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Irradiance and Temperature Effects on Time of Development and Flower Size in Chrysanthemum*

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ABSTRACT

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The effects of day temperature (DT), night temperature (NT) and photosynthetic photon flux (PPF), on rate of development and flower size were studied in chrysanthemum (*Dendranthema grandiflora* Tzvelev. cultivar 'Bright Golden Anne'). DT and NT ranged from 10 to 30°C and PPF from 1.8 to 21.6 mol $day^{-1}m^{-2}$. Flower initiation did not occur after 100 short days (SD) at low PPF levels (1.8 mol $day^{-1}m^{-2}$) in combination with high DT or NT (30°C). The number of days to flower varied from 58 to 140 days among plants grown under environmental conditions allowing flower initiation within 100 SD. The time to flower from start of SD decreased nonlinearly as PPF increased. Increasing PPF by 9.9 mol $day^{-1}m^{-2}$ at 20°C accelerated flowering 20 days when the initial PPF was 1.8 mol $day^{-1}m^{-2}$, but only 10 days when the initial PPF was 11.7 mol $day^{-1}m^{-2}$. The DT and NT for most rapid flower development were estimated from a model predicting time to flower. Independent of PPF in the range from 2 to 20 mol $day^{-1}m^{-2}$, the optimum DT was 17°C and the optimum NT was 18°C. Total flower area per plant varied from 14 to 310 cm^2. The flower size increased linearly as PPF increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at a constant temperature of 20°C. The optimum DT/NT combination for largest flower size changed from 21/14° to 20/18°C as PPF increased from 5 to 20 mol $day^{-1}m^{-2}$.

Keywords: *Chrysanthemum morifolium; Dendranthema grandiflora;* irradiance response, modeling; temperature.

Abbreviations: ADT = average daily temperature; DT = day temperature; NT = night temperature; PPF = photosynthetic photon flux; SD = short days.

INTRODUCTION

Knowledge of plant development is necessary for scheduling greenhouse production. In the case of chrysanthemums, cultivars are classified into re-

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sponse groups according to the expected number of SD to flower (Machin and Scopes, 1978). The rate of development can be modified, however, by irradiance and temperature conditions (Cathey, 1955; Karlsson, 1984), and production schedules must be varied as the seasons change. Therefore, quantitative environmental effects on plant development must be known in order precisely to control growth and to schedule production.

We previously described chrysanthemum flowering response to PPF, DT and NT based on 15 treatment combinations selected by using a central composite statistical design (Karlsson and Heins, 1986). In models developed using data from a central composite statistical design, greatest accuracy is attained near the center of the treatment ranges (Gardiner et al., 1967). To develop models with improved predictability at environmental extremes, additional data must be collected at extreme temperature and irradiance values. This paper presents new models for flowering in chrysanthemum based on a larger data base.

MATERIALS AND METHODS

Rooted cuttings of *Dendranthema grandiflora* Tzvelev. cultivar 'Bright Golden Anne' were individually planted in 10-cm pots filled with a commercial peat-lite medium (Michigan Peat Co.) and placed in growth chambers. Long day conditions were maintained for 7 days with 325 μmol $s^{-1}m^{-2}$ (16 h day^{-1}, 18.7 mol $day^{-1}m^{-2}$) and 20°C DT and NT. On the seventh day after potting, a SD photoperiod was initiated (10-h light, 14-h dark), and plants were pinched to 6 nodes and placed under appropriate treatment combinations (see Table 1) with the thermoperiod coinciding with the photoperiod. A 15.6 mM daminozide solution was applied as a foliar spray 7 and 14 days after the start of SD (Crater, 1980). Ten days after the start of SD, the number of lateral shoots was reduced to 3 $plant^{-1}$. The uppermost shoot was numbered 1 and the basal shoot 3. Lateral flower buds were removed when they were large enough to be detached without damaging the terminal flower bud.

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, and the shelves were lowered as necessary to maintain the desired PPF level at the canopy top. Average daily temperature fluctuated ± 1°C from the setpoint, and PPF varied $\pm 10\%$ over the canopy.

Plants were irrigated 1–3 times daily, depending on plant size and environmental conditions. Nutrition consisted of 14.3 mol m^{-3} (14.3 mM) N and 5.1 mol m^{-3} (5.1 mM) K added through the watering system. Media 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 combi-

TABLE 1

Time required for flower development, flower diameter, and total flower area plant^{-1} as affected by PPF, DT and NT in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne')

Environment			Average daily temp	Average time to flowering (days)[1]			Flower diam. (cm)			Plant flower area (cm^2)[1]
PPF	Temp (°C)			Shoot 1	Shoot 2	Shoot 3	Shoot 1	Shoot 2	Shoot 3	
(mol day^{-1} m^{-1}	DT	NT								
1.8	10	10[2]	10.0	126± 5.8	125± 4.4	-	4.0	6.6	1.2	51±31
1.8	30	10[2,3]	18.3	-	-	-	-	-	-	-
1.8	20	20	20.0	93± 4.2	90± 1.3	-	7.4	9.0	1.2	111±29
1.8	10	30[2,3]	21.7	-	-	-	-	-	-	-
1.8	30	30[2,3]	30.0	-	-	-	-	-	-	-
5.8	14	14	14.0	68± 0.8	71± 2.9	-	11.5	8.4	4.5	178±28
5.8	26	14	19.0	87± 5.5	81± 3.1	-	6.4	8.8	4.8	107±34
5.8	20	20[2]	20.0	66± 2.5	68± 2.1	73± 7.1	10.1	9.7	9.8	229±19
5.8	14	26	21.0	83± 5.9	86± 6.7	-	6.6	5.1	3.4	68±34
5.8	26	26	26.0	100± 5.9	109±15.5	-	4.6	3.9	2.6	41±17
11.7	20	10	14.2	68± 1.5	74± 5.9	77± 9.0	12.4	9.9	8.7	260±46
11.7	10	20	15.8	70± 4.6	74± 3.8	-	8.6	7.5	5.8	132±18
11.7	20	20	20.0	64± 1.2	66± 3.7	68± 1.8	10.7	10.4	10.0	253±10
11.7	30	20	24.2	105±14.6	101±14.6	108±16.5	4.9	6.0	4.8	83±34
11.7	20	30	25.8	92±14.7	87± 9.4	-	5.4	6.1	3.4	71±16
17.6	14	14	14.0	68± 2.9	68± 1.5	70± 4.4	11.9	11.9	10.2	310±23
17.6	26	14	19.0	73± 4.4	72± 1.9	76± 8.1	11.6	11.9	9.7	290±38
17.6	20	20[2]	20.0	64± 5.0	64± 5.0	66± 2.2	11.1	11.5	10.7	280±13
17.6	14	26	21.0	70± 1.1	68± 1.5	77± 6.1	8.1	8.6	5.5	137±13
17.6	26	26	26.0	88±20.6	90±18.1	85±14.9	6.6	6.9	7.0	134±41
21.6	10	10[2]	10.0	79± 6.3	79± 5.8	86±10.4	11.3	11.3	9.7	277±33
21.6	30	10[2]	18.3	81±19.0	86±10.1	-	8.4	8.9	7.8	135±59
21.6	20	20	20.0	57± 1.8	58± 1.5	59± 1.0	11.7	11.3	9.7	285±23
21.6	10	30[2]	21.7	87± 6.6	89± 3.3	91± 3.6	6.4	6.1	4.9	80±71
21.6	30	30[2]	30.0	140± 5.0	136± 5.1	-	2.5	1.9	2.1	14±10

[1] ± standard deviation.
[2] Treatments added to the basic central composite design.
[3] No flower initiation after 100 SD.

nations (Gardiner et al., 1967; Armitage et al., 1981). The PPF levels ranged from 1.8 to 21.6 mol day^{-1}m^{-2} (50–600 μmol s^{-1}m^{-2}, 10 h day^{-1}), and both DT and NT ranged from 10° to 30°C. Earlier studies indicated that additional treatments with plants growing under conditions at the extremes of the experimental ranges were necessary for a better understanding of the environmental effects (Karlsson and Heins, 1986). The 15 treatments required in the statis-

tical design were therefore supplemented to give a total of 25 treatments (see Table 1).

Data were collected on 5 randomly selected plants every 10 days during development. The experiment was terminated at flowering or after 100 SD if the terminal apex was still vegetative. A shoot was considered in flower when the outermost petals had reflexed to a horizontal position. Flowering dates for shoots not in flower at the final sampling date were estimated based on bud size. The analysis of time to flower was based on data from the two acropetal shoots, and the analysis of flower size was done on total flower area per plant. Flower area was calculated assuming that each flower was circular. Treatments in which plants did not initiate flowers were assigned a value of 200 SD for regression analysis of developmental time and a value of 0 cm^2 for regression analysis of flower size. Days to flower, flower area and PPF were natural-log transformed prior to regression analysis.

Regression analyses of data on time to flower and flower size were initially performed using the subroutine "BMDP9R, all possible subsets regression" (Dixon et al., 1985) with linear, quadratic and interaction terms of DT, NT, PPF and ADT as independent variables. Model selection was based on the Mallows' Cp statistic (Draper and Smith, 1981), significance of included independent variables, r^2 and F values of the regression models, and the adequacy of prediction. All variables included in the final models were significant at the 1% level as indicated by a 2-tailed t-test. Isopleth graphs were created using the developed models and the Surfer graphing package (Golden Software, 1987).

RESULTS

Time required from start of SD to flower decreased as PPF increased (Table 1). Time to flower of Shoot 1 (acropetal shoot) decreased 29 days as PPF increased from 1.8 to 11.7 mol $day^{-1}m^{-2}$ at a constant 20 °C. Further increases in PPF to 21.6 mol $day^{-1}m^{-2}$ at 20 °C accelerated development by 7 days. Increasing PPF also increased uniformity of flowering among shoots on a plant. On plants grown at 1.8 mol $day^{-1}m^{-2}$, Shoot 1 flowered in 93 days and Shoot 3 did not reach flowering in 100 SD, while plants grown at 21.6 mol $day^{-1}m^{-2}$ flowered on Shoots 1 and 3 in 57 and 59 days, respectively (Table 1).

Temperature affected days to flower at each PPF level (Table 1). An increase in both DT and NT from 14 to 26 °C delayed flowering more than 30 days at 5.8 mol $day^{-1}m^{-2}$, but about 20 days at 17.6 mol $day^{-1}m^{-2}$.

High DT or NT combined with low PPF levels prevented flower initiation under SD conditions. No flower buds were present after 100 SD when the PPF was 1.8 mol $day^{-1}m^{-2}$ and either DT or NT was 30 °C (Table 1). The unfavorable effects of temperature on flower initiation were overcome by increasing

TABLE 2

Regression coefficients and confidence intervals of independent variables in selected models for prediction of days to flower and plant flower area (cm^2) in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne')

Independent variable	Regression coefficient	Confidence interval (0.95)		
ln (days to flower)				
Intercept	5.4933	5.2933	-	5.6932
ln(PPF)	-1.7215×10^{-1}	-2.1550×10^{-1}	-	-1.2880×10^{-1}
DT×NT	-1.1588×10^{-2}	-1.4194×10^{-2}	-	-0.8981×10^{-2}
DT×NT^2	3.1748×10^{-4}	2.3505×10^{-4}	-	3.9990×10^{-4}
DT^2×NT	3.2368×10^{-4}	2.4101×10^{-4}	-	4.0635×10^{-4}
DT^2×NT^2	-0.8591×10^{-5}	-1.1436×10^{-5}	-	-0.5746×10^{-5}
ln (plant flower area)				
Intercept	3.1912	2.7441	-	3.6353
ln(PPF)	1.0094	0.6461	-	1.3728
ln(PPF)×DT^2	-1.4702×10^{-3}	-1.8040×10^{-3}	-	-1.1363×10^{-3}
ln(PPF)×NT^2	-3.8692×10^{-3}	-4.7752×10^{-3}	-	-2.9632×10^{-3}
(ln(PPF))^2×NT	-1.7401×10^{-2}	-2.7605×10^{-2}	-	-0.7197×10^{-2}
(ln(PPF))^2×NT^2	1.0323×10^{-3}	0.6095×10^{-3}	-	1.4551×10^{-2}
DT×NT^2	3.5950×10^{-4}	2.5994×10^{-4}	-	4.5905×10^{-4}
DT^2×NT	2.3777×10^{-4}	1.5517×10^{-4}	-	3.2036×10^{-4}
DT^2×NT^2	-2.3545×10^{-5}	-2.6694×10^{-5}	-	-2.0396×10^{-5}
ln(PPF)×DT×NT	3.7049×10^{-3}	3.2314×10^{-3}	-	4.1783×10^{-3}

PPF levels. Flowering occurred on plants grown at 21.6 mol $day^{-1}m^{-2}$ under all DT and NT combinations studied, including constant 30°C.

The selected model (Table 2) predicting time to flower was

$$\text{Days to flower} = 243.05\times\exp(a1)\times PPF^{-0.17215}$$

where

$$a1 = (-1.1588\times10^{-2}\times DT\times NT) + (3.1748\times10^{-4}\times DT\times NT^2) + (3.2368\times10^{-4}\times DT^2\times NT) + (-8.5909\times10^{-6}\times DT^2\times NT^2)$$

(Mallows' Cp = 5.1, $r^2 = 0.68$).

Predicted days to flower, as DT and NT simultaneously increased from 10 to 30°C at 5, 10 and 15 mol $day^{-1}m^{-2}$, are shown in Fig. 1. A similar deviation from the optimum temperature for most rapid development resulted in greater flowering delay at low PPF than at high PPF.

The number of DT and NT combinations which resulted in flowering in less than 75 days increased with PPF (Fig. 2). Under a specific PPF, the largest flowering delay occurred with simultaneously high DT and NT. The optimum

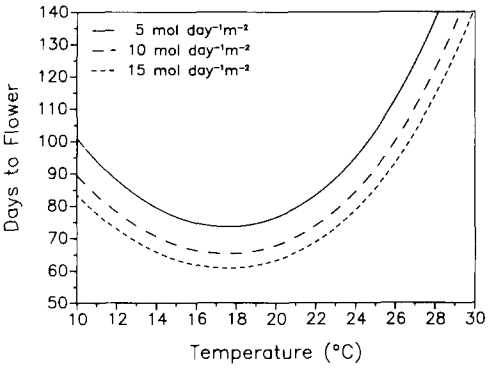

Fig. 1. Predicted number of days from start of SD to flower as influenced by a simultaneous increase in DT and NT at PPF of 5, 10 and 15 mol $day^{-1}m^{-2}$ in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne'). The graph was created using a regression model.

DT and NT combination for development did not vary with PPF (Fig. 2). The selected model predicted the most rapid development at 18°C DT and 17°C NT independent of PPF in the range from 2 to 20 mol $day^{-1}m^{-2}$.

Total flower area increased from 111 to 185 cm^2 $plant^{-1}$ as PPF increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at a constant 20°C (Table 1). These flower areas corresponded to an average flower diameter of 7 cm at the lowest PPF and 11 cm at the highest PPF. The plants grown at 5.8 mol $day^{-1}m^{-2}$ always had smaller flowers than plants grown at the same temperature combinations at 17.6 mol $day^{-1}m^{-2}$.

Total flower area $plant^{-1}$ decreased as either DT or NT deviated from the optimum at a given PPF level. As DT and NT increased from 14 to 26°C, flower area decreased from 178 to 41 cm^2 at 5.8 mol $day^{-1}m^{-2}$ and from 310 to 134 cm^2 at 17.6 mol $day^{-1}m^{-2}$ (Table 1). The flowers formed at a constant 30°C and a PPF of 21.6 mol $day^{-1}m^{-2}$ were small (2 cm in diameter). Plants grown at 30°C and 1.8 mol $day^{-1}m^{-2}$ had not initiated flowers after 100 SD.

The selected model (Table 2) predicting flower size was

$$\text{Flower area } (cm^2) = 3.1912 \times \exp(a1) \times PPF^{a2}$$

where

$$a1 = (3.5950 \times 10^{-4} \times DT \times NT^2) + (2.3777 \times 10^{-4} \times DT^2 \times NT) + (-2.3545 \times 10^{-5} \times DT^2 \times NT^2).$$

$$a2 = 1.0094 - (1.4702 \times 10^{-3} \times DT^2) - (3.8692 \times 10^{-3} \times NT^2) - (3.4802 \times 10^{-2} \times NT) + (2.0646 \times 10^{-3} \times NT^2) + (3.7049 \times 10^{-3} \times DT \times NT)$$ (Mallows' $Cp = 8.5$, $r^2 = 0.98$).

Predicted flower area increased to a maximum and then rapidly decreased as the temperature increased from 10 to 30°C (Fig. 3). Maximum flower area

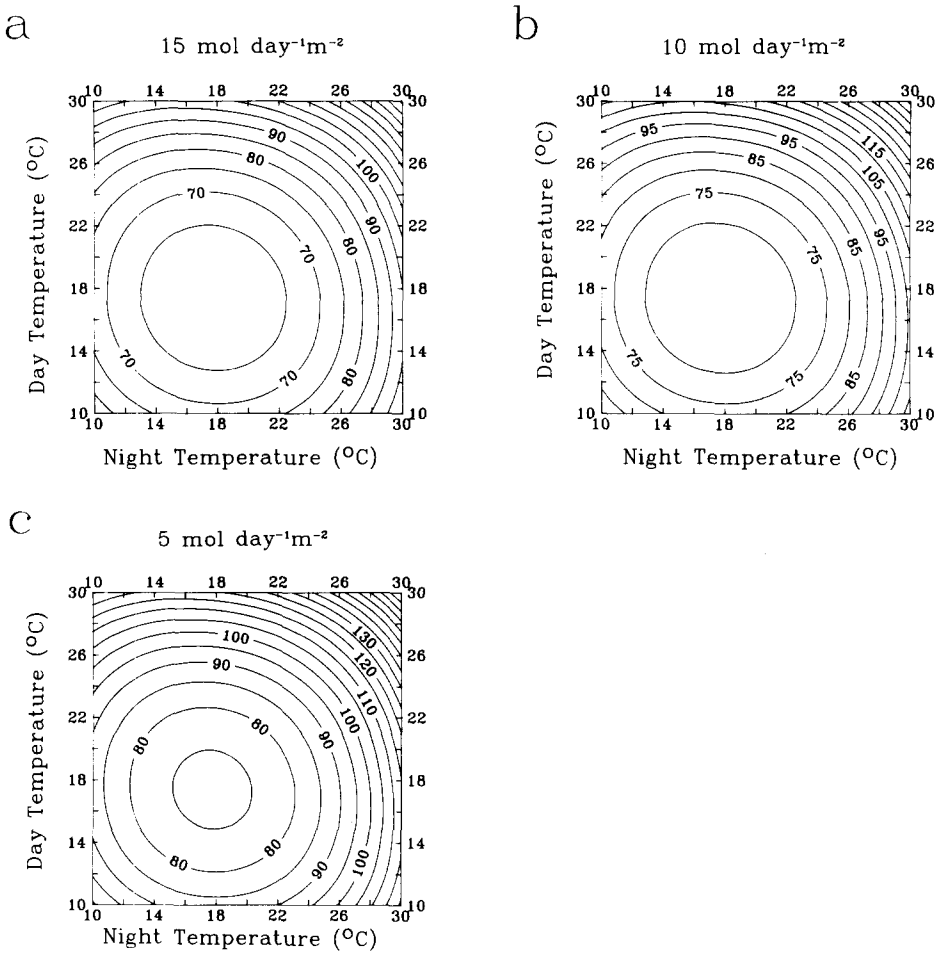

Fig. 2. Days from start of SD to flower as affected by DT and NT in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne') at PPF of (a) 15, (b) 10, (c) 5 mol day^{-1}m^{-2}. The graphs were created using a regression model.

at 5, 10 or 15 mol day^{-1}m^{-2} was predicted at a constant DT and NT of 17, 18, or 19°C, respectively. Predicted flower area per plant decreased faster when both DT and NT increased simultaneously from the optimum than when only either DT or NT increased (Fig. 4). A DT below the optimum reduced flower size and total flower area more than an NT below the optimum. The optimum DT/NT combinations for largest flower size were calculated to be 20°/15° at 5, 20°/15° at 10 and 20°/16°C at 15 mol day^{-1}m^{-2}.

DISCUSSION

Seasonal changes in time required for chrysanthemum flowering have been correlated with the variations in natural PPF levels (Schwabe, 1953; Vince,

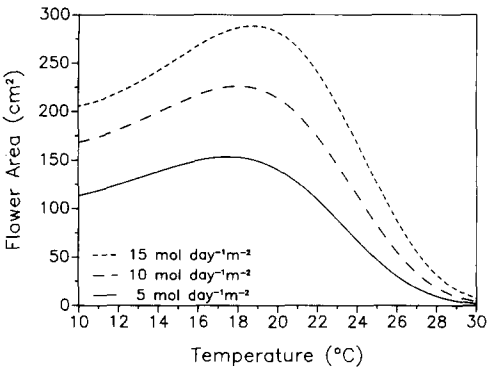

Fig. 3. Predicted total plant flower area as influenced by a simultaneous increase in DT and NT at PPF of 5, 10 and 15 mol $day^{-1}m^{-2}$ in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne'). The graph was created using a regression model.

1960; Mason and Vince, 1962; Cockshull and Hughes, 1972; Hughes and Tsujita, 1981; Hicklenton, 1984). Our results confirm these observations. They also explain why supplemental irradiation has a greater effect on time to flower under low natural irradiance levels than under high levels. Supplementing natural irradiance with 6.8 mol $day^{-1}m^{-2}$ hastened development 6 and 9 days under fall conditions for the cultivars 'Yellow Paragon' and 'Copper Anne', but did not significantly affect time to flower under spring conditions (Hicklenton and McRae, 1984). In our experiment, flowering decreased more than 20 days when the PPF was increased by 4 mol $day^{-1}m^{-2}$ at an initial 1.8 mol $day^{-1}m^{-2}$ and 20°C constant temperature. A similar PPF increase at 17.6 mol $day^{-1}m^{-2}$ only slightly accelerated development (Table 1).

The optimum temperature for flower initiation and development in chrysanthemum has been reported as 16°C (Cathey, 1955) and 22° DT/18°C NT (Bonaminio and Larson, 1980). The optimum DT and NT for fastest development in our experiment (18°C) is comparable with these previous reports. The small differences in observed optimum temperature for development could be due to differences in cultivars, environmental conditions during LD-treatment and/or cultural practices.

The model presented here, better describes how DT, NT and PPF determine chrysanthemum developmental rate in the range from 10 to 30°C and 2–20 mol $day^{-1}m^{-2}$, than a model previously reported (Karlsson and Heins, 1986). The old model underestimated time to flower at extreme DT and NT compared with the model presented in the present paper. The largest discrepancy between the two models in predicting the rate of development occurred at PPF levels below 5 mol $day^{-1}m^{-2}$.

Flower size and flower area per plant increased with increasing PPF (Table 1, Fig. 3). Larger flowers and more uniform flower size among shoots have been observed in other research as a result of supplemental lighting (Cockshull and

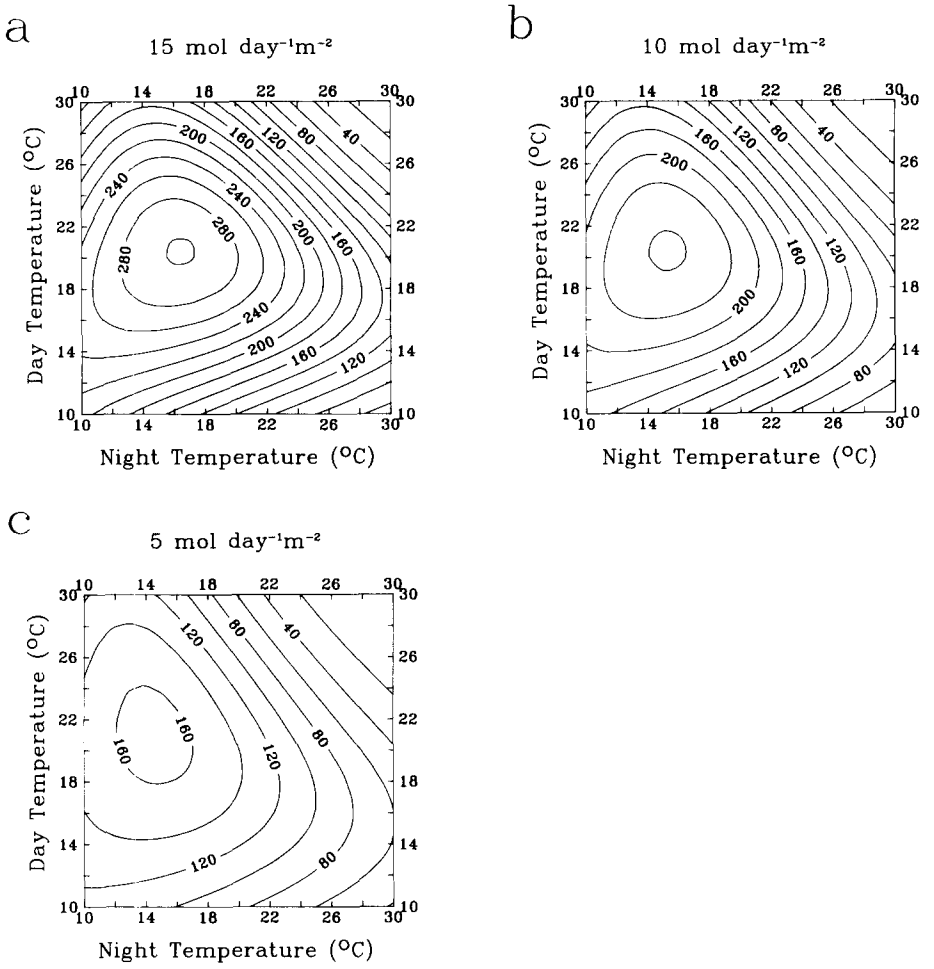

Fig. 4. Total plant flower area as affected by DT and NT in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne') at PPF of (a) 15, (b) 10, (c) 5 mol $day^{-1}m^{-2}$. The graphs were created using a regression model.

Hughes, 1971; Machin and Scopes, 1978; Mason and Vince, 1962). Similarly, in our study, the difference in average flower diameter among shoots on one plant at a constant 20°C temperature decreased from 8 cm at 1.8 mol $day^{-1}m^{-2}$ to 2 cm at 21.6 mol $day^{-1}m^{-2}$ (Table 1). In addition to greater uniformity, total flower area increased from 111 to 285 cm^2 as PPF increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at 20°C.

The larger flower size under high PPF may be a result of increased floret number. Cockshull and Hughes (1971) found that PPF determines in part the number of florets initiated in the flower; 300 florets were initiated per flower at 17 mol $day^{-1}m^{-2}$ compared with c. 200 at a PPF level of 1.5 mol $day^{-1}m^{-2}$. Temperature did not affect floret number in studies by Vince (1960), but plants grown at 10°C had larger flowers than plants grown at 16°C. Vince (1960)

concluded that the larger flowers at low temperature were a result of increased floret length.

The predicted changes in flower area were similar using either the model presented here or the earlier model (Karlsson and Heins, 1986) at NT above 20°C. The model based on results from experiments using the basic central composite design indicated that flower size continued to increase as the NT decreased from 20 to 10°C. The additional information from plants grown at 10 or 30°C revealed that at a particular DT and PPF there was an optimum NT in the range between 10 and 30°C. This optimum NT was not predicted in the previous model.

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