and internode length resulted in predicted values within 1 SD of observed shoot lengths.

In summary, the appearance of 2-mm flower buds were predicted to occur within 100 SD at any combination of DT and NT between 10° and 30°C when PPF was above 10.8 mol·day^{-1}·m^{-2}. The number of leaves formed below the flower increased with increasing DT and NT, while increasing PPF resulted in a small leaf number decrease. Leaf unfolding rate was determined by the average daily temperature and internode length by the difference between DT and NT.

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