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FOR MODEL DEVELOPMENT IN CHRYSANTHEMUM

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CHARACTERIZATION OF DEVELOPMENT AND GROWTH RESPONSES TO IRRADIANCE AND TEMPERATURE FOR MODEL DEVELOPMENT IN CHRYSANTHEMUM

By

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ABSTRACT

CHARACTERIZATION OF DEVELOPMENT AND GROWTH RESPONSES TO IRRADIANCE AND TEMPERATURE FOR MODEL DEVELOPMENT IN CHRYSANTHEMUM

By

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Quantitative relationships were developed to describe chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') growth processes to photosynthetic photon flux (PPF), day temperature (DT) and night temperature (NT). The number of leaves formed prior to flower initiation increased at an increasing rate as DT and NT increased from 20° to 30°C. Rate of leaf unfolding was a linear function of average daily temperature (ADT). Internode length was linearly correlated with the difference between DT and NT (DIF) rather than absolute temperature. Increasing DIF from -12° to 12°C resulted in progressively longer internodes. Total plant flower area increased linearly as PPF increased from 2 to 20 mol $day^{-1}m^{-2}$. The estimated optimum DT/NT combination for largest flower size increased from 19°/16° to 20°/17°C as the PPF level increased from 5 to 20 mol $day^{-1}m^{-2}$. Number of days required to complete development from start of short days to flower at 20°C decreased rapidly as PPF

increased from 2 to 10 mol $day^{-1}m^{-2}$. Further increasing PPF level to 20 mol $day^{-1}m^{-2}$ only resulted in a small decrease of flowering time. The optimum DT for fastest development to flower increased from 17° to 18° and the optimum NT decreased from 18° to 16°C as the PPF level increased from 5 to 20 mol $day^{-1}m^{-2}$. Four developmental phases were studied during reproductive growth. The four phases were from start of short days to a 2 mm large terminal flower bud (visible bud), from visible bud to a 10 mm large terminal flower bud (disbud), from disbud to a flower bud showing color, and from color to flower. Fastest plant development during any phase occurred when plants were grown at 18° to 20°C. Conditioning effects of temperatures from previous phases on time required for subsequent development under optimal temperatures were observed during the second and third phase but not during the fourth phase. Low temperature (10°) during the first phase delayed development rate during the second phase. Plant development during the third phase was delayed after plants had been exposed to a high temperature (30°C) during the first and second phase. Total plant biomass varied from 3.6 to 17.2 g at flowering. Greatest biomass was accumulated in plants grown under high PPF and temperature conditions. Proportion root biomass increased while proportion leaf biomass decreased with increasing PPF levels. Partitioning to roots decreased as DT increased.

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TABLE OF CONTENTS

	Page
LIST OF TABLES	viii
LIST OF FIGURES	xi
INTRODUCTION	1
SECTION I Influence of photosynthetic photon flux, day and night temperature on internode and leaf development in chrysanthemum	3
Abstract	4
Introduction	5
Materials and Methods	7
Results and Discussion	10
Literature Cited	21
SECTION II Path analysis of chrysanthemum growth and development	36
Abstract	37
Literature Cited	47
SECTION III Rate of development during four phases of chrysanthemum growth as affected by preceding and prevailing temperature exposure	53
Abstract	54
Introduction	55
Materials and Methods	58
Results and Discussion	61
Literature Cited	69
SECTION IV Irradiance and temperature effects on time of development and flower size in chrysanthemum	82
Abstract	83

Page

Introduction 84
Materials and Methods 86
Results and Discussion 89
References 95

SECTION V Chrysanthemum biomass allocation patterns along irradiance and temperature gradients 109
Abstract 110
Introduction 111
Materials and Methods 113
Results 116
Discussion 122
Literature cited 130

LIST OF TABLES

Table Page

SECTION I

1. Influence of photosynthetic photon flux (PPF), day temperature, and night temperature on number of leaves in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') . . . 24

2. Influence of photosynthetic photon flux (PPF), day temperature, and night temperature on shoot and internode length in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') 25

SECTION II

1. Influence of photosynthetic photon flux (PPF), day temperature, and night temperature on time to flower and total plant dry weight at flowering in chrysanthemum (*Dendranthema grandiflora* Tzvelev.) 50

SECTION III

1. Actual temperature and photosynthetic photon flux from start of short days (SD) to visible bud (VB), from VB to removal of lateral flower buds (disbud, DB), from DB to buds showing first color (C), from C to flower (FLW), and from SD to FLW 72

2. Time of development from start of short days (SD) to visible bud (VB), from VB to removal of lateral flower buds (disbud, DB), from DB

Table Page

to buds showing first color (C), from C to flower (FLW), from SD to FLW, and leaf number per shoot for *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' grown under different constant temperatures 73

3. Influence of temperature before and during a particular phase of development in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'. The plants were held at the first temperature from start of short days until start of the second phase 74

4. Regression coefficients for functions relating temperature with time of development from start of short days (SD) to visible bud (VB), from VB to disbud (DB), from DB to buds showing color (C), and from C to flower (FLW) in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' 75

SECTION IV

I. Time required for flower development, flower diameter and total flower area per plant as affected by photosynthetic photon flux (PPF), day temperature and night temperature in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' 98

SECTION V

1. Influence of photosynthetic photon flux (PPF), day and night temperature on total biomass and resource allocation at flowering in *Dendranthema grandiflora* Tzvelev. 134

2. Number of independent variables, F-values and r^2 values for regression equations developed to study biomass accumulation over time in roots, stems, leaves and flowers of

Table Page

Dendranthema grandiflora Tzvelev. Stepwise regression analysis with linear, higher order terms and interaction terms of environmental variables (photosynthetic photon flux, day temperature and night temperature) and time on a normalized basis available for addition. Biomass was normalized to values between 0 and 1 by dividing the data values with the maximum value observed prior to analysis. All independent variables included in the equations were significant at $P < 0.05$. 135

3. Regression coefficients for functions relating normalized quantity of biomass in roots, stems, leaves and flowers over normalized time (NDAY) from start of short days to flowering in *Dendranthema grandiflora* Tzvelev. Biomass and time required for flowering were scaled to attain values between 0 and 1. (Regression variables significant at $P < 0.05$.) 136

4. Regression coefficients for functions relating maximum amount of biomass in roots, stems, leaves and flowers during the growth period from start of short days to flowering in *Dendranthema grandiflora* Tzvelev. (Regression variables significant at $P < 0.05$.) 137

LIST OF FIGURES

Figure — Page

SECTION I

1. Predicted flower initiation or continued vegetative growth under short day conditions in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') as affected by day and night temperature at a photosynthetic photon flux of 1.8 mol $day^{-1}m^{-2}$ (50 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}. Flower initiation is predicted not to occur within the shaded area 27

2. The effect of day (DT) and night temperature (NT) on number of leaves formed per shoot prior to flower initiation in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') at a photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$ (325 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}). The functional relationship used to create the graph was: Leaf number = $12.6349 - 0.6278 * DT + 0.0222 * DT^2 + 0.0041 * NT^2 - 0.7 * 10^{-8} * PPF * DT^2 * NT^2$ 29

3. Number of chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') leaves unfolded per day as a function of average daily temperature 31

4. Number of days after pinch and start of short days required for the first leaf to appear in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') with average

Figure Page

daily temperature (ADT) from 10° to 30°C and photosynthetic photon flux (PPF) from 1.8 to 21.6 mol $day^{-1}m^{-2}$ (50 to 600 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}). The functional relationship used to create this graph was: Days to first leaf = 19.1892 - 0.7475 * PPF - 0.6078 * ADT + 0.0264 * PPF * ADT. Flower initiation is not predicted to occur within the shaded region 33

5. The effect of the difference between day and night temperature (DIF) and average daily temperature (ADT) on internode length (cm) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'). Observed internode lengths are indicated on the graph and areas with combinations of DIF and ADT outside the studied range are shaded. The functional relationship used to create the graph was: Internode length = 1.7637 + 0.2274 * DIF + 0.0013 * DIF^2 - 0.0080 * DIF * ADT 35

SECTION II

1. Path diagram indicating the possible interrelationships in chrysanthemum a) among increments of relative dry weight accumulation (G) during 4 developmental phases and total relative dry weight increase, b) among days of 4 developmental phases (T) and total number of days to flower, and c) among relative growth rates (dry weight gain day^{-1}, R) of 4 developmental phases and total relative dry weight increase.
The 4 developmental phases were from start of short day to a 4 mm large terminal flower bud (visible bud), from visible bud to a 10 mm large terminal flower bud (disbud), from disbud to a flower bud showing color, and from color to flower. Numbers correspond to path coeffi-

Figure Page

cients. Asterisks define the level of significance: *** $p < 0.001$ and ** $p < 0.01$ 52

SECTION III

1. Time to flower for *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' grown at an initial temperature and shifted to a second temperature at visible bud, disbud or color and allowed to complete the development in the second temperature. Initial temperature at a) 30°, b) 25°, c) 20°, d) 20° day temperature and 16° night temperature, e) 15°, and f) 10°C 77

2. Effect of temperature on rate of development from start of short days (SD) to visible bud (VB) stage in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' 79

3. Effect of plant exposure to a temperature early in development on time required to complete subsequent phases of development in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.
a) Time to complete development from visible bud (VB) to disbud (DB) as affected by the temperature from VB to DB and the temperature from start of short days (SD) to VB.
b) Time to complete development from DB to the flower first showing color (C) as affected by the temperature from DB to C and the temperature from SD to DB.
c) Time to complete development from C to flowering (FLW) as affected by the temperature from C to FLW and the temperature from SD to C 81

Figure Page

SECTION IV

1. Predicted number of days from start of short days to flower and first derivative (days/mol $day^{-1}m^{-2}$) as influenced by photosynthetic photon flux (PPF) at a constant 20°C day (DT) and night temperature (NT) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'). Asterisks indicate observed number of days to flower.
The functional relationship used to create graph was: Days to flower = exp(5.8915 - (0.4332 * ln(PPF)) - (0.0179 * DT * NT) + (0.0314 * ln(PPF) * (average daily temperature)) - (0.6047 * 10^{-3} * ln(PPF) * DT^2) - (0.6130 * 10^{-3} * ln(PPF) * NT^2) + (0.4867 * 10^{-3} * DT * NT^2) + (0.5175 * 10^{-3} * DT^2 * NT) - (0.1410 * 10^{-4} * DT^2 * NT^2) + (0.4356 * 10^{-3} * ln(PPF) * DT * NT)).
(Mallows' C_p = 10.00, r^2 = 0.68) 100

2. Predicted number of days from start of short days to flower as influenced by a simultaneous increase in day (DT) and night temperature (NT) at photosynthetic photon flux (PPF) levels of 5, 10 and 15 mol $day^{-1}m^{-2}$ in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne').
The functional relationship used to create this graph was: Days to flower = exp(5.8915 - (-0.4332 * ln(PPF)) - (0.0179 * DT * NT) + (0.0314 * ln(PPF) * (average daily temperature)) - (0.6047 * 10^{-3} * ln(PPF) * DT^2) - (0.6130 * 10^{-3} * ln(PPF) * NT^2) + (0.4867 * 10^{-3} * ln(PPF) * NT^2) + (0.4867 * 10^{-3} * DT * NT^2) + (0.5175 * 10^{-3} * DT^2 * NT) - (0.1410 * 10^{-4} * DT^2 * NT^2) + (0.4356 * 10^{-3} * ln(PPF) * DT * NT)).
(Mallows' C_p = 10.00, r^2 = 0.68) 102

3. Days from start of short days to flower as

Figure Page

affected by day (DT) and night temperature (NT) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne', at a photosynthetic photon flux (PPF) of a) 15, b) 10, and c) 5 mol $day^{-1}m^{-2}$. The functional relationship used to create these graphs was: Days to flower = exp(5.8915 - (0.4332 * ln(PPF)) - (0.0179 * DT * NT) + (0.0314 * ln(PPF) * ADT) - ($0.6047 * 10^{-3}$ * ln(PPF) * DT^2) - ($0.6130 * 10^{-3}$ * ln(PPF) * NT^2) + ($0.4867 * 10^{-3}$ * DT * NT^2) + ($0.5175 * 10^{-3}$ * DT^2 * NT) - ($0.1410 * 10^{-4}$ * DT^2 * NT^2) + ($0.4356 * 10^{-3}$ * ln(PPF) * DT * NT)). (Mallows' C_p = 10.00, r^2 = 0.68) 104

4. Predicted total plant flower area as influenced by a simultaneous increase in day (DT) and night temperature (NT) at photosynthetic photon flux of 5, 10 and 15 mol $day^{-1}m^{-2}$ in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'). The functional relationship used to create this graph was: Flower area (cm^2) = exp(2.2318 + (1.2847 * ln(PPF)) + (0.0829 * NT) - ($0.1402 * 10^2$ * ln(PPF) * DT^2) - ($0.4822 * 10^{-2}$ * ln(PPF) * NT^2) - (0.0259 * $(ln(PPF))^2$ * NT) + ($0.1390 * 10^{-2}$ * $(ln(PPF))^2$ * NT^2) * NT^2) + ($0.2669 * 10^{-3}$ *DT * NT^2) + ($0.1892 * 10^{-3}$ * DT^2 * NT) - ($0.2057 * 10^{-4}$ DT^2 * NT^2) + $0.4036 * 10^{-2}$ * ln(PPF) * DT * NT)). Mallows' C_p = 10.84, r^2 = 0.98) 106

5. Total plant flower area as affected by day (DT) and night temperature (NT) in chrysanthemum (*Dendranthema grandiflora* 'Bright Golden Anne') at a photosynthetic photon flux (PPF) of a) 15, b) 10, and c) 5 mol $day^{-1}m^{-2}$. The functional relationship used to create these graphs was: Flower area (cm^2) =

Figure Page

exp(2.2318 + 1.2847 * ln(PPF) + 0.0829 * NT
- 0.1402 * 10^{-2} * ln(PPF) * DT^2 - 0.4822
* 10^{-2} * ln(PPF) * NT^2 - 0.0259 * $(\ln(PPF))^2$
* NT + 0.1390 * 10^{-2} * $(\ln(PPF))^2$ * NT^2 +
0.2669 * 10^{-3} * DT * NT^2 + 0.1892 * 10^{-3} *
DT^2 * NT - 0.2057 * 10^{-4} * DT^2 * NT^2 + 0.4036
* 10^{-2} * ln(PPF) * DT * NT)).
Mallows' C_p = 10.84, r^2 = 0.98) 108

SECTION V

1. Relative biomass accumulation in roots, leaves, stems and flowers plotted against relative time from start from short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev 139

2. Gain of biomass in roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. Biomass in the different plant parts was estimated by developed functions. Root biomass, stem biomass added to root biomass, leaf biomass added to root and stem biomass and flower biomass added to root, stem and leaf biomass were plotted to show accumulated plant biomass. Observed values are plotted with standard deviations.
a) Photosynthetic photon flux (PPF) of 1.8 mol $day^{-1}m^{-2}$ with day temperature (DT) and night temperature (NT) at 20 C. Observed time to flower was 90 days.
b) PPF level of 21.6 mol $day^{-1}m^{-2}$ with DT and NT at 20 C. Observed time to flower was 60 days 141

3. Gain of biomass in roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora*

Figure Page

Tzvelev. Biomass in the different plant parts was estimated by developed functions. Root biomass, stem biomass added to root biomass, leaf biomass added to root and stem biomass and flower biomass added to root, stem and leaf biomass were plotted to show accumulated plant biomass. Observed values are plotted with standard deviations. a) Day temperature (DT) at 10 C with night temperature (NT) at 20 C and photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days. b) DT at 30 C with NT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 90 days 143

4. Gain of biomass in roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. Biomass in the different plant parts was estimated by developed functions. Root biomass, stem biomass added to root biomass, leaf biomass added to root and stem biomass and flower biomass added to root, stem and leaf biomass were plotted to show accumulated plant biomass. Observed values are plotted with standard deviations. a) Night temperature (NT) at 10 C with day temperature (DT) at 20 C and photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days. b) NT at 30 C with DT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 80 days 145

5. Estimated biomass allocation to roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. using developed functional relationships.

a) Photosynthetic photon flux (PPF) of 1.8 mol $day^{-1}m^{-2}$ with day temperature (DT) and night temperature (NT) at 20 C. Observed time to flower was 90 days and observed total plant dry matter at flowering was 3.6 g.
b) PPF level of 21.6 mol $day^{-1}m^{-2}$ with DT and NT at 20 C. Observed time to flower was 60 days and observed total plant dry matter at flowering was 15.3 g. 147

6. Estimated biomass allocation to roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. using developed functional relationships.
a) Day temperature (DT) at 10 C with night temperature (NT) at 20 C and photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days and observed total plant dry matter at flowering was 5.9 g.
b) DT at 30 C with NT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 90 days and observed total dry matter at flowering was 10.6 g 149

7. Estimated biomass allocation to roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. using developed functional relationships.
a) Night temperature (NT) at 10 C with day temperature (DT) at 20 C and photosynthetic photon flux of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days and observed total plant dry matter at flowering was 5.9 g.
b) NT at 30 C with DT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 80 days and observed total plant dry matter at flowering was 9.3 g 151

INTRODUCTION

Chrysanthemum is the second most important plant in the flowering pot plant industry today. In 1986, 33.4 million pots of chrysanthemums were produced in the United States with a value of $87.3 million. Many cultivars with a wide range of flower types, sizes, and colors are available. The large diversity in plant and flower characteristics have created a demand for flowering potted chrysanthemums year around.

Chrysanthemum is propagated by cuttings and plants are flowered by exposure to short day conditions after a pinch. The critical photoperiod is shorter for flower development than the critical photoperiod for flower initiation. The length of the critical photoperiods vary with cultivars and can be modified by temperature. Under conditions with day lengths shorter than the critical photoperiods, plant morphology and rate of development are determined by genetic and environmental factors.

Greenhouse production allows for control of plant development by adjustments in the environment. The use of computers for greenhouse environmental control further increases the opportunities to maintain an optimum environment for desired plant growth. Suitable software

can be developed when the environmental effects on plant growth have been quantitatively described. This study was initiated to define such quantitative relationships for chrysanthemum. Functional relationships for the effects of photosynthetic photon flux, day temperature and night temperature on rate of development and morphological characteristics were developed for chrysanthemum growth under short day conditions.

SECTION I

INFLUENCE OF PHOTOSYNTHETIC PHOTON FLUX, DAY AND NIGHT TEMPERATURE ON INTERNODE AND LEAF DEVELOPMENT IN CHRYSANTHEMUM

Influence of Photosynthetic Photon Flux, Day and Night Temperature on Internode and Leaf Development in Chrysanthemum

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Abstract

The effects of photosynthetic photon flux (PPF), day temperature (DT) and night temperature (NT) on leaf number, first leaf appearance, leaf unfolding rate and shoot length were studied in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'). A functional relationship was developed to predict if flower initiation would occur under a given set of environmental conditions. The number of leaves formed prior to flower initiation increased quadratically as DT and/or NT increased from 10° to 30°C. Increasing PPF levels from 1.8 to 21.6 mol $day^{-1}m^{-2}$ resulted in 1 or 2 leaves less per shoot. Number of days from pinching to first leaf appearance was determined by the PPF level and average daily temperature. Rate of leaf unfolding was a linear function of average daily temperature. The difference between DT and NT (DIF = DT - NT) and DIF interacting with average daily temperature were highly correlated with internode length. Increasing DIF from -12° to 12° resulted in progressively longer internodes. Increasing average daily temperature resulted in longer internodes when DIF was negative but shorter internodes when DIF was positive.

Introduction

Modeling plant growth and development requires an understanding of the functional relationships between plant processes and the environmental factors which influence them. In commercial production of chrysanthemum (*Dendranthema grandiflora* Tzvelev., (1)), plants are flowered by exposing the plants to short day (SD) conditions. Most plants are pinched prior to SD (10). Plant development of pinched plants under SD starts with the formation of lateral shoots and the appearance of leaves. The apical shoot meristem changes from vegetative to reproductive. Time from pinch to visible flower bud is determined by the number of leaves initiated prior to the transition of the vegetative meristem to a reproductive meristem and the rate of leaf unfolding.

Plant height is an important factor for quality in chrysanthemum pot plant production. Many plants adapt to a wide range of environmental conditions by changes in partitioning pattern and morphological characteristics (17,27). Height in chrysanthemum is such a plant feature demonstrating large adaptability to the environment (11,18,20). An understanding of how the environment determines final height is necessary to precisely produce plants with desirable height characteristics.

Climatic conditions alter the morphology of chrysanthemum. Leaf number, meristem transition from

vegetative to reproductive, and leaf appearance rate are plant variables involved in determining time required to complete the development from start of SD to the appearance of flower buds. Plant height influences quality. All four variables must be quantified before models of development can be constructed. This study was initiated to define quantitative relationships between photosynthetic photon flux (PPF), day temperature (DT), and night temperature (NT) and leaf number, flower initiation, leaf unfolding rate and plant height in chrysanthemum.

Materials and Methods

Rooted cuttings of 'Bright Golden Anne' were planted individually in 10 cm pots and placed in growth chambers for 7 days under a PPF of 18.7 mol $day^{-1}m^{-2}$ (325 μmol $s^{-1}m^{-2}$, 16 hr day^{-1}) and a constant temperature of 20°C. SD (10 hr light, 14 hr dark) were initiated on the seventh day and plants were pinched to 6 nodes. The PPF, DT and NT were then altered in the chamber to provide one of the treatment combinations shown in Table 1. The DT and NT paralleled the photoperiod and skotoperiod. A 15.6 mM daminozide solution was applied as a foliar spray 7 and 14 days after the start of SD (10). The number of lateral shoots was reduced to 3/plant ten days after the start of SD. Lateral flower buds were removed when they were large enough to be detached without damaging the terminal bud.

The PPF was provided by cool-white fluorescent lamps (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 plants were lowered as necessary to maintain the desired PPF at the canopy top. Average daily temperature fluctuated $\pm$ 1°C from the setpoint and PPF varied $\pm$ 10% over the canopy.

Plants were grown in a commercial peat-lite medium and irrigated as necessary to prevent water stress. The nutritional program 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 $\pm$ 0.2 by adjusting water pH with nitric acid.

A central composite statistical design was used to select treatment combinations (14,19). The PPF levels ranged from 1.8 to 21.6 mol $day^{-1}m^{-2}$ (50 to 600 μmol $s^{-1}m^{-2}$, 10 hr day^{-1}) 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 for determining leaf area, leaf number, shoot length and dry weight of the original shoot and the 3 lateral shoots. A leaf was recorded as unfolded when it was 1 cm or longer in length. The experiment was terminated at flowering or if no sign of flower initiation was apparent after 100 SD.

Leaf number was linearly regressed with time to obtain estimates of average leaf unfolding rates for each treatment. Days to first leaf appearance were calculated using these estimated leaf unfolding rates. Multiple linear regression analyses were performed using the SPSS subroutine 'New regression' (23) and the Systat statistical package (33). The unit for PPF used in the analyses was mol $day^{-1}m^{-2}$. Surface and isopleth graphs were created using the selected functions and the Surfer graphing program

(15).

Stepwise regression analysis with linear, quadratic and interaction terms of DT, NT, PPF and average daily temperature (ADT) was initially used to select a functional relationship for each development or growth process. In the analysis of internode length, the difference between DT and NT (DIF = DT - NT) was also added to the variables available for inclusion. Efforts were made to improve the resulting equations by addition and deletion of independent variables using both the terms available in the stepwise regression analysis 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

It was necessary to first establish whether flower initiation would occur under a given set of environmental conditions. After 100 SD, plants in some treatment conditions had not initiated flowers (Table 1). Models based on relationships between apex size and stage of development have been developed previously to describe the transition from a vegetative to a reproductive meristem (5,28). These models ignored the effects of environmental conditions controlling rate of meristem transition. A model considering environmental conditions was therefore developed.

Plants that did not develop visible 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 utilized in model development. The selected regression function based on the data was mathematically manipulated to give a 'flower initiation index' greater than 1.0 when flower initiation had occurred, and an index less than or equal to 1.0 when flower initiation had not occurred after 100 SD. The flower initiation index was developed by dividing the function by 20 and then inverting it. The final model to determine if flower initiation occurred was:

$$\text{Flower initiation index} = 1 / (1.4815 - (0.0796 * DT) + (0.0025 * DT^2) - (0.0465 * NT) + (0.0016 * NT^2) - (0.00004 * PPF * DT * NT))$$

Combinations of DT and NT where flower initiation was not predicted to occur after 100 SD at a PPF level of 1.8 mol $day^{-1}m^{-2}$ are shown in Figure 1. At this PPF level, flower initiation was not predicted at 30°C DT with any combination of NT. Flower initiation was also not predicted to occur at 30° NT when the DT was 10° or between 23° and 30°. The number of DT and NT combinations in the range from 10° to 30° where flower initiation was not predicted to occur decreased as PPF increased to 10.8 mol $day^{-1}m^{-2}$. Flowering was predicted to occur under all DT and NT combinations between 10° and 30° at PPF levels above 10.8 mol $day^{-1}m^{-2}$. These predictions are consistent with the observed results (Table 1).

The number of leaves formed prior to flower initiation could not be determined for all treatments due to lack of flower initiation. Data from plants in treatments that did not initiate flowers in 100 days were therefore excluded in the continued analyses. The functional relationships for leaf number, time to first leaf appearance and leaf unfolding rate were developed under the assumption that flower initiation had occurred. These plant processes related to the appearance of leaves can therefore only be predicted with the functional relationships discussed below

when flower initiation first has been established.

No significant differences ($P < 0.05$) in leaf number or shoot length existed between the two uppermost lateral shoots on plants within a treatment. Leaf number and shoot length of the third shoot were significantly different from shoot 1 and/or shoot 2 in certain treatments (Table 1,2). Analyses of leaf number, shoot length and internode length were performed on the combined data from the first and second lateral shoot.

Number of leaves formed per shoot prior to flower initiation was modified by the environment (Table 1). Leaf number increased in response to either high DT or NT. The response to DT being larger such that plants grown with 30°C DT had a higher leaf number than plants grown with 30° NT. Plants grown at a PPF of 11.7 mol $day^{-1}m^{-2}$ with a 30° NT and 20° DT had 11 leaves per shoot. When DT and NT were reversed at the same PPF, plants had 14 leaves per shoot (Table 1). The functional relationship selected to predict leaf number for the first and the second lateral shoot was:

$$\text{Leaf number} = 12.6349 - (0.6278 * DT) + (0.0222 * DT^2) + (0.0041 * NT^2) - (0.7 * 10^{-8} * PPF * DT^2 * NT^2) \qquad (r^2 = 0.79)$$

The effect of DT and NT on predicted leaf number in chrysanthemum at 11.7 mol $day^{-1}m^{-2}$ (325 μmol $s^{-1}m^{-2}$, 10 hr day^{-1}) is shown in Figure 2. The greatest number of leaves

were formed when both DT and NT were 30°C. Only small changes in leaf number were predicted below 20°.

High temperatures during SD result in "heat delay" (24). More leaves are formed per shoot leading to delayed morphological flower initiation (4,32). A heat tolerant cultivar was shown to form 3 more leaves and a heat sensitive cultivar 4 more leaves when the temperature was increased from 22° DT/18° NT to 30° DT/26°C NT (32). At the PPF level (21 mol $day^{-1}m^{-2}$) used by Whealy et al. (32), our functional relationship predicted a 5 leaf increase when DT is increased from 22° to 30° and NT is increased from 18° to 26°.

Many studies have shown greater leaf number at reduced PPF levels (6,7,8,31). The plants in our experiment were placed under a PPF level of 18.7 mol $day^{-1}m^{-2}$ for 1 week prior to start of SD. In contrast, the plants where grown at the same PPF level during LD and SD in other studies. The small increase in leaf number observed at lower PPF levels in our experiment may be due to the relatively high PPF conditions provided during LD. The developed regression function predicts only an additional 2 leaves per shoot when the PPF level is decreased from 21.6 to 1.8 mol $day^{-1}m^{-2}$ while maintaining 20°C DT and NT.

Rate of leaf appearance in several species has been found to increase linearly as temperature increases to some maximum rate (2,13,21,25,29). Cockshull et al. (9) reported leaf appearance in chrysanthemum was also an 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 ADT as the independent variable (Figure 3).

$$\text{Leaves day}^{-1} = 0.0271 + (0.0174 * \text{ADT}) \qquad (r^2 = 0.95)$$

Efforts to improve this relationship by adding higher order terms were ineffective. A 1°C increase in ADT is predicted to increase chrysanthemum leaf unfolding by 0.017 leaves/day. This rate of increase in leaf unfolding per 1° increase in ADT is comparable to pea with 0.020 leaves/day (2) and for sunflower with 0.022 leaves/day (25). However, the rate of leaf unfolding was 5 times faster in Easter lily at 0.094 leaves/day (21) and in maize 4 times faster at 0.067 leaves/day (29).

Cockshull et al. (9) did not present a functional relationship for leaf unfolding in chrysanthemum. Their (9) reported leaf unfolding rate at 10° was similar to the rate observed in this study at 10° but their rate at 20°C was 39% higher than we observed. The difference may be due to cultivar differences, LD treatment or cultural practices.

The appearance of the first leaf after pinch is a combination of the rates of shoot formation and leaf unfolding. Number of days required to produce a 1 cm long leaf on the two uppermost lateral shoots was a function of PPF levels and ADT (Figure 4).

Days to first leaf = 19.1892 - (0.7457 * PPF) - (0.6078 * ADT) + (0.0264 * PPF * ADT)

(r^2 = 0.88)

High ADT and PPF levels resulted in first leaf appearance after 3 days. The rate of development immediately after SD was independent of PPF level at an ADT above 27°C. Similarly, at the highest PPF level the effect of ADT was insignificant.

Transition from a vegetative to a reproductive meristem under SD conditions in chrysanthemum was dependent on cultivar and PPF levels (30). Two cultivars classified in the 10 week response group completed leaf initiation in 10 to 14 SD. Cultivars in shorter and longer response groups formed a reproductive meristem in 3 to 7 and 14 to 17 SD, respectively. Cockshull and Hughes (7) found the meristem transition to occur faster at 5.8 mol $day^{-1}m^{-2}$ PPF (200 μmol $s^{-1}m^{-2}$, 8 hr day^{-1}) compared to 3.7 mol $day^{-1}m^{-2}$ (130 μmol $s^{-1}m^{-2}$, 8 hr day^{-1}). Faster leaf initiation also occurred in chrysanthemum when the PPF level increased from 1.3 to 20.2 mol $day^{-1}m^{-2}$ (3,8). The rapid first leaf appearance observed with high PPF (Figure 4) was likely a result of faster leaf initiation and meristem transition, since the leaf unfolding rate was found to be an ADT response.

Supplemental lighting and relatively high temperatures

during early development under SD are beneficial in chrysanthemum production. Flowering occurred 2 to 4 days earlier when 6 mol $day^{-1}m^{-2}$ (140 μmol $s^{-1}m^{-2}$, 12 hr day^{-1}) supplemental irradiation was provided for the first 2 weeks of SD (26). The cultivar 'Yellow Paragon' flowered 6 days earlier and 'Copper Ann' 9 days earlier when supplemental irradiation (6.8 mol $day^{-1}m^{-2}$, 190 μmol $s^{-1}m^{-2}$, 9 hr day^{-1}) was supplied for the first 5 weeks of SD (16). Temperatures above 16° favored fast development prior to the visible bud stage while temperatures below 16°C hasten development after visible bud (4). The functional relationship developed for first leaf appearance on the newly formed shoots also indicated that favorable PPF and temperature conditions facilitated the development immediately after transfer to SD.

Temperature was found to be the determining factor influencing shoot length, PPF was nonsignificant (11). A high DT in combinations with a high NT resulted in tall plants (Table 2). Plants grown at a constant 14° had on average 16 cm long shoots compared to 29 or 31 cm long shoots at a constant 26°C. Shoots also increased in length with increasing DT. When the DT was increased from 14° to 26° with a NT of 14° and a PPF level of 5.8 or 17.6 mol $day^{-1}m^{-2}$, the shoots doubled in length from 16 to 33 cm at the lower PPF level and from 15 to 28 cm (shoot 1) at the higher PPF level. No such increase in shoot length occurred when NT was increased from 14° to 26° with the DT

at 14°.

The number of leaves formed prior to flower initiation increased with increasing temperatures and decreased slightly with increasing PPF (Table 1, Figure 2). Plants with many leaves always grew tall, but two groups of tall plants could be distinguished (Table 2). The first group of tall plants had internode lengths similar to that of the short plants but had more internode segments. The second group had a similar number of internodes as the shorter plants, but of greater length. A plant showing morphologically delayed flower initiation (14 or 15 leaves/shoot) will grow tall unless the internodes are exceptionally short.

The important factor for monitoring and controlling height during development appeared to be internode length, since the leaf number was set during the first weeks of SD (30). Shoot length among plants exhibiting 10 or 11 leaves was 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* (12). A large positive DIF resulted in longer internodes. Examination of observed internode length (Table 2) suggested DIF to be of similar significance for chrysanthemum. The regression analysis resulted in an

equation with DIF, DIF^2 and DIF*ADT as significant independent variables.

$$\text{Internode length} = 1.7637 + (0.2274 * DIF) + (0.0013 * DIF^2) - (0.0080 * DIF * ADT) \qquad (r^2 = 0.79)$$

The predicted internode lengths with DIF ranging from -12° to 12° and of ADT ranging from 10° to 30°C are shown in Figure 5 along with observed internode lengths. The internode length increased with increasing DIF. Under conditions with a higher NT than DT (a negative DIF) the internode length was predicted to be longer as the ADT increased. At positive DIF values however, an increasing ADT was calculated to give shorter internodes. Prediction of total shoot length using the functions for leaf number and internode length resulted in predicted values within one standard deviation of observed shoot lengths.

Extreme differences between DT and NT may result in slower and abnormal plant development and growth (22). The relationship between environmental conditions and internode length may change when DIF approaches values of -20° or 20°. The selected experimental conditions did not provide a good distribution of DIF values, since the importance of DIF was not anticipated at the initiation of this study. Based on earlier observations with chrysanthemum (11,18,19,20) and Easter lily (12) the validity of the

developed function appear relevant. The areas in Figure 5 with combinations of ADT and DIF outside the range of values studied have been shaded.

Flower initiation was delayed morphologically as temperature increased and more leaves had to unfold before the flower bud became visible. Delayed chronological initiation has also been observed under high temperatures (30). Since the rate of leaf unfolding was a linear ADT response in the range from 10° to 30°C and flower initiation occurred during this period, most rapid leaf unfolding may result in delayed meristem transition and continued development of florets (30).

The rate of development from start of SD to visible bud was dependent on rate of meristem transition, total leaf number, and the rate of leaf unfolding. High PPF levels produced the highest leaf initiation rates and the fastest transition from a vegetative to a reproductive meristem. The number of leaves formed before the meristem became reproductive was determined primarily by DT and NT, while the rate of leaf unfolding was an ADT response.

Shoot length was a function of leaf number/shoot and the internode length. Plants grown with a high DT always grew tall. When the high DT was combined with a high NT, tall plants with many leaves developed. A high DT accompanied with a low NT resulted in plants with long internodes. The internode length was determined by DIF and ADT. The more positive DIF became, the longer the

internodes. Increasing ADT resulted in longer internodes at negative DIF values but in shorter internodes at positive DIF values.

The developed quantitative relationships for the growth and development processes from SD to visible flower buds provided a summary of the environmental effects and enable model development for initial chrysanthemum development under reproductive conditions. The functions for leaf number and internode length gave an understanding of the factors governing height and an opportunity to construct a model for height control based on environmental options.

Literature Cited

1. Anderson, N.O. 1987. Reclassification of the genus *Chrysanthemum* L. HortScience 22:313.

2. Balvoll, G. and A.H. Bremer. 1965. Varmesum og planteavl i samband med vekst og utvikling av ymse grønsaksvokstrar. Meldinger fra Norges Landbruks-høgskole, Rpt. No. 20, 44:1-18.

3. Berg, A.R. and E.G. Cutter. 1969. Leaf initiation rates and volume growth rates in the shoot apex of chrysanthemum. Amer. J. Bot. 56:153-159.

4. Cathey, H.M. 1955. A study of the effects of light and temperature upon the flowering of *Chrysanthemum morifolium* and *Tulipa gesneriana*. Ph.D. Thesis, Cornell University, Ithaca.

5. Charles-Edwards, D.A., K.E. Cockshull, J.S. Horridge, and J.H.M. Thornley. 1979. A model of flowering in chrysanthemum. Ann. Bot. 44:557-566.

6. Cockshull, K.E. and A.P. Hughes. 1971. The effects of light intensity at different stages in flower initiation and development of *Chrysanthemum morifolium*. Ann. Bot. 35:915-926.

7. Cockshull, K.E. and A.P. Hughes. 1972. Flower formation in *Chrysanthemum morifolium*: the influence of light level. J. Hort. Sci. 47:113-127.

8. Cockshull, K.E. 1979. Effects of irradiance and temperature on flowering of *Chrysanthemum morifolium* Ramat. in continuous light. Ann. Bot. 44:451-460.

9. Cockshull, K.E., D.W. Hand, and F.A. Langton. 1981. The effect of day and night temperature on flower initiation and development in chrysanthemum. Acta Hort. 125:101-110.

10. Crater, G.D. 1980. Pot mums, p. 261-285. In: R.A. Larson (ed.). Introduction to floriculture. Academic Press, New York.

11. Erwin, J.E. 1986. Environmental and physiological factors influencing the response of *Chrysanthemum morifolium* cvs. 'Bright Golden Anne' and 'Circus' to daminozide. MS Thesis, Michigan State University, E. Lansing.

12. Erwin, J.E., R.D. Heins, and M.G. Karlsson. 1987. Thermomorphogenesis in *Lilium longiflorum* Thunb. Amer. J.Bot. (in review).

13. Friend, D.J.C., V.A. Helson, and J.E. Fisher. 1962. Leaf growth in marquis wheat, as regulated by temperature, light intensity, and daylength. Can. J, Bot. 40:1299-1311.

14. Gardiner, D.A., R.G. Cragle, and P.T. Chandler. 1967. The response surface method as a biological tool. Tenn. Agr. Expt. Sta. Bul. 429:25-40.

15. Golden Software, Inc. 1987. Surfer, version 3.00. Golden, Colorado.

16. Hicklenton, P.R. and K.B. McRae. 1984. Vegetative growth and flowering of pot chrysanthemums in response to supplemental HPS radiation and split-night temperatures. J.Amer. Soc. Hort. Sci. 109:30-33.

17. Hickman J.C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). Jour. Ecol. 63:689-701.

18. Karlsson, M.G. 1984. Influence of temperature and irradiance on growth and development of *Chrysanthemum morifolium* 'Bright Golden Anne'. MS Thesis, Michigan State University, E. Lansing.

19. Karlsson, M.G. and R.D. Heins. 1986. Response surface analysis of flowering in chrysanthemum 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253-259.

20. Karlsson, M.G., R.D. Heins, and W.H. Carlson. 1983. Development of environmental strategies based on plant growth models. Acta Hort. 147:153-160.

21. Karlsson, M.G., R.D. Heins, and J.E. Erwin. 1988. Quantifying temperature controlled leaf unfolding rates in *Lilium longiflorum* Thunb. 'Nellie White'. J. Amer. Soc. Hort. Sci. 113:xxx-xxx.

22. Mastalerz, J.W. 1977. The greenhouse environment. John Wiley & Sons, New York.

23. Nie, N.E., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent. 1975. Statistical package for the social sciences (SPSS). 2nd edition. McGraw-Hill Inc., New York.

24. Post, K. and D.B. Lacey. 1951. High temperature produces long day effect on chrysanthemums. Bull. N.Y. St. Flower Grs. 76:4.

25. Rawson, H.M. and J.H. Hindmarsh. 1982. Effects of temperature on leaf expansion in sunflower. Aust. J. Plant Physiol. 9:209-219.

26. Stefanis, J.P. and R.W. Langhans. 1982. Quantum flux density studies of chrysanthemum in a controlled environment with high pressure sodium lamps. II. Long day and short day studies. J. Amer. Soc. Hort. Sci. 107:461-464.

27. Thompson, K. and A.J.A. Stewart. 1981. The measurement and meaning of reproductive effort in plants. Am. Nat. 117:205-211.

28. Thornley, J.H.M and K.E. Cockshull. 1980. A catastrophe model for the switch from vegetative to reproductive growth in the shoot apex. Ann. Bot. 46:333-341.

29. Tollenaar, M., T.B. Daynard, and R.B. Hunter. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Science 19:363-366.

30. Van Ruiten, J.E.M. and J. De Jong. 1984. Speed of flower induction in *Chrysanthemum morifolium* depends on cultivar and temperature. Scientia Hortic. 23:287-294.

31. Vince, D. 1960. Low temperature effects on the flowering of *Chrysanthemum morifolium* Ramat. J. Hort. Sci. 35:161-175.

32. Whealy, C.A., T.A. Nell, J.E. Barrett, and R.A. Larson. 1987. High temperature effects on growth and floral development of chrysanthemum. J. Amer. Soc. Hort. Sci. 112:464-468.

33. Wilkenson, L. 1986. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.

Table 1. Influence of photosynthetic photon flux (PPF), day temperature, and night temperature on number of leaves in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne').

Environment			Average			
PPF[z]	Temp(°C)		daily	Number of leaves[y]		
mol day^{-1}m^{-2}	Day	Night	temp (°C)	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[x v]	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[x v]	21.7	21 ± 1.0	20 ± 0.4	14 ± 0.5 *
1.8	30	30[x v]	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]10 hr irradiation day^{-1}.
[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 (at 5% level) or nonsignificantly different from shoot 1 and/or shoot 2, respectively.
Differences between shoot 1 and shoot 2 were all nonsignificant.

Table 2. Influence of photosynthetic photon flux (PPF), day temperature, and night temperature on shoot and internode length in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne').

Environment			Day temp.	Shoot length (cm)[y]			Internode length (cm)		
PPF[z]	Temp(°C)		minus night						
mol day^{-1}m^{-2}	Day	Night	temp. (°C)	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] 10 hr irradiation day^{-1}.
[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 (at 1% or 5% level) or nonsignificantly different from shoot 1 and/or shoot 2, respectively.
Differences between shoot 1 and shoot 2 were all nonsignificant.

Figure 1. Predicted flower initiation or continued vegetative growth under short day conditions in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') as affected by day and night temperature at a photosynthetic photon flux of 1.8 mol $day^{-1}m^{-2}$ (50 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}). Flower initiation is predicted not to occur within the shaded area.

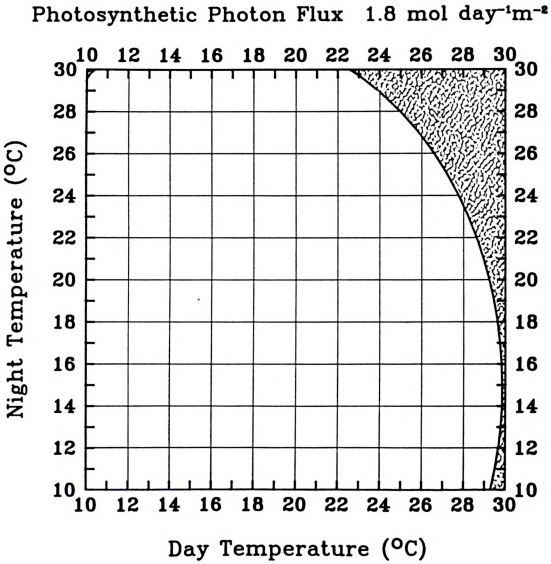

Photosynthetic Photon Flux 1.8 mol day⁻¹m⁻²
Night Temperature (°C)
Day Temperature (°C)
10 12 14 16 18 20 22 24 26 28 30

Figure 2. The effect of day (DT) and night temperature (NT) on number of leaves formed per shoot prior to flower initiation in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') at a photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$ (325 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}). The functional relationship used to create the graph was: Leaf number = 12.6349 - 0.6278 * DT + 0.0222 * DT^2 + 0.0041 * NT^2 - 0.7 * 10^{-8} * PPF * DT^2 * NT^2.

Photosynthetic Photon Flux 11.7 mol day^{-1}m^{-2}

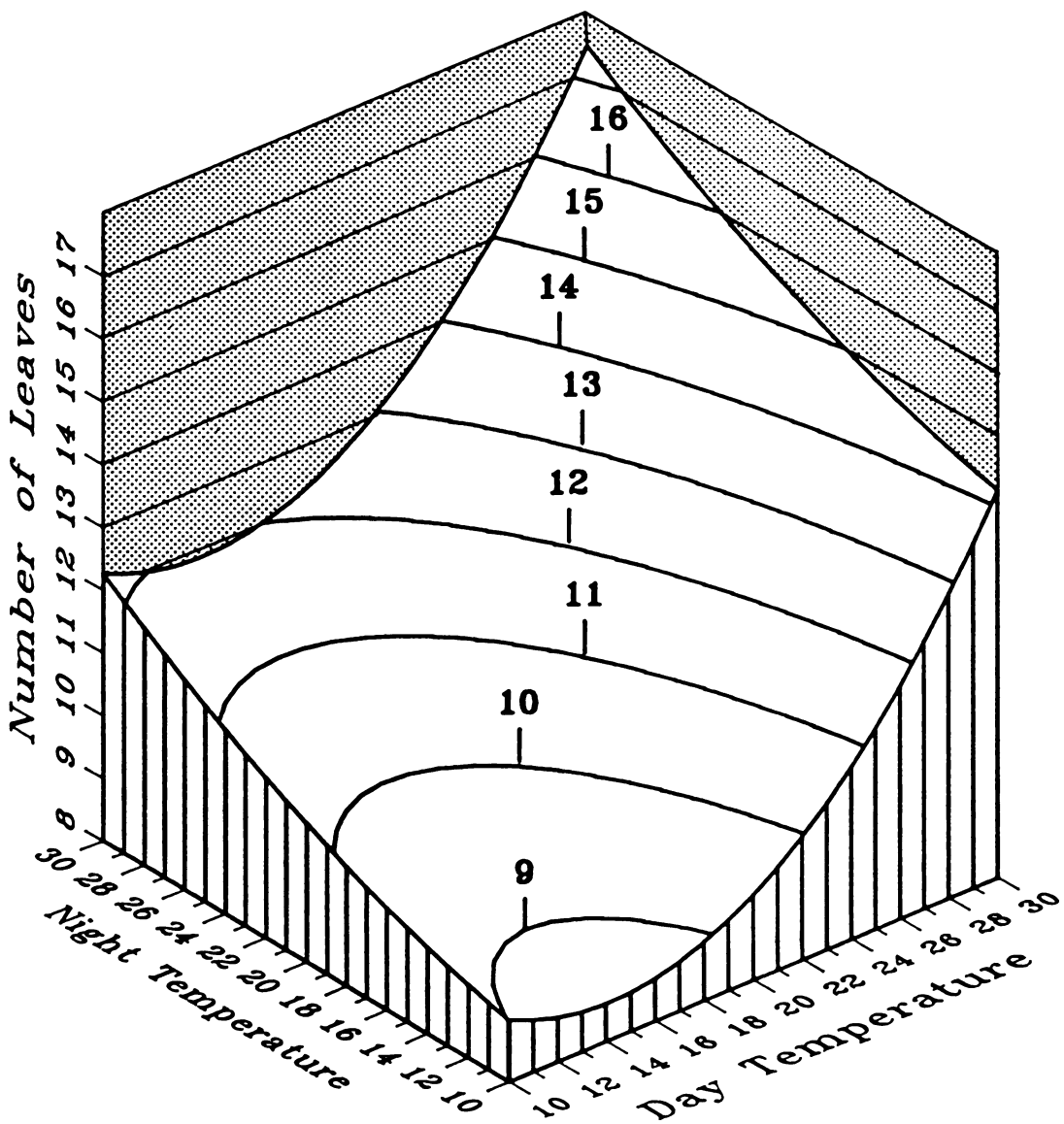


Figure 3. Number of chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') leaves unfolded per day as a function of average daily temperature.

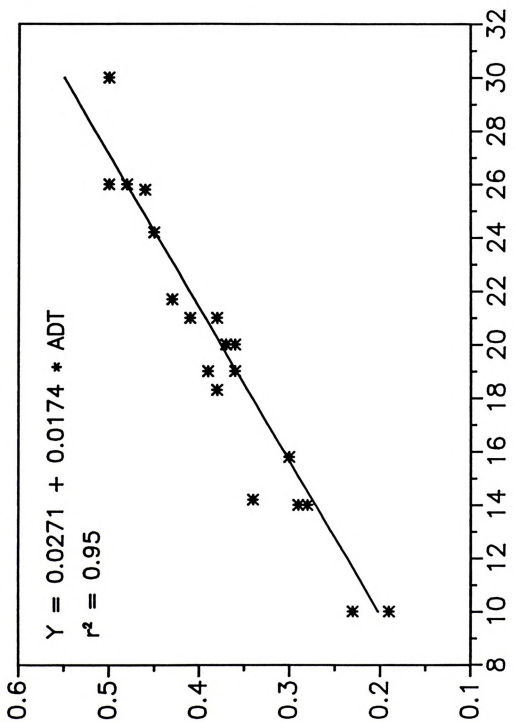

Y = 0.0271 + 0.0174 * ADT
r² = 0.95
Leaves Day⁻¹
0.6
0.5
0.4
0.3
0.2
0.1
8 10 12 14 16 18 20 22 24 26 28 30 32
Average Daily Temperature (°C)

Figure 4. Number of days after pinch and start of short days required for the first leaf to appear in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') with average daily temperatures (ADT) from 10° to 30°C and photosynthetic photon flux (PPF) from 1.8 to 21.6 mol $day^{-1}m^{-2}$ (50 to 600 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}). The functional relationship used to create this graph was: Days to first leaf = 19.1892 - 0.7457 * PPF - 0.6078 * ADT + 0.0264 * PPF * ADT. Flower initiation is not predicted to occur within the shaded region.

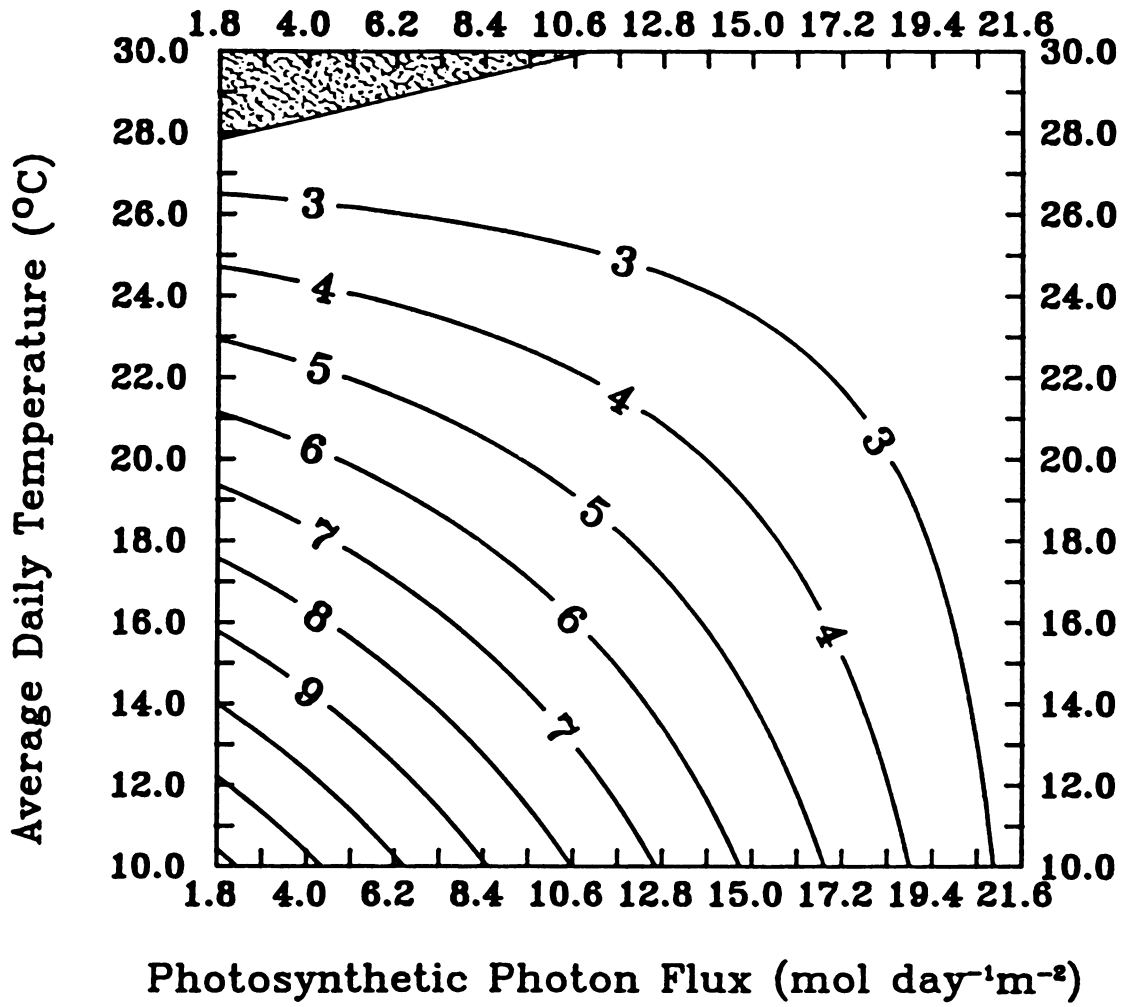
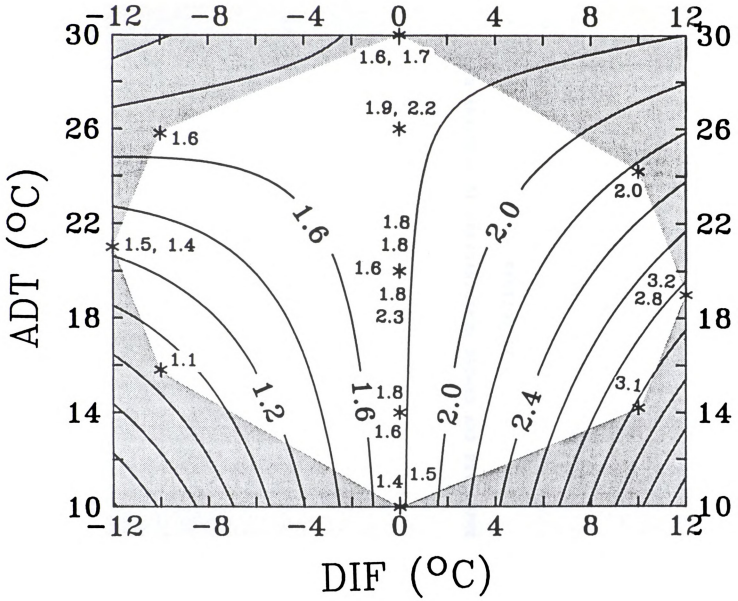

1.8 4.0 6.2 8.4 10.6 12.8 15.0 17.2 19.4 21.6
30.0
28.0
26.0
24.0
22.0
20.0
18.0
16.0
14.0
12.0
10.0
3
4
5
6
7
8
9
Average Daily Temperature (°C)
Photosynthetic Photon Flux (mol day⁻¹m⁻²)

Figure 5. The effect of the difference between day and night temperature (DIF) and average daily temperature (ADT) on internode length (cm) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'). Observed internode lengths are indicated on the graph and areas with combinations of DIF and ADT outside the studied range are shaded. The functional relationship used to create the graph was: Internode length = 1.7637 + 0.2274 * DIF + 0.0013 * DIF^2 - 0.0080 * DIF * ADT.


ADT (°C)
DIF (°C)
−12
−8
−4
0
4
8
12
30
26
22
18
14
10
1.6, 1.7
1.9, 2.2
1.6
2.0
1.5, 1.4
1.8
1.8
1.6
1.8
2.3
3.2
2.8
1.1
3.1
1.8
1.6
1.4
1.5
1.6
1.2
2.0
2.4

SECTION II

PATH ANALYSIS OF CHRYSANTHEMUM GROWTH AND DEVELOPMENT

Path Analysis of Chrysanthemum Growth and Development

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Additional index words. plant growth analysis, phasic development, dry weight accumulation, *Chrysanthemum morifolium*, *Dendranthema grandiflora*

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Abstract

Plants of *Dendranthema grandiflora* Tzvelev. were grown under one of 25 irradiance and temperature combinations from start of short days to flower. Four phases of development were defined as the start of short days to the appearance of 4 mm terminal flower buds (phase I), appearance of 4 mm terminal flower buds to removal of lateral flower buds when the terminal flower bud was 7-8 mm (phase II), removal of lateral flower buds to flower buds showing first color (phase III), and flower buds showing color to flowering (phase IV). Path analysis was used to study the influence of development time and relative dry weight gain during each of these four phases on development time and relative dry weight gain of subsequent phases. Relative dry matter accumulation during Phase I, II, III, and IV significantly influenced cumulative relative dry weight gain with phase I having the greatest influence. Increasing relative dry weight gain during Phase I had a significant negative effect on relative dry weight gain in Phase II. Time within each phase significantly affected total time to flower. Under the constant environmental conditions of this experiment, time in one phase did not influence the length of time in later phases.

Recommendations have been developed to help growers produce high quality flowering pot plants at low cost in minimal time. These recommendations often define a set of environmental conditions which are maintained during development through flowering (19,20); however, constant environmental conditions throughout plant development may not optimize plant growth. If the plants respond differently to the environment during different phases of development, it should be possible to distinguish which phases of development are most important in determining total time of development and final plant characteristics. When these phasic responses have been quantified, it may be possible to more precisely monitor and control the environment during critical phases while tolerating less control during other phases.

Wright (29,30) developed a statistical method termed "path analysis" to quantify interactions among yield components and measure their contribution to total yield. In path analysis, the direct effects of independent variables are studied with the indirect effects removed. The advantage of such an analysis is that the effect of one component on another can be isolated from influences of other components. A high path coefficient between two components indicates that a change in one will result in a substantial relative change in the other when additional influences are removed. Path coefficients not significantly

different from zero indicate that a change in one component will have little direct effect on a corresponding component. Path coefficients can only be calculated if their dependence structure is known. Yield components for example, often develop sequentially and those which develop late cannot affect early components. The directionality of dependencies can be determined in these situations.

Path analysis has been used by agronomists (8,9) and horticulturists (11,23,25,26) in problems involving yield. Analogies can be made between individual yield components and growth during discrete intervals, and between yield and final plant size. Yield components interact multiplicatively to produce yield and a log transformation is used to make the dependence structure linear (24,27). A log transformation is also used in the analysis of plant growth so dry matter accumulation can be expressed linearly when the percentage dry weight increase is constant (16). This transformation also serves to equalize residual variance among young and mature plants, and removes any potential bias in favor of later growth phases. Both yield components and growth phases develop sequentially and the dependence structure can easily be determined.

Although several workers have described the growth of chrysanthemums by mathematical models (1,7,12,14,15,18), none have determined how variation in growth during a particular developmental phase influence subsequent

development and time to flower. The objectives of this study were to determine how relative growth rate and developmental time in one phase influenced relative growth rate and time in later phases and to identify the most critical developmental phases for total dry matter accumulation and time to flower in chrysanthemum.

Rooted cuttings of *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' (2) were planted in 10 cm pots and placed in growth chambers under 18.7 mol $day^{-1}m^{-2}$ (325 μmol $s^{-1}m^{-2}$, 16 hr day^{-1}) photosynthetic photon flux (PPF) and a constant temperature of 20°C for 7 days. A short day (SD) photoperiod was initiated (10 hr light, 14 hr dark) on the seventh day and plants were pinched to six nodes. The PPF, day temperature (DT), and night temperature (NT) were altered in the chamber to provide one of 25 treatment combinations (Table 1).

The PPF was provided by cool-white fluorescent and incandescent lamps with an input wattage of 80:20, respectively. Average daily temperature fluctuated $\pm$ 1°C from the setpoint and PPF varied $\pm$ 10% over the plant canopy.

Plants were grown in a commercial peat-lite medium (Michigan Peat Co.) and irrigated up to three times daily to prevent water stress conditions. Fertilizer program 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 $\pm$ 0.2 by adjusting water pH with nitric acid.

A central composite design was used to select treatment combinations (3,10). Temperatures ranged from 10° to 30°C and PPF from 1.8 to 21.6 mol $day^{-1}m^{-2}$ (50 to 600 μmol $s^{-1}m^{-2}$, 10 hr day^{-1}). 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 stages of development were distinguished: start of SD, visible bud (VB, appearance of 4 mm terminal flower buds), disbud (DB, removal of lateral flower buds when the terminal bud was 7-8 mm in diameter), flower buds showing first color, and flowering (outermost petals reflexed to a horizontal position). Four developmental phases were defined as the intervals between the five stages. Dry weight of roots, stems, leaves and flowers was determined on five randomly selected plants at the five developmental stages. Dry matter accumulation during each phase and the length of each phase were calculated based on the observations at the five sampling occasions.

In a growth model where W_0 through W_4 are dry weights at five developmental stages, four phases of dry weight accumulation can be created which are related to total plant dry weight gain from start of SD to flower.

$$(\ln W_1 - \ln W_0) + (\ln W_2 - \ln W_1) + (\ln W_3 - \ln W_2) + (\ln W_4 - \ln W_3) = \ln W_4 - \ln W_0 = \ln(\text{total relative dry weight gain})$$

By letting G_1 through G_4 represent the relative dry weight gain during each of the four developmental phases ($G_i = \ln W_i - \ln W_{i-1}$), one can perform a path analysis to quantify the effect of G_{i-1} on G_i, G_{i+1}, etc. variables and total plant relative dry weight gain at flowering (G_T). A similar analysis can be performed with the time intervals of each phase (T_1, T_2, T_3, and T_4) treated as components of the total time to flower.

The G_i variables were used to define growth as the relative dry weight increase for each developmental phase, but this analysis ignores the time required to complete the development from one stage to another (T_1 through T_4). An additional analysis was therefore performed using the mean relative growth rates (R_i variables) of each phase.

$$R_i = (\ln W_i - \ln W_{i-1})/(t_i - t_{i-1})$$

where W_{i-1} and W_i are plant dry weights at the beginning and end of the phase, and $(t_i - t_{i-1})$ is the time required to complete a particular phase (6).

Path analysis was performed on the defined variables using SPSS subprogram 'regression' (22). A series of least

square regressions was computed with one variable at a time as the dependent variable and the preceding variables in the path as the independent variables. The standardized beta values were used as the path coefficients.

The potential interrelations among the G_i variables are diagrammed in Figure 1a. The number corresponding to each path is the relative direct effect (path coefficient) of one developmental phase on another with the indirect effects removed. G_1 had the greatest effect on G_T, while subsequent phases exhibited decreasing effects. Previous studies with chrysanthemum have shown that optimal growing conditions during the first few weeks after planting improve final size (5,13,28).

One might expect a large relative growth rate during one phase to allow for even greater relative growth during subsequent phases. This was not the case in chrysanthemum (Figure 1a). G_1 (from SD to VB) had a significant negative effect (path coefficient = -0.606) on G_2 (from VB to DB). This means as G_1 became larger, G_2 became smaller. All other path coefficients indicating direct effects of relative dry weight gain on successive relative dry weight gain were non-significant.

The length of time in phase I was generally longer than the length of time in phase II, and more dry weight could accumulate during phase I compared to phase II. The negative effect of G_1 on G_2 might therefore be related to

the different length of phase I and II. Variations in T_1, T_2, T_3, and T_4 significantly contributed to variations in total time to flower, but the influence of the T variables on each other was not significant (Figure 1b). These results suggest that when the environmental conditions were kept constant throughout chrysanthemum development, the plants responded directly to the environment without conditioning effects from earlier phases. The plant response to an earlier phase however is affected if the environment is changed from one phase to another (17).

The R_1 variable, like the G_1 variable, was significantly related to G_T (Figure 1c). No other R_i variables were significantly associated with later R_i variables or G_T. These results again suggest that early growth had the greatest influence on final plant size. In addition, when dry weight accumulation was expressed as a relative growth rate, i.e. taking the length of time to complete each phase into consideration (R_i), no negative effect of phase I on phase II was observed.

Phasic analysis of plant growth can provide insight into growth and development of a plant. The G variables for all four phases significantly affected G_T. G_1 and R_1 were most highly associated with G_T when the influences of intermediate phases were removed. This suggests that it is most critical to optimize environmental conditions during early development. An early large relative dry weight gain

was expected to result in a large leaf area and, therefore, sequentially larger relative dry weight gains. However, neither the analysis of G variables or R variables supported this hypothesis (Figure 1a,c).

A plant with a large initial relative dry weight gain may have a different partitioning pattern than a plant with a smaller initial relative dry weight gain. Large initial relative dry weight gains are likely to occur under different environmental conditions than small initial relative dry weight gains. These different environmental conditions may result in different partitioning patterns. For example, the increased dry weight may be directed to supportive tissues such as roots and stems rather than to leaves, resulting in a relatively smaller dry weight increase during the second phase. PPF was most important of the 3 environmental factors in determining total dry matter accumulation (17) and it also modified partitioning patterns. Total dry matter at flowering increased from 3.6 to 15.3 g/plant as the PPF level increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at a DT and NT of 20°C (Table 1). As the PPF level increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ the proportion of dry matter at flowering decreased in leaves from 40% to 22%, increased in stems from 20% to 24% and increased in roots from 8% to 24% (17). The decrease in partitioning to leaves as PPF increases has also been shown in other studies (4,21).

A second possible explanation for large initial relative dry weight gains not resulting in subsequent large relative dry weight gains may be that environmental conditions favoring early development are not as favorable for growth later in development. A large relative dry weight gain during the first phase may still be desirable, since a plant with a strong root system and stem strength can potentially produce larger flowers.

In summary, relative dry weight gain during phase I, II, III, and IV (G_1, G_2, G_3 and G_4) significantly influenced cumulative relative dry weight gain (G_T) with G_1 having the greatest influence. Increasing G_1 had a negative effect on G_2. An increasing relative growth rate during phase I (R_1) increased G_T whereas the other R_i variables were not significantly correlated with later R_i variables or G_T. Time required to complete one phase of development was relatively independent of the time duration during previous phases.

Literature Cited

1. Acock, B., D.A. Charles-Edwards, and S. Sawyer. 1979. Growth responses of a chrysanthemum crop to the environment. III. Effects of radiation and temperature on dry matter partitioning and photosynthesis. Ann. Bot. 44:289-300.

2. Anderson, N.O. 1987. Reclassification of the genus *Chrysanthemum* L. HortScience 22:313.

3. Armitage, A.M., W.H. Carlson, and C.E. Cress. 1981. Determination of flowering time and vegetative habit of *Tagetes patula* through response surface techniques. J. Amer. Soc. Hort. Sci. 106:632-638.

4. Björkman, O. 1981. Responses to different quantum flux densities, p. 57-107. In: O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler (eds.). Encyclopedia of plant physiology, Volume 12A, Physiological plant ecology I, response to the physical environment. Springer-Verlag, New York.

5. Carpenter, W.J. 1975. High intensity lighting of pot chrysanthemum. Flor. Rev. 156:19-20, 59-60.

6. Causton, D.R. 1983. A biologist's basic mathematics. Edward Arnold, London.

7. Charles-Edwards, D.A., K.E. Cockshull, J.S. Horridge, and J.H.M. Thornley. 1979. A model of flowering in chrysanthemum. Ann. Bot. 44:547-556.

8. Dewey, D.R. and K.H. Lu. 1959. A correlation and path coefficient analysis of components of crested wheatgrass seed production. Agron. J. 51:515-518.

9. Duarte, R.A. and M.W. Adams. 1972. A path coefficient analysis of some yield component relationships in field beans (*Phaseolus vulgaris*). Crop Sci. 12:579-582.

10. Gardiner, D.A., R.G. Cragle, and P.T. Chandler. 1967. The response surface method as a biological tool. Tenn. Agr. Expt. Sta. Bul. 429:25-40.

11. Hancock, J.F., M.P. Pritts, and J.H. Siefker. 1984. Yield components of strawberries maintained in ribbons and matted rows. Crop Res. 24:37-43.

12. Heins, R.D., M.G. Karlsson, J.A. Flore, and W.H. Carlson. 1986. Effects of photosynthetic rate maximization on growth and development in chrysanthemum. J. Amer. Soc. Hort. Sci. 111:42-46.

13. Hicklenton, P.R. 1984. Response of pot chrysanthemum to supplemental irradiation during rooting, long day, and short day production stages. J. Amer. Soc. Hort. Sci. 109:468-472.

14. Hughes, A.P. 1973. A comparison of the effects of light intensity and duration on *Chrysanthemum morifolium* cv. Bright Golden Anne in controlled environments. I. Growth analysis. Ann. Bot. 37:267-274.

15. Hughes, A.P. and K.E. Cockshull. 1971. The effects of light intensity and carbon dioxide concentration on the growth of *Chrysanthemum morifolium* cv. Bright Golden Anne. Ann. Bot. 35:899-914.

16. Hunt, R. 1978. Plant growth analysis. Edward Arnold Ltd., London.

17. Karlsson, M.G. 1987. Characterization of growth responses to irradiance and temperature for model development in chrysanthemum. Ph.D. Dissertation, Michigan State University, E. Lansing.

18. Karlsson, M.G. and R.D. Heins. 1986. Response surface analysis of flowering in chrysanthemum 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253-259.

19. Larson, R.A. (ed.). 1980. Introduction to floriculture. Academic Press, New York.

20. Laurie, A., D.C. Kiplinger, and K.S. Nelson. 1969. Commercial flower forcing. McGraw-Hill, New York.

21. Lee, S.M. and P.B. Cavers. 1979. The effect of shade on growth, development and resource allocation patterns of three species of foxtail (*Setaria*). Can. J. Bot. 59:1776-1786.

22. Nie, N.E., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent. 1975. Statistical package for social sciences (SPSS). 2nd edition. McGraw-Hill, New York.

23. Pritts, M.P., J.H. Siefker, and J.F. Hancock. 1984. Yield component variation in wild and cultivated blueberries. Proc. Blueberry Res. Workers Conf. 5:30-37.

24. Pritts, M.P. and J.F. Hancock. 1985. Lifetime biomass partitioning and yield component relationships in the highbush blueberry, *Vaccinium corymbosum* L. (*Ericaceae*). Amer. J. Bot. 72:446-452.

25. Ranalli, P., M. DiCandilo, I. Giordano, and B. Casarini. 1981. Correlation and path analysis in peas (*Pisum sativum* L.) for processing. Z. Pflanzenzuchtung 86:81-86.

26. Shasha'a, N.S., W.P. Nye, and W.F. Campbell. 1973. Path coefficient analysis of correlation between honey bee activity and seed yield in *Allium cepa* L. J. Amer. Soc. Hort. Sci. 98:341-347.

27. Siefker, J.H. and J.F. Hancock. 1986. Yield component interactions in cultivars of the highbush blueberry. J. Amer. Soc. Hort. Sci. 111:606-608.

28. Stephanis, J.P. and R.W. Langhans. 1982. Quantum flux density studies of chrysanthemum in a controlled environment with high-pressure sodium lamps. II. Long day and short day studies. J. Amer. Soc. Hort. Sci. 107:461-464.

29. Wright, S. 1921. Correlation and causation. J. Agr. Res. 20:557-585.

30. Wright, S. 1934. The method of path coefficients. Ann. Math. Stat. 5:161-215.

Table 1. Influence of photosynthetic photon flux (PPF), day temperature, and night temperature on time to flower and total plant dry weight at flowering in *Dendranthema grandiflora* Tzvelev.

Environment			Days to experimental termination[z]	Total plant dry matter at flowering (g)[y]
PPF	Temp(°C)			
mol day^{-1}m^{-2}	Day	Night		
1.8	10	10[x]	120	3.8 ± 0.02
1.8	30	10[x v]	---	---
1.8	20	20	90	3.6 ± 0.14
1.8	10	30[x v]	---	---
1.8	30	30[x v]	---	---
5.8	14	14	70	5.3 ± 0.10
5.8	26	14	80	5.9 ± 0.09
5.8	20	20[x]	70	6.2 ± 0.07
5.8	14	26	80	6.6 ± 0.10
5.8	26	26	90	8.6 ± 0.38
11.7	20	10	70	10.7 ± 0.09
11.7	10	20	70	5.9 ± 0.07
11.7	20	20	70	10.0 ± 0.22
11.7	30	20	90	10.6 ± 0.05
11.7	20	30	80	9.3 ± 0.16
17.6	14	14	70	10.9 ± 0.40
17.6	26	14	75	14.3 ± 0.42
17.6	20	20[x]	70	10.7 ± 0.19
17.6	14	26	70	11.0 ± 0.14
17.6	26	26	80	17.2 ± 0.56
21.6	10	10[x]	80	10.5 ± 0.18
21.6	30	10[x]	80	11.6 ± 0.38
21.6	20	20	60	15.3 ± 0.12
21.6	10	30[x]	90	14.6 ± 0.41
21.6	30	30[x]	120	14.5 ± 0.23

[z]When the flowers had reflexed their outermost petals to a horizontal position.

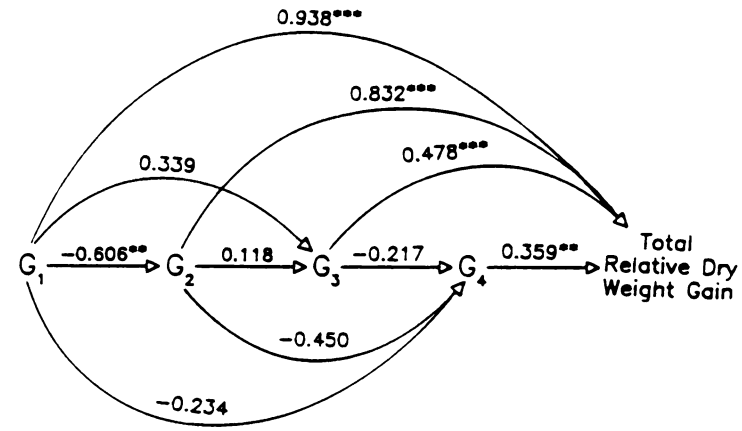
[y]± SE.

[x]Treatments added to the 15 basic treatments in the central composite design.

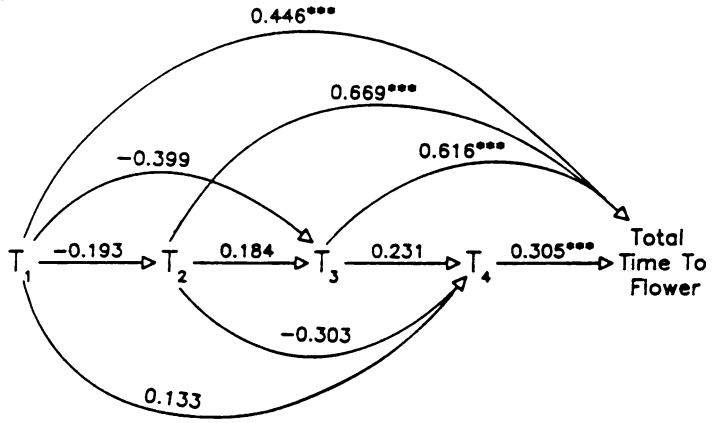
[v]Not used in analysis due to lack of flower initiation.

Figure 1. Path diagram indicating the interrelationships in chrysanthemum (*Dendranthema grandiflora* Tzvelev.) a) among increments of relative dry weight accumulation (G) during 4 developmental phases and total relative dry weight increase, b) among days of 4 developmental phases (T) and total number of days to flower, and c) among relative growth rates (dry weight gain day^{-1}, R) of 4 developmental phases and total relative dry weight increase.
The 4 developmental phases were from start of short day to a 4 mm large terminal flower bud (visible bud), from visible bud to a 10 mm large terminal flower bud (disbud), from disbud to a flower bud showing color, and from color to flower. Numbers correspond to path coefficients. Asterisks define the level of significance: *** = $P < 0.001$ and ** = $P < 0.01$.

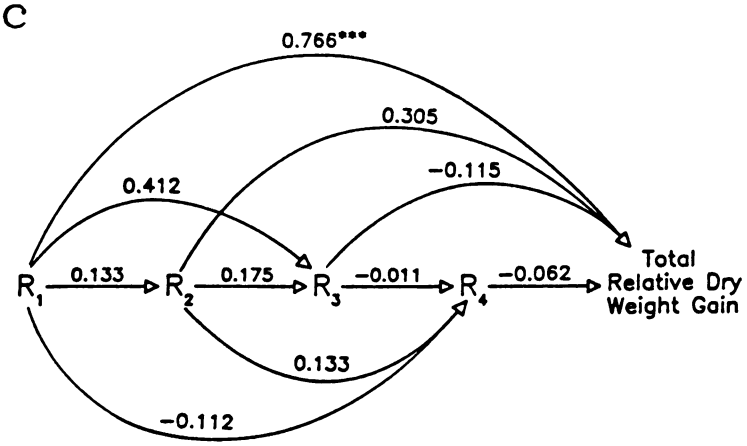
a


0.938***
0.832***
0.339
0.478***
G1
−0.606**
G2
0.118
G3
−0.217
G4
0.359**
Total Relative Dry Weight Gain
−0.450
−0.234

b


0.446***
0.669***
−0.399
0.616***
T1
−0.193
T2
0.184
T3
0.231
T4
0.305***
Total Time To Flower
−0.303
0.133

c


0.766***
0.305
0.412
−0.115
R1
0.133
R2
0.175
R3
−0.011
R4
−0.062
Total Relative Dry Weight Gain
0.133
−0.112

SECTION III

RATE OF DEVELOPMENT DURING FOUR PHASES OF CHRYSANTHEMUM GROWTH AS AFFECTED BY PRECEDING AND PREVAILING TEMPERATURE EXPOSURE

Rate of Development during Four Phases of Chrysanthemum Growth as Affected by Preceding and Prevailing Temperature Exposure

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Additional index words. temperature response, *Chrysanthemum morifolium*, *Dendranthema grandiflora*, average temperature, optimum temperature

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Abstract

Time required to complete four developmental phases in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' was determined under temperatures ranging from 10° to 30°C. The 4 defined phases were from start of short days to a 2 mm large terminal flower bud (visible bud), from visible bud to a 10 mm large terminal flower bud (disbud), from disbud to a flower bud showing color, and from color to flower. Fastest development during any phase occurred on plants grown in the 18° and 20° treatments. The developmental rate was delayed as the temperature varied from these temperatures. Conditioning effects of temperature from previous phases were observed during phase II and III but not during phase IV. A low temperature (10°) during phase I delayed development in phase II while phase III was delayed after plants had been exposed to high temperature (30°) during phase I and II. The developmental rate during phase IV was determined only by the temperature during that phase. Functional relationships were developed for prediction of required time to complete each phase with the temperature before and during the phase as the independent variables. Optimum temperatures for development were calculated to 21.3°, 20.3°, 23.1°, and 19.1° for the four phases.

Introduction

Optimum temperatures for growth and development have been found to vary in many plant species as the plant develops (2,3,8,16,19,24). Blaauw et al. (2) defined organ initiation, preparation for elongation, and development from visible bud to flower as phases of tulip bulb development. The optimum temperatures for the three phases were 17-20°, 9°, and 20°C, respectively. Similar temperature schedules for optimum growth have been developed for several other bulbs and are widely used in commercial production (8).

Changes in optimum temperature during development have also been observed in chrysanthemum. Temperatures above 16° favored quick development prior to the visible bud stage while temperatures below 16°C hastened development after visible bud (3). A 10° temperature increased the number of leaves formed prior to flower initiation and delayed development compared to 16° (23). Low temperatures (5° or 10°) after buds were visible only caused small delays in time to flower. The reproductive development in chrysanthemum was delayed at temperatures above 20° after disbud, although the rate of dry weight gain increased (13).

The temperature effect on dry weight accumulation during plant development has been found to be affected by plant age. In snapdragon, the optimum temperature for dry

weight accumulation decreased with increasing plant age (16). A decreasing optimum temperature appeared to be related to the larger size of the plant rather than to physiological age. Similarly in tomato, the optimum temperature for dry weight accumulation decreased gradually from 25° to 17°C (24).

Sachs (19) studied temperature effects during germination, seedling growth, vegetative growth, flowering and fruiting on several species including *Zea mays*, *Curcubita pepo* and *Pisum sativum*. In the species studied, each phase had a minimum temperature below which no growth occurred, an optimum temperature where optimal growth occurred, and a maximum temperature above which no growth occurred. Temperatures either above or below the optimum temperature resulted in delayed growth. The shortest time to complete development could be determined when the optimum temperature requirements were known for each phase.

The temperature during one phase of development can influence how the plants respond to the environment during subsequent phases. Chrysanthemums grown at 21° under long days (LD) and shifted to 16° at start of short days (SD) flowered 7 days later than plants grown at 16° under LD and allowed to complete development under SD at 16°C (3). Temperatures of 5° or 10° compared to 16° during the LD period also delayed subsequent development under SD at 16°. An increased number of leaves accompanied the delayed development at 10° (23). Chrysanthemum cuttings taken from

stock plants at 27°, 21°, and 16° flowered at different times when allowed to develop at 10° from planting to flowering. The fastest development occurred for cuttings taken from stock plants kept at 21° (3). Poinsettia cuttings taken from stock plants at 12° or 15° initiated flowers faster when allowed to develop at 21° than cuttings taken from stock plants at temperatures above 15° (10).

Temperature is often manipulated to control growth in greenhouse production. Knowledge of the relationships between temperature and plant growth is necessary for appropriate temperature adjustments. This study was initiated to determine optimum temperatures for maximum chrysanthemum growth rates during 4 developmental phases and to determine the importance of preceding temperature exposure on subsequent growth rate.

Material and Methods

One thousand rooted cuttings of *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' (1) were planted individually in 10 cm pots on 31 Oct. 1985, and placed in a greenhouse with a temperature of 20°±1°C (24 hr average temperature). The natural daylength was extended to 16 hr day^{-1} with incandescent lamps. After 7 days, 810 plants were selected for uniformity, pinched and placed in greenhouse sections with heating set points of 20° day temperature (DT) and 16° night temperature (NT) or in greenhouse sections with heating setpoints of 10°, 15°, 20°, 25°, or 30° throughout the day (cooling setpoints were 2° higher than the heating setpoints). A SD photoperiod (10 hr light, 14 hr dark) was initiated and maintained through flowering by pulling an opaque curtain at 1800 HR and retracting at 0800 HR. The 20° DT and 16° NT treatment will be addressed as the 18° treatment for simplicity, since the average desired temperature was 17.7°.

Plants were grown in a commercial peat-lite medium (Michigan Peat Co.) and watered daily as required to maintain nonstressed conditions. Nutrition consisted of 14.3 mol m^{-3} (14.3 mM) N and 5.1 mol m^{-3} (5.1 mM) K at every watering using ammonium nitrate and potassium nitrate. A 15.6 mM daminozide solution was applied as a foliar spray 7 and 14 days after the start of SD (7).

Greenhouse temperatures were controlled using a

greenhouse climate control computer (Oglevee Computer Systems, Connelsville, Pa) and monitored by a datalogger (Digistrip III, Kaye Instruments Co., New Bedford, Conn.) using iron/constantan thermocouples. Photosynthetic photon flux (PPF) was monitored with a LI-190SB quantum sensor. Actual temperatures and PPF levels were measured every ten seconds and averaged to provide hourly mean values. Average temperatures and PPF levels incurred during the experiment in the different greenhouse sections were calculated from the hourly means and used in the analyses (Table 1).

The four defined developmental phases were: phase I - from start of SD to a 2 mm terminal flower bud (visible bud, VB), phase II - from VB to a 10 mm terminal flower bud (disbud, DB), phase III - from DB to a flower bud showing color, and phase IV - from color to when the outermost petals had reflexed to a horizontal position (flower). A plant was considered at a developmental stage when one shoot on the plant had developed the desired characteristics.

Ten preselected plants from each greenhouse section were moved to each of the other sections at VB, DB, and color. Each plant was moved individually when it had reached the chosen stage for the temperature shift. The plants remained in the second section (temperature) until flowering (plants were moved from, but not to the 20° DT 16°C NT section). The number of SD was recorded as each

developmental stage was reached.

Functional relationships were developed for prediction of time required to complete a phase of development with the temperatures before and during the phase as the independent variables. An optimum temperature for development would be expected to occur with delayed development as the temperature deviated from the optimum (3,19). This type of growth response can be described in multiple linear regression analysis by second order terms. Forward stepwise regression analysis (17) was therefore performed using linear and second order terms with significance levels for addition and deletion at 0.05. In an effort to improve the developed equations, higher order terms were also considered but rejected as addition of higher order terms only slightly improved the coefficients of determination, while decreasing the F values of the equations. Furthermore, they did not improve the prediction in any of the developmental phases. Surface graphs were created using the selected functions and the Surfer graphing program (11).

The experiment was repeated with SD starting on 11 March, 1986. Results and trends were similar in the two experiments. Greenhouse temperature control was better during the first experiment and therefore only those results are presented.

Results and Discussion

The time required to complete each phase and total time to flower for plants grown at the same temperature throughout development are presented in Table 2. More time was required to complete phase I and II than phase III and IV. Time required to complete phases I through IV averaged 40%, 35%, 10%, and 15% of total time to flower respectively, when plants were grown at constant temperatures throughout development. Development was fastest at 18° and 20°C during all 4 phases with slower development as the temperature either increased or decreased. Plants grown at 10° during phase I were delayed more than plants grown at 30°, while during phase IV, plants grown at 30° were delayed more than plants grown at 10°. In phase II and III the rate of development was similar at 10° and 30°. Preliminary experiments also showed that low temperature (below 20°) slowed development from SD to VB and that low temperature accelerated subsequent development (13).

Number of leaves below the flower was morphologically determined during the first developmental phase. Five more leaves were formed per shoot on plants grown at 30° compared to plants grown at 15°-20°C, indicating delayed morphological flower initiation (Table 2). Delay in morphological flower initiation also occurred on plants in the 10° treatment but to a lesser extent; 12 leaves were

formed on these plants. Although the leaf number was different, a similar number of days was required to complete phase I for plants at 10° and 30°.

Flowering in plants grown at the lowest (10°) and the highest (30°C) temperatures, was delayed ca. 60 days. The delay in development at 10° vs. 30° is likely due to different causes. Delayed flowering in chrysanthemum at low temperatures has been observed both in association with no change in leaf number and with an increase in leaf number (23). The higher number of leaves occurred under reduced PPF levels. Four to 5 more leaves were formed below the flower on plants grown under 2.9 mol $day^{-1}m^{-2}$ PPF compared with plants grown at 5.8 mol $day^{-1}m^{-2}$ PPF (4). Flower initiation and development in chrysanthemum are affected by interactions between PPF levels and temperatures (5,12,14,20,23). The low PPF level encountered during phase I in our experiment (3.9 mol $day^{-1}m^{-2}$, Table 1) is likely responsible for the increase in leaf number at 10°.

Increased leaf number and delayed development at high temperature is commonly referred to as "heat delay" in chrysanthemum. The increase in leaf number due to "heat delay" appears to be independent of prevailing PPF levels. Plants grown under 5.8 or 17.6 mol $day^{-1}m^{-2}$ PPF formed 5 or 4 more leaves at 26° than plants grown at 14°C (14). A heat tolerant cultivar formed 3 more leaves and a heat sensitive cultivar 4 more leaves at a PPF level of 21 mol $day^{-1}m^{-2}$ when the temperature was changed from 22° DT/18°

NT to 30° DT/26° NT (25).

Rate of leaf unfolding in several plant species has been found to increase linearly as temperature increases to some maximum rate (6,9,15,18,21). From data given by Cockshull et al. (6), the average leaf unfolding rate in chrysanthemum can be calculated to 0.20 leaves/day at 10° and 0.53 leaves/day at 20°C. Since the rate of leaf unfolding is slower at 10° than 20° (6), the delay at low temperatures during phase I is likely a combination of delayed chronological flower initiation and slower bud development (22). Even though plants growing in the 30° temperature produced more leaves, the length of the leaf unfolding period was likely similar to 20° due to the expected increased leaf unfolding rate at 30° (6). The delayed development during phase I at 30° was therefore attributed to delayed development after flower initiation rather than delayed chronological initiation (25).

The effect of temperatures early in development on developmental rate during later phases was studied by shifting plants at different stages to a second temperature. Time to flower when plants were shifted to a second temperature at the start of phase II, III or IV and allowed to flower in the second temperature is shown in Figure 1. No benefits in regard to time to flower were attained when plants were shifted from 18°C to a second temperature. In general, fastest development occurred when plants were shifted to 15° or 20° from 15°, 18° or 20°.

Shifting plants at VB from a less favorable temperature (e.g. 10° or 30°) to 15° or 20° resulted in faster flowering than shifts at DB or color. A transfer of plants from 15°, 18° or 20° to a second temperature of 10°, 25° or 30° resulted in delayed development compared to plants maintained at 15°, 18° or 20°.

The effect of prior temperature exposure on time required to complete phase II, III and IV is presented in Table 3. The number of days required to complete the development from VB to DB (phase II) varied from 25 days at 20° to 69 days at 30°C. A 10° temperature in phase I resulted in slower development in phase II for plants shifted to a warmer temperature compared to plants grown continually at constant temperatures above 10° during phase I and II. Temperatures of 15° and 30° in phase I also delayed development when combined with 25° or 30° in phase II. A low prior temperature (10°) delayed development in phase II while phase III was delayed after plants had been exposed to high temperature (30°). There was a trend for faster development at lower prevailing temperature independent of temperature exposure prior to phase IV.

Functional relationships between time of a phase and temperature before and during the phase were developed (Table 4). Only the direct effect to temperature was studied during phase I since all plants were grown at constant 20°C prior to the start of the experiment. The developmental time response to temperature during phase I

is shown in Figure 2. Figure 3 illustrates the observed effects of temperature on time of development during phase II, III and IV. Figure 3a clearly shows that the development during phase II was influenced both by temperature during phase II and phase I. Low temperatures during phase I delayed development in phase II more than high temperatures. In contrast to development in phase II, developmental rate during phase III was not greatly influenced by low temperature prior to DB (start of phase III). High temperature prior to phase III however delayed development under all temperatures during phase III (Table 3, Figure 3b). Temperature exposure up to color had only a small effect on time of development during phase IV (Table 3, Figure 3c). The response surface to temperature during phase IV had a valley at intermediate temperatures and development was delayed as the temperatures increased or decreased.

Optimum temperatures for fastest development during phase I was calculated to 21.3°C using the functional relationship given in Table 4. The optimum temperatures for phase II, III, and IV were calculated to 20.3°, 23.1° and 19.1° when the calculated optimum temperature for earlier phases were used as the previous temperatures. Similar lengths of development were predicted for a range of temperatures around the calculated optimum. The developed function for phase I predicted 32 days as the fastest rate of development to VB at 21.3°. Predicting

time of development during phase I to within 1 day of the minimum 32 days was possible with temperatures from 21.3° ± 2.5°. Predicting time of development during phase II, III and IV within 1 day of the minimum (21, 6 and 14 days respectively) was possible with temperatures of 20.3° ± 3.2°, 23.1° ± 5.9° and 19.1° ± 4.3°.

The range of optimum temperatures for each phase provide flexibility in greenhouse temperature control. Temperatures within the range will result in similar number of days to complete development while increased or decreased temperatures to outside the optimum range only will delay development.

Optimum temperatures for development have been found to decrease with plant age (3,16,24). Preliminary experiments showed that DT and NT above 20°C accelerated development until VB in chrysanthemum, but slowed development during later phases (13). Optimum temperatures for development in this study decreased except for the phase from DB to color. The third phase was shortest (10% of time required for flowering) and had the widest range of temperatures displaying developmental rates within 1 day of the optimum rate. One specific optimum temperature for phase III may therefore be unjustified since there appear to be a plateau at the optimum.

Cathey (3) found development in chrysanthemum occurs faster at temperatures above 16° prior to VB and at temperatures below 16°C after VB. We found a similar

lowering of the optimum temperature after VB but not to the extent observed by Cathey (3). A regression analysis on time required to complete the development from VB to flower (phase II, III and IV) as a function of temperature gave an equation with an optimum temperature of 19.3°. The change in optimum temperature for the development from SD to VB and from VB to flower was 2° (from 21.3° to 19.3°). Although the optimum temperature decreased, it was still above 16°. The difference in optimum temperatures found here and by Cathey (3) could be due to differences in cultivars, environmental conditions before SD or irradiance conditions.

The results presented on rate of development indicate that chrysanthemum experiences temperature conditioning. Rate of development during phase II and III at a specific temperature varied depending on what the temperature had been prior to the studied phase (Figure 3a,b). Previous unfavorable temperatures for development such as 10° or 30°C from SD to VB cannot be negated in phase II by maintaining an optimum temperature. The effect of the less optimum temperature during phase I is carried over to phase II and will cause delayed development even at an optimum temperature for phase II. Similarly, the effects of an unfavorable temperature during phase I and II was carried over to phase III. During phase IV the plants exhibited less temperature conditioning and time required to complete development was determined by the temperature of that

phase.

Temperature requirements with a minimum, an optimum, and a maximum temperature for the different phases of growth and development as hypothesized by Sachs (19) can be modified by previous temperature exposure. In chrysanthemum, temperature conditioning alters the developmental rate response to later temperatures. Phasic development in chrysanthemum can therefore only be predicted if the preceding temperature conditions are accounted for.

Literature Cited

1. Anderson, N.O. 1987. Reclassification of the genus *Chrysanthemum* L. HortScience 22:313.

2. Blaauw, A.H., I. Luyten, and A.M. Hartsema. 1936. The limits of flower formation and the growth of iris bulbs II. Proc. Konikle Ned. Akad. Wetenschap 39:928-936, 1074-1078.

3. Cathey, H.M. 1955. A study of the effects of light and temperature upon the flowering of *Chrysanthemum morifolium* and *Tulipa gesneriana*. Ph.D. Thesis, Cornell University, Ithaca.

4. Cockshull, K.E. and A.P. Hughes. 1971. The effect of light intensity at different stages in the flower initiation and development of *Chrysanthemum morifolium*. Ann. Bot. 35:915-926.

5. Cockshull, K.E. and A.P. Hughes. 1972. Flower formation in *Chrysanthemum morifolium*: the influence of light level. J. Hort. Sci. 47:113-127.

6. Cockshull, K.E., D.W. Hand, and F.A. Langton. 1981. The effect of day and night temperature on flower initiation and development in chrysanthemum. Acta Horticulturae 125:101-110.

7. Crater, G.D. 1980. Pot mums, p. 261-285. In: R.A. Larson (ed.). Introduction to floriculture. Academic Press, New York.

8. De Hertogh, A.A. 1985. Holland bulb forcer's guide. 3rd ed. The International Flower-Bulb Center, Hillegom, The Netherlands.

9. Friend, D.J.C., V.A. Helson, and J.E. Fisher. 1962. Leaf growth in marquis wheat, as regulated by temperature, light intensity, and daylength. Can. J. Bot. 40:1299-1311.

10. Gislerød, H.R. and B. Litlere. 1976. Temperature effects on poinsettia (*Euphorbia pulcherrima* Willd.) under long day conditions. Acta Hort. 64:205-209

11. Golden Software, Inc. 1987. Surfer, version 3.00. Golden, Colorado.

12. Hughes, A.P. and K.E. Cockshull. 1971. The effect of light intensity and carbon dioxide concentration on the growth of *Chrysanthemum morifolium* cv. Bright Golden Anne. Ann. Bot. 35:899-914.

13. Karlsson, M.G., R.D. Heins, and M.P. Pritts. 1985. Influence of temperature and photosynthetic active radiation during different developmental phases of *Chrysanthemum morifolium* 'Bright Golden Anne'. HortScience 20:111. (Abstr.)

14. Karlsson, M.G. and R.D. Heins. 1986. Response surface analysis of flowering in chrysanthemum 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253-259.

15. Karlsson, M.G., R.D. Heins, and J.E. Erwin. 1988. Quantifying temperature controlled leaf unfolding rates in *Lilium longiflorum* Thunb. 'Nellie White'. J. Amer. Soc. Hort. Sci. 113:xxx-xxx.

16. Miller, R.O. 1962. Variations in optimum temperatures of snapdragons depending on plant size. Proc. Amer. Soc. Hort. Sci. 81:535-543.

17. Nie, N.E., C.H. Hull, J.G. Jenkins, K. Steinbrenner, and D.H. Bent. 1975. Statistical package for the social sciences (SPSS). 2nd edition. McGraw-Hill Inc., New York.

18. Rawson, H.M. and J.H. Hindmarsh. 1982. Effects of temperature on leaf expansion in sunflower. Aust. J. Plant Physiol. 9:209-219.

19. Sachs, J. 1860. Physiologische Untersuchungen über die Abhängigkeit der Keimung von der Temperatur. Jb. Wiss. Botan. 2:338-377.

20. Schwabe, W.W. 1952. Effects of temperature, day length and light intensity in the control of flowering in the chrysanthemum. Proc. 13th Int. Hort. Congr. 2:952-960.

21. Tollenaar, M., T.B. Daynard, and R.B. Hunter. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Science 19:363-366.

22. Van Ruiten, J.E.M and J. De Jong. 1984. Speed of flower induction in *Chrysanthemum morifolium* depends on cultivar and temperature. Scientia Hortic. 23:287-294.

23. Vince, D. 1960. Low temperature effects on the flowering of *Chrysanthemum morifolium* Ramat. J. Hort. Sci. 35:161-175.

24. Went, F.W. 1957. Some theoretical aspects of effects of temperature on plants, 163-174. In: F.H. Johnson (ed.). Influence of temperature on biological systems. Waverly Press, Baltimore.

25. Whealy, C.A., T.A. Nell, J.E. Barrett, and R.A. Larson. 1987. High temperature effects on growth and floral development of chrysanthemum. J. Amer. Soc. Hort. Sci. 112:464-468.

Table 1. Actual temperature and photosynthetic photon flux from start of short days (SD) to visible bud (VB), from VB to removal of lateral flower buds (disbud, DB), from DB to buds showing first color (C), from C to flower (FLW), and from SD to FLW.

Setpoint Temperature (°C)	Phase				
	SD to VB	VB to DB	DB to C	C to FLW	SD to FLW
	Actual average temperature (°C)[y]				
10	11.0 ± 0.1	11.4 ± 0.2	11.4 ± 0.2	10.5 ± 0.5	11.1 ± 0.1
15	14.6 ± 0.2	15.9 ± 0.1	17.1 ± 0.3	16.8 ± 0.2	15.6 ± 0.2
18[z]	18.5 ± 0.1	18.7 ± 0.1	18.9 ± 0.5	19.6 ± 0.4	18.8 ± 0.1
20	20.1 ± 0.1	20.4 ± 0.2	19.9 ± 0.6	21.0 ± 0.2	20.3 ± 0.1
25	26.3 ± 0.3	27.7 ± 0.3	25.9 ± 0.1	25.3 ± 0.1	26.5 ± 0.2
30	31.2 ± 0.2	30.7 ± 0.3	32.7 ± 0.2	31.1 ± 0.2	31.1 ± 0.2
	Photosynthetic photon flux (mol $day^{-1}m^{-2}$)[y]				
10	3.9 ± 0.3	6.2 ± 0.4	11.7 ± 1.1	11.5 ± 1.6	6.6 ± 0.4
15	3.4 ± 0.3	5.3 ± 0.4	7.0 ± 1.0	5.3 ± 0.8	4.6 ± 0.3
18[z]	3.4 ± 0.4	5.3 ± 0.4	8.0 ± 0.3	6.5 ± 0.8	4.5 ± 0.3
20	3.4 ± 0.4	4.3 ± 0.3	7.8 ± 0.3	6.4 ± 0.8	4.5 ± 0.3
25	3.4 ± 0.3	5.4 ± 0.4	5.7 ± 1.0	6.0 ± 0.9	4.8 ± 0.3
30	3.8 ± 0.3	6.0 ± 0.4	10.5 ± 1.2	11.5 ± 1.3	6.6 ± 0.4

[z]Day temperature at 20° and night temperature at 16°C.
[y]± SE.

Table 2. Time of development from start of short days (SD) to visible bud (VB), from VB to removal of lateral flower buds (disbud, DB), from DB to buds showing first color (C), from C to flower (FLW), from SD to FLW, and leaf number per shoot for *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' grown under different constant temperatures.

Temperature (°C)	Days of Development					Leaf number per shoot
	SD to VB	VB to DB	DB to C	C to FLW	SD to FLW	
10	52 d	53 c	16 c	17 b	138 d	12 b
15	38 b	27 ab	7 a	14 a	86 b	10 a
18[z]	34 a	25 a	6 a	12 a	77 a	10 a
20	33 a	25 a	6 a	14 a	78 a	10 a
25	37 b	31 b	11 b	17 b	96 c	12 b
30	48 c	52 c	15 c	22 c	137 d	15 c

[z]Day temperature at 20° and night temperature at 16°C.
Mean separation within columns by Duncan's multiple range test, 0.1% level.

Table 3. Influence of temperature before and during a particular phase of development in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'. The plants were held at the first temperature from start of short days until start of the second phase.

Temperature		Phases[z]		
1st	2nd	VB to DB (days)	DB to C (days)	C to FLW (days)
10	10	53 b	16 b	17 a
15	10	34 a	12 a	17 a
18[y]	10	32 a	10 a	16 a
20	10	32 a	11 a	18 ab
25	10	30 a	15 b	20 b
30	10	33 a	20 c	20 b
10	15	39 b	10 b	15 ab
15	15	27 a	7 a	14 ab
18[y]	15	28 a	7 a	13 a
20	15	27 a	8 a	14 ab
25	15	25 a	11 b	16 bc
30	15	27 a	14 c	18 c
10	20	40 b	9 b	13 a
15	20	29 a	7 a	13 a
18[y]	20	25 a	6 a	13 a
20	20	25 a	6 a	14 ab
25	20	25 a	10 b	15 b
30	20	27 a	13 c	15 b
10	25	48 c	10 b	14 a
15	25	38 b	8 a	14 a
18[y]	25	31 a	7 a	16 ab
20	25	32 a	8 a	15 ab
25	25	31 a	11 b	17 b
30	25	33 a	14 c	16 ab
10	30	69 d	11 b	19 a
15	30	47 b	9 a	23 b
18[y]	30	41 a	8 a	23 b
20	30	42 a	9 a	22 ab
25	30	41 a	11 b	23 b
30	30	52 c	15 c	22 ab

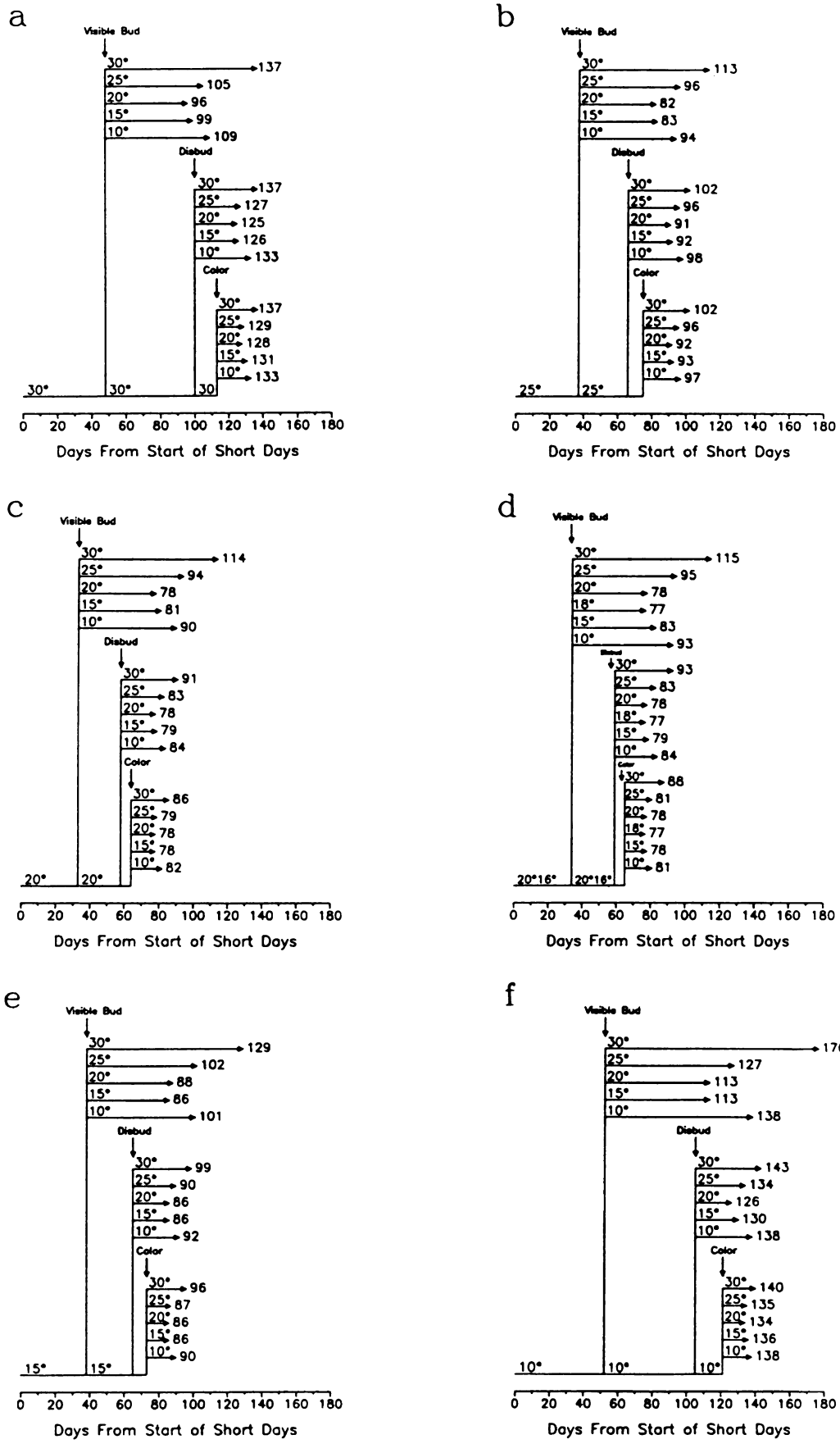
[z] VB=visible bud, DB=disbud, C=color, FLW=flower.
[y] Day temperature at 20° and night temperature at 16°C.
Mean separation within columns with the same 2nd temperature by Duncan's multiple range test, 0.1% level.

Table 4. Regression coefficients for functions relating temperature with time of development from start of short day (SD) to visible bud (VB), from VB to disbud (DB), from DB to buds showing color (C), and from C to flower (FLW) in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

Regression[z] variable	Time of Development (days)			
	SD to VB	VB to DB	DB to C	C to FLW
Constant	107.6160	105.6318	44.6060	30.6927
T_1	-7.0448	-2.0318	-1.9315	-0.2680
T_2	---	-3.2967	-1.8386	-1.6791
$(T_1)^2$	0.1650	0.0305	0.0500	0.0279
$(T_2)^2$	---	0.1337	0.0403	0.0291
$T_1 \times T_2$	---	-0.2039	0.0054	---
$T_1 \times (T_2)^2$	---	---	-0.0001	0.0017
$(T_1)^2 \times T_2$	---	0.0049	---	-0.0018
r^2	0.92	0.82	0.82	0.75

[z] T_1=Temperature from start of SD to beginning of the considered phase, T_2=Temperature during the considered phase.

Figure 1. Time to flower for *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' grown at an initial temperature and shifted to a second temperature at visible bud, disbud or color and allowed to complete the development in the second temperature. Initial temperature at a) 30°, b) 25°, c) 20°, d) 20° day temperature and 16° night temperature, e) 15°, and f) 10°C.


a
Visible Bud
30° 137
25° 105
20° 96
15° 99
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Disbud
30° 137
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20° 125
15° 126
10° 133
Color
30° 137
25° 129
20° 128
15° 131
10° 133
30° 30° 30
0 20 40 60 80 100 120 140 160 180
Days From Start of Short Days
b
Visible Bud
30° 113
25° 96
20° 82
15° 83
10° 94
Disbud
30° 102
25° 96
20° 91
15° 92
10° 98
Color
30° 102
25° 96
20° 92
15° 93
10° 97
25° 25°
0 20 40 60 80 100 120 140 160 180
Days From Start of Short Days
c
Visible Bud
30° 114
25° 94
20° 78
15° 81
10° 90
Disbud
30° 91
25° 83
20° 78
15° 79
10° 84
Color
30° 86
25° 79
20° 78
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0 20 40 60 80 100 120 140 160 180
Days From Start of Short Days
d
Visible Bud
30° 115
25° 95
20° 78
18° 77
15° 83
10° 93
30° 93
25° 83
20° 78
18° 77
15° 79
10° 84
30° 88
25° 81
20° 78
18° 77
15° 78
10° 81
20°16° 20°16°
0 20 40 60 80 100 120 140 160 180
Days From Start of Short Days
e
Visible Bud
30° 129
25° 102
20° 88
15° 86
10° 101
Disbud
30° 99
25° 90
20° 86
15° 86
10° 92
Color
30° 96
25° 87
20° 86
15° 86
10° 90
15° 15°
0 20 40 60 80 100 120 140 160 180
Days From Start of Short Days
f
Visible Bud
30° 176
25° 127
20° 113
15° 113
10° 138
Disbud
30° 143
25° 134
20° 126
15° 130
10° 138
Color
30° 140
25° 135
20° 134
15° 136
10° 138
10° 10° 10°
0 20 40 60 80 100 120 140 160 180
Days From Start of Short Days

Figure 2. Effect of temperature on rate of development from start of short days (SD) to visible bud (VB) stage in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

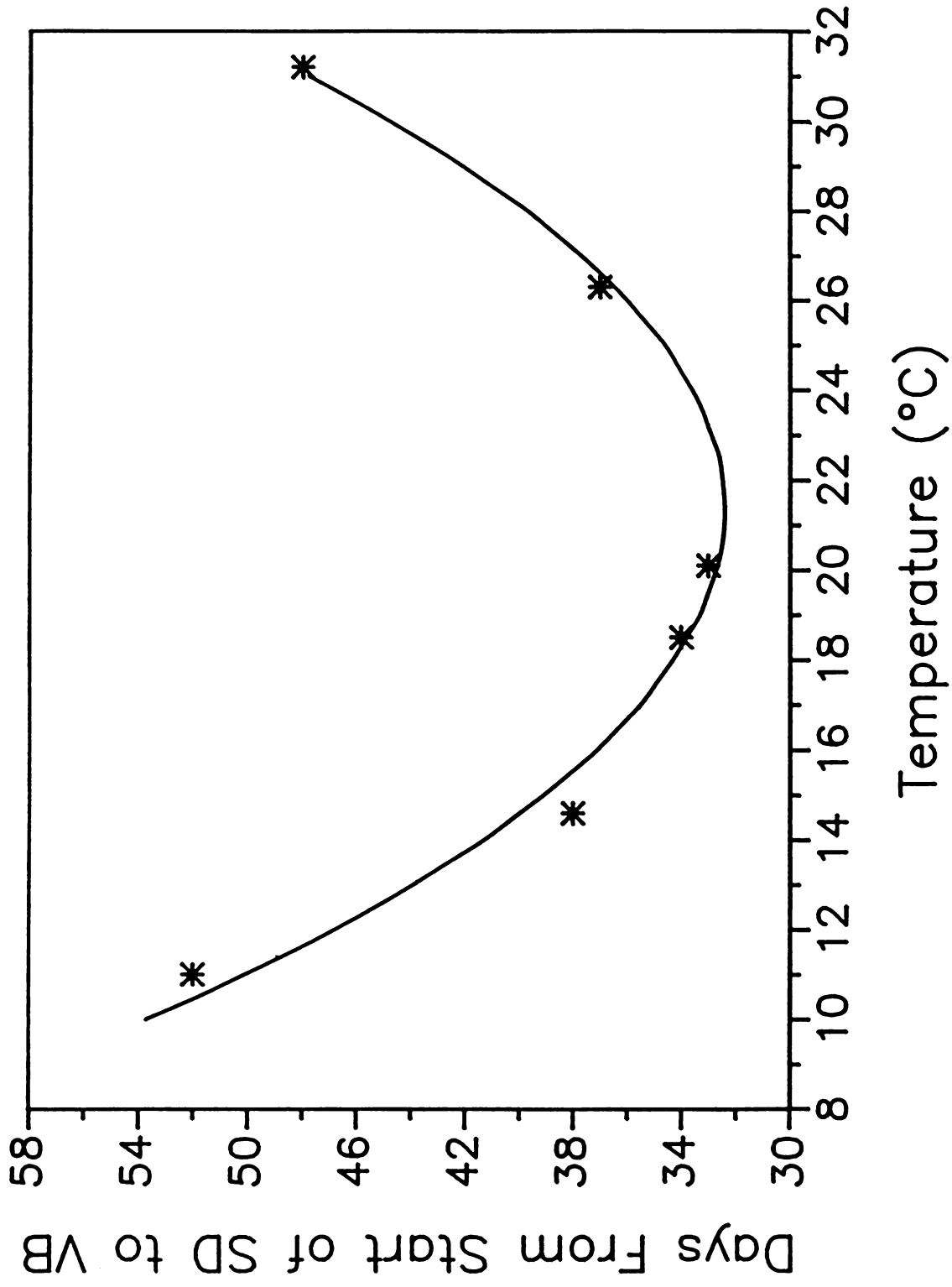

Days From Start of SD to VB
58
54
50
46
42
38
34
30
8
10
12
14
16
18
20
22
24
26
28
30
32
Temperature (°C)

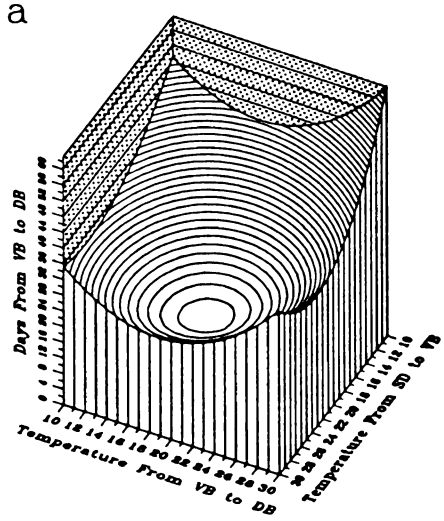
Figure 3. Effect of plant exposure to a temperature early in development on time required to complete subsequent phases of development in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

a) Time to complete development from visible bud (VB) to disbud (DB) as affected by the temperature from VB to DB and the temperature from start of short days (SD) to VB.

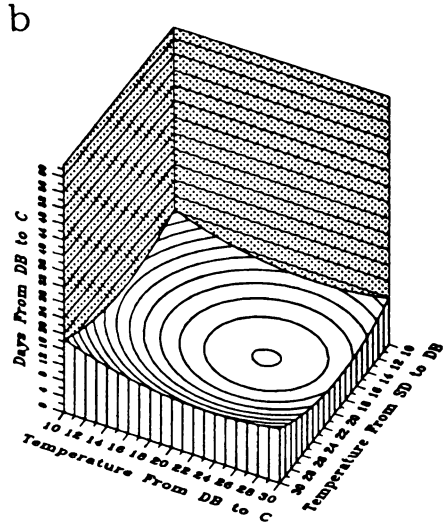
b) Time to complete development from DB to the flower first showing color (C) as affected by the temperature from DB to C and the temperature from SD to DB.

c) Time to complete development from C to flowering (FLW) as affected by the temperature from C to FLW and the temperature from SD to C.

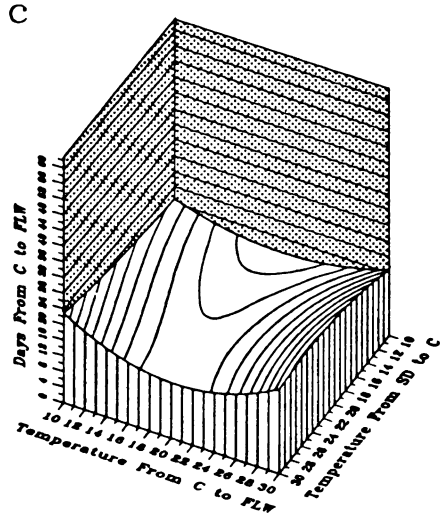
a


Days From VB to DB
Temperature From VB to DB
Temperature From SD to VB

b


Days From DB to C
Temperature From DB to C
Temperature From SD to DB

c


Days From C to FLW
Temperature From C to FLW
Temperature From SD to C

SECTION IV

IRRADIANCE AND TEMPERATURE EFFECTS ON TIME OF DEVELOPMENT AND FLOWER SIZE IN CHRYSANTHEMUM

IRRADIANCE AND TEMPERATURE EFFECTS ON TIME OF DEVELOPMENT AND FLOWER SIZE IN CHRYSANTHEMUM

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ABSTRACT

Karlsson, M.G. and Heins, R.D., _____. Irradiance and temperature effects on time of development and flower size in chrysanthemum. *Scientia Hortic.*,_____.

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. 'Bright Golden Anne'). Flower initiation did not occur after 100 short days at low PPF levels (1.8 mol $day^{-1}m^{-2}$) in combination with high DT or NT (30°C). Number of days to flower decreased rapidly from 90 to 70 days as PPF increased from 1.8 to 11.7 mol $day^{-1}m^{-2}$ at 20°C. Further increasing PPF to 21.6 mol $day^{-1}m^{-2}$ resulted in only a small (10 days) decrease in flowering time. The optimum DT and NT for fastest development were estimated from a function predicting time to flower. The optimum DT increased from 17° to 18°C and the optimum NT decreased from 18° to 16°C as the PPF level increased from 5 to 20 mol $day^{-1}m^{-2}$. Total plant flower area increased linearly as PPF increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at a constant 20°C. The optimum DT/NT combination for largest flower size was estimated from a function predicting flower size. The optimum increased from 19°/16° to 20°/17°C as the PPF level increased from 5 to 20 mol $day^{-1}m^{-2}$.

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

INTRODUCTION

Knowledge about time requirements for plant development is necessary to plan and schedule greenhouse production. Chrysanthemum cultivars are classified into response groups which indicate the expected number of days from start of short days to flower (Machin and Scope, 1978). The rate of development can, however, be modified by the irradiance and temperature conditions plants are exposed to during development (Cathey, 1955; Karlsson, 1984) and production schedules must be varied as the season change. The quantitative effect of the environment on plant development must be known before the progression of growth can be corrected by climatic adjustments and production planning become more precise.

Flower size is an important determinant of quality in chrysanthemum. Many plants adapt to a wide range of environmental conditions by changes in dry weight partitioning patterns and morphological characteristics (Hickman, 1975; Thompson and Stewart, 1981). The flower size of chrysanthemum has been found to be largely determined by how well the plant adapts to the environment (Cathey, 1955; Karlsson, 1984). Plant plasticity allows plant production for different market demands and quality control in chrysanthemum production to be accomplished by adjustments in the environment.

The effects of irradiance and temperature conditions

on rate of chrysanthemum development and flower size were studied with the objective to quantify these responses to day temperature (DT), night temperature (NT) and photosynthetic photon flux (PPF).

MATERIALS AND METHODS

Rooted cuttings of *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' (Anderson, 1987) were planted individually in 10 cm pots filled with a commercial peat-lite medium (Michigan Peat Co.) and placed in growth chambers. Long day conditions were kept 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 short day (SD) photoperiod was initiated (10 h light, 14 h dark), and plants were pinched to 6 nodes and placed under appropriate treatment combinations (Table I) with the thermoperiod paralleling 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 per plant. The uppermost shoot was considered shoot 1 and the basal, shoot 3. Lateral flower buds were removed when they were large enough to safely be detached without damaging the terminal flower bud.

The PPF was provided by cool-white fluorescent lamps (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 $\pm$ 1°C from the setpoint and

PPF varied ± 10% over the canopy.

Plants were irrigated 1 to 3 times daily, depending on plant size and environmental conditions. Nutritional program 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 water pH with nitric acid.

A central composite statistical design was used to select treatment combinations (Gardiner et al., 1967; Armitage et al., 1981). The PPF levels ranged from 1.8 to 21.6 mol $day^{-1}m^{-2}$ (50 to 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 endpoints of the experimental ranges, were necessary for a better understanding of the environmental effects (Karlsson and Heins, 1986). The 15 treatments required in the statistical design were therefore supplemented with 10 additional treatments to give a total of 25 treatments (Table I).

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 done on data from the two uppermost shoots and the analysis of flower size was done on total flower area per

plant. Flower area was calculated assuming each flower had a circular shape. Treatments with plants not initiating flowers were assigned a value of 200 SD for the developmental time regression analysis and a value of 0 cm^2 for the flower size regression analysis. Days to flower, flower area and PPF were natural log transformed prior to statistical analysis.

Regression analysis was initially performed on time to flower and flower size using the subroutine 'BMDP9R, all possible subsets regression' (Dixon et al., 1985) with linear, quadratic and interactions terms of DT, NT, PPF and average daily temperature (ADT) as independent variables. Equation selection was based on the Mallows' C_p statistic (Draper and Smith, 1981), significance of included independent variables, r^2 and F values of the equations and the adequacy of prediction. All variables included in the final equations were significant at the 5% level as indicated by a two-tailed t-test. Isopleth graphs were created using the developed functions and the Surfer graphing package (Golden Software, 1987).

RESULTS AND DISCUSSIONS

Environmental conditions with high DT or NT combined with low PPF levels prevented flower initiation. No flower buds were present after 100 SD when the PPF was 1.8 mol $day^{-1}m^{-2}$ and either the DT or the NT was 30°C (Table I). The unfavorable effects of temperature on flower initiation were overcome by increasing PPF levels. Flowering occurred on plants grown at 21.6 mol $day^{-1}m^{-2}$ after ca. 80 SD when the DT was 30° and NT 10°C and after 90 SD when the DT was 10° and NT 30°C. Flowering also occurred on plants grown with both DT and NT at 30°C and 21.1 mol $day^{-1}m^{-2}$ but only after 140 days.

Time required to complete development from start of SD to flower decreased with an increasing PPF level. Flowering time decreased more than 20 days when the PPF was increased from 1.8 to 5.8 mol $day^{-1}m^{-2}$ at a 20°C constant temperature (Table I). Further increases in the PPF level from 5.8 to 21.6 mol $day^{-1}m^{-2}$ at 20°C only slightly accelerated development (Figure 1). Seasonal changes in time required for flowering was correlated with the variations in natural PPF levels (Schwabe, 1953; Vince, 1960; Mason and Vince, 1962; Cockshull and Hughes, 1972; Hicklenton, 1984; Hughes and Tsujita, 1981). These results confirm observations that supplemental irradiation has a greater effect on time to flower under low natural irradiance conditions than high natural irradiance levels. Supplementing the natural

irradiance with 6.8 mol $day^{-1}m^{-2}$ hasten development 6 and 9 days under fall conditions for the cultivars 'Yellow Paragon' and 'Copper Anne' but had no significant effect on time to flower during spring conditions (Hicklenton and McRae, 1984). The timing of supplemental irradiation is also critical as increasing the PPF level only for a limited time during early reproductive growth resulted in faster flowering (Stefanis and Langhans, 1982; Hicklenton, 1984; Carpenter, 1975; Cockshull and Hughes, 1972).

Temperature determined days to flower at a specific PPF level. An increase in both DT and NT from 14° to 26°C at 5.8 mol $day^{-1}m^{-2}$ delayed flowering more than 30 days (Table I). Time to flower was delayed 20 days at 17.6 mol $day^{-1}m^{-2}$ when the temperature was increased from 14° to 26°C. Predicted days to flower as both DT and NT increased from 10° to 30°C at 5, 10 and 15 mol $day^{-1}m^{-2}$ are shown in Figure 2. A temperature deviation from the optimum at a low PPF levels resulted in a greater delay than a similar deviation at high PPF levels. These results show that temperature control is more critical under reduced irradiance conditions.

The time required to flower from the start of SD also increased as either DT or NT deviated from the optimum temperature combination. An increase in either DT or NT from 20°C resulted in slower development at all PPF levels (Table I). Figure 3 illustrates isopleth plots of time to flower at 3 PPF levels (5, 10, and 15 mol $day^{-1}m^{-2}$) and DT

and NT from 10° to 30°C. The range of DT and NT combinations which result in flowering within 75 days was larger at a high PPF level. This again indicates, that precise temperature control is more important at low PPF levels for fastest development than at high PPF levels (Figure 3). Largest delay in development occurred when DT and NT increased simultaneously (Figure 3).

The optimum DT and NT combination for fastest development did not vary much among PPF levels (Figure 3). The developed function predicted fastest development to occur at 17°, 18° and 18°C DT in combination with NT of 18°, 17° and 17°C as the PPF level increased from 5 to 10 to 15 mol $day^{-1}m^{-2}$. Cathey (1955) reported the optimum temperature for flower initiation and development in chrysanthemum was 16°C. A temperature combination of 22° DT and 18°C NT resulted in the least number of days to flower in another study with chrysanthemums (Bonaminio and Larson, 1978). The small differences in observed optimum temperature for development could be due to differences in cultivars, environmental conditions during long day treatment and cultural practices.

The PPF level was an important determinant of flower size (Table I). Total plant flower area increased from 111 to 285 cm^2 as the PPF level increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at a constant 20°C. This corresponds to an average flower diameter of 7 cm at the lower PPF level and 11 cm at 21.6 mol $day^{-1}m^{-2}$. The plants grown at 5.8 mol

$day^{-1}m^{-2}$ had smaller flowers than plants grown at the same temperature combinations at 17.6 mol $day^{-1}m^{-2}$.

Flower area decreased as the temperature deviated from an optimum temperature at a specific PPF level. 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 $day^{-1}m^{-2}$ as DT and NT increased from 14° to 26°C (Table I). Flower area also decreased when either DT or NT was increased individually from 14° to 26°C. The flowers formed at a constant 30°C and a PPF level of 21.6 mol $day^{-1}m^{-2}$ were small (2 cm in diameter). Plants grown at 30°C and 1.8 mol $day^{-1}m^{-2}$ did not initiate flowers after 100 SD. Figure 4 shows the predicted effect of temperature on flower area with equal DT and NT. Flower area increased to a maximum as the temperature increased from 10° to 17°, 18°, or 19°C at 5, 10 or 15 mol $day^{-1}m^{-2}$ and then decreased rapidly as the temperature was further increased to 30°C.

Maximum flower size occurred at an optimum combination of DT and NT. Figure 5 illustrates the effects of DT and NT on total plant flower area as predicted by the selected functional relationship at 5, 10 and 15 mol $day^{-1}m^{-2}$. Flower area decreased faster when both DT and NT increased simultaneously from the optimum compared to an increase in only DT or NT. A DT below the optimum resulted in a larger decrease in flower size than a NT below the optimum. The optimum DT and NT combinations for flower size were calculated to 19°/16°C at 5 mol $day^{-1}m^{-2}$, 20°/16°C at 10

mol $day^{-1}m^{-2}$, and 20°/16°C NT at 15 mol $day^{-1}m^{-2}$. Under 15 mol $day^{-1}m^{-2}$, the flower area increased more rapidly as the temperature approached the optimum temperature combination compared to similar temperature changes under 10 and 5 mol $day^{-1}m^{-2}$.

Cockshull and Hughes (1971) found the number of florets initiated in the flower to be determined by the PPF level. At 17 mol $day^{-1}m^{-2}$, 300 florets were initiated per flower while only ca. 200 were initiated at a PPF level of 1.5 mol $day^{-1}m^{-2}$. The larger flower size under high PPF levels in this study may be a result of increased floret number. Florets per flower, however, were not determined in this study. Temperature did not affect floret number but was an important factor for floret length in studies by Vince (1960). Under a given PPF level the largest flowers can be expected to develop under temperature combinations allowing for optimal floret growth.

PPF was an important factor in determining both number of SD required for flowering and flower size. The rate of development and flower size increased as the PPF level increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$. At a specific PPF level, either decreasing or increasing DT and NT from an optimum combination resulted in delayed development and smaller flowers.

ACKNOWLEDGMENTS

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REFERENCES

Anderson, N.O., 1987. Reclassification of the genus *Chrysanthemum* L. HortScience 22:313.

Armitage, A.M., Carlson, W.H. and Cress, C.E., 1981. Determination of flowering time and vegetative habit of *Tagetes patula* through response surface techniques. J. Amer. Soc. Hort. Sci. 106:632-638.

Bonaminio, V.P. and Larson, R.A., 1980. Influence of reduced night temperatures on growth and flowering of 'May Shoesmith' chrysanthemums. J. Amer. Soc. Hort. Sci. 103:752-756.

Carpenter, W.J., 1975. High intensity lighting of pot chrysanthemum. Florists' Review 156(4034):19-20,59-60).

Cathey, H.M., 1955. A study of the effects of light and temperature upon the flowering of *Chrysanthemum morifolium* and *Tulipa gesneriana*. Ph. D. Thesis, Cornell University, Ithaca.

Crater, G.D., 1980. Pot mums, p. 261-285. In: R.A. Larson (editor), Introduction to floriculture. Academic Press, New York.

Cockshull, K.E. and Hughes, A.P., 1971. The effect of light intensity at different stages in flower initiation and development of *Chrysanthemum morifolium*. Ann. Bot. 35:915-926.

Cockshull, K.E. and Hughes, A.P., 1972. Flower formation in *Chrysanthemum morifolium*: the influence of light level. J.Hort. Sci. 47:113-127.

Dixon, W.J., Brown, M.B., Engelman, L., Frane, J.W., Hill, M.A., Jennrich, R.I. and Toporek, J.D., 1985. BMDP Statistical software, 1985 printing. University of California Press, Los Angeles.

Draper, N.R. and Smith, H., 1981. Applied regression analysis. 2nd edition. John Wiley & Sons, New York.

Gardiner, D.A., Cragle R.G. and Chandler, P.T., 1967. The response surface method as a biological research tool. Tenn. Agr. Expt. Sta. Bul. 429:25-40.

Golden Software, Inc. 1987. Surfer, version 3.00. Golden, Colorado

Hicklenton, P.R. 1984. Response of pot chrysanthemum to supplemental irradiance during rooting, long day, and short day production stages. J. Amer. Soc. Hort. Sci. 109:468-472.

Hicklenton, P.R. and McRae, K.B., 1984. Vegetative growth and flowering of pot chrysanthemums in response to supplemental HPS radiation and split-night temperatures. J.Amer. Soc. Hort.Sci. 109:30-33.

Hickman, J.C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). Jour. Ecol. 63:689-701.

Hughes, B.R. and Tsujita, M.J., 1981. The effect of supplemental HPS lighting during propagation on rooting and quality of 'White Marble' cut chrysanthemum. J. Amer. Soc. Hort. Sci. 106:613-615.

Karlsson, M.G., 1984. Influence of temperature and irradiance on growth and development of *Chrysanthemum morifolium* 'Bright Golden Anne'. M.S. Thesis, Michigan State University, E. Lansing.

Karlsson, M.G. and Heins, R.D., 1986. Response surface analysis of flowering in chrysanthemum 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253-259.

Machin, B. and Scopes, N., 1978. Chrysanthemums, year-round growing. Blandford Press Ltd. Poole, Dorset.

Mason, D.T. and Vince, D., 1962. The pattern of growth in chrysanthemum as a response to changing seasonal environment. Proc. 15th Int. Hort Congr. 1958, 2:374-383.

Schwabe, W.W., 1953. Effects of temperature, daylength and light intensity in the control of flowering in the chrysanthemum. Rep. 13th Int. Hort. Congr. 1952, 2:952-960.

Stefanis, J.P. and Langhans, R.W., 1982. Quantum flux density studies of chrysanthemum in a controlled environment with high-pressure sodium lamps. II. Long day and short day studies. J. Amer. Soc. Hort. Sci. 107:461-464.

Thompson, K. and Stewart, A.J.A., 1981. The measurement and meaning of reproductive effort in plants. Am. Nat. 117:205-211.

Vince, D., 1960. low temperature effects on the flowering of *Chrysanthemum morifolium* Ramat. J. Hort. Sci. 35:161-175.

Table I. Time required for flower development, flower diameter and total flower area per plant as affected by photosynthetic photon flux (PPF), day temperature and night temperature in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

Environment			Aver.	Days to	Aver. time to flw (days)			Flw diam. (cm)			Plant flw
PPF[z]	Temp (°C)		daily	termi-	Shoot			Shoot			area
mol day^{-1}m^{-2}	Day	Night	temp	nation[y]	1	2	3	1	2	3	(cm^2)
1.8	10	10[x]	10.0	120	126± 5.8	125± 4.4	—	4.0	6.6	1.2	51±31
1.8	30	10[x v]	18.3	—	—	—	—	—	—	—	—
1.8	20	20	20.0	90	93± 4.2	90± 1.3	—	7.4	9.0	1.2	111±29
1.8	10	30[x v]	21.7	—	—	—	—	—	—	—	—
1.8	30	30[x v]	30.0	—	—	—	—	—	—	—	—
5.8	14	14	14.0	70	68± 0.8	71± 2.9	—	11.5	8.4	4.5	178±28
5.8	26	14	19.0	80	87± 5.5	81± 3.1	—	6.4	8.8	4.8	107±34
5.8	20	20[x]	20.0	70	66± 2.5	68± 2.1	73± 7.1	10.1	9.7	9.8	229±19
5.8	14	26	21.0	80	83± 5.9	86± 6.7	—	6.6	5.1	3.4	68±34
5.8	26	26	26.0	90	100± 5.9	109±15.5	—	4.6	3.9	2.6	41±17
11.7	20	10	14.2	70	68± 1.5	74± 5.9	77± 9.0	12.4	9.9	8.7	260±46
11.7	10	20	15.8	70	70± 4.6	74± 3.8	—	8.6	7.5	5.8	132±18
11.7	20	20	20.0	70	64± 1.2	66± 3.7	68± 1.8	10.7	10.4	10.0	253±10
11.7	30	20	24.2	90	105±14.6	101±14.6	108±16.5	4.9	6.0	4.8	83±34
11.7	20	30	25.8	80	92±14.7	87± 9.4	—	5.4	6.1	3.4	71±16
17.6	14	14	14.0	70	68± 2.9	68± 1.5	70± 4.4	11.9	11.9	10.2	310±23
17.6	26	14	19.0	75	73± 4.4	72± 1.9	76± 8.1	11.6	11.9	9.7	290±38
17.6	20	20[x]	20.0	70	64± 5.0	64± 5.0	66± 2.2	11.1	11.5	10.7	280±13
17.6	14	26	21.0	70	70± 1.1	68± 1.5	77± 6.1	8.1	8.6	5.5	137±13
17.6	26	26	26.0	80	88±20.6	90±18.1	85±14.9	6.6	6.9	7.0	134±41
21.6	10	10[x]	10.0	80	79± 6.3	79± 5.8	86±10.4	11.3	11.3	9.7	277±33
21.6	30	10[x]	18.3	80	81±19.0	86±10.1	—	8.4	8.9	7.8	135±59
21.6	20	20	20.0	60	57± 1.8	58± 1.5	59± 1.0	11.7	11.3	9.7	285±23
21.6	10	30[x]	21.7	90	87± 6.6	89± 3.3	91± 3.6	6.4	6.1	4.9	80±71
21.6	30	30[x]	30.0	130	140± 5.0	136± 5.1	—	2.5	1.9	2.1	14±10

[z]10 hr irradiance day^{-1}.
[y]When ca. 50% of the flowers had reflexed their outermost petals to a horizontal position.
[x]Treatments added to the basic central composite design.
[v]No flower initiation after 100 SD.

Figure 1. Predicted number of days from start of short days to flower and first derivative (days/mol $day^{-1}m^{-2}$) as influenced by photosynthetic photon flux (PPF) at a constant 20°C day (DT) and night temperature (NT) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'). Asterisks indicate observed number of days to flower.
The functional relationship used to create this graph was:
Days to flower = $\exp(5.8915 - (0.4332 * \ln(PPF)) - (0.0179 * DT * NT) + (0.0314 * \ln(PPF) * (\text{average daily temperature})) - (0.6047 * 10^{-3} * \ln(PPF) * DT^2) - (0.6130 * 10^{-3} * \ln(PPF) * NT^2) + (0.4867 * 10^{-3} * DT * NT^2) + (0.5175 * 10^{-3} * DT^2 * NT) - (0.1410 * 10^{-4} * DT^2 * NT^2) + (0.4356 * 10^{-3} * \ln(PPF) * DT * NT))$.
(Mallows' $C_p = 10.00$, $r^2 = 0.68$)

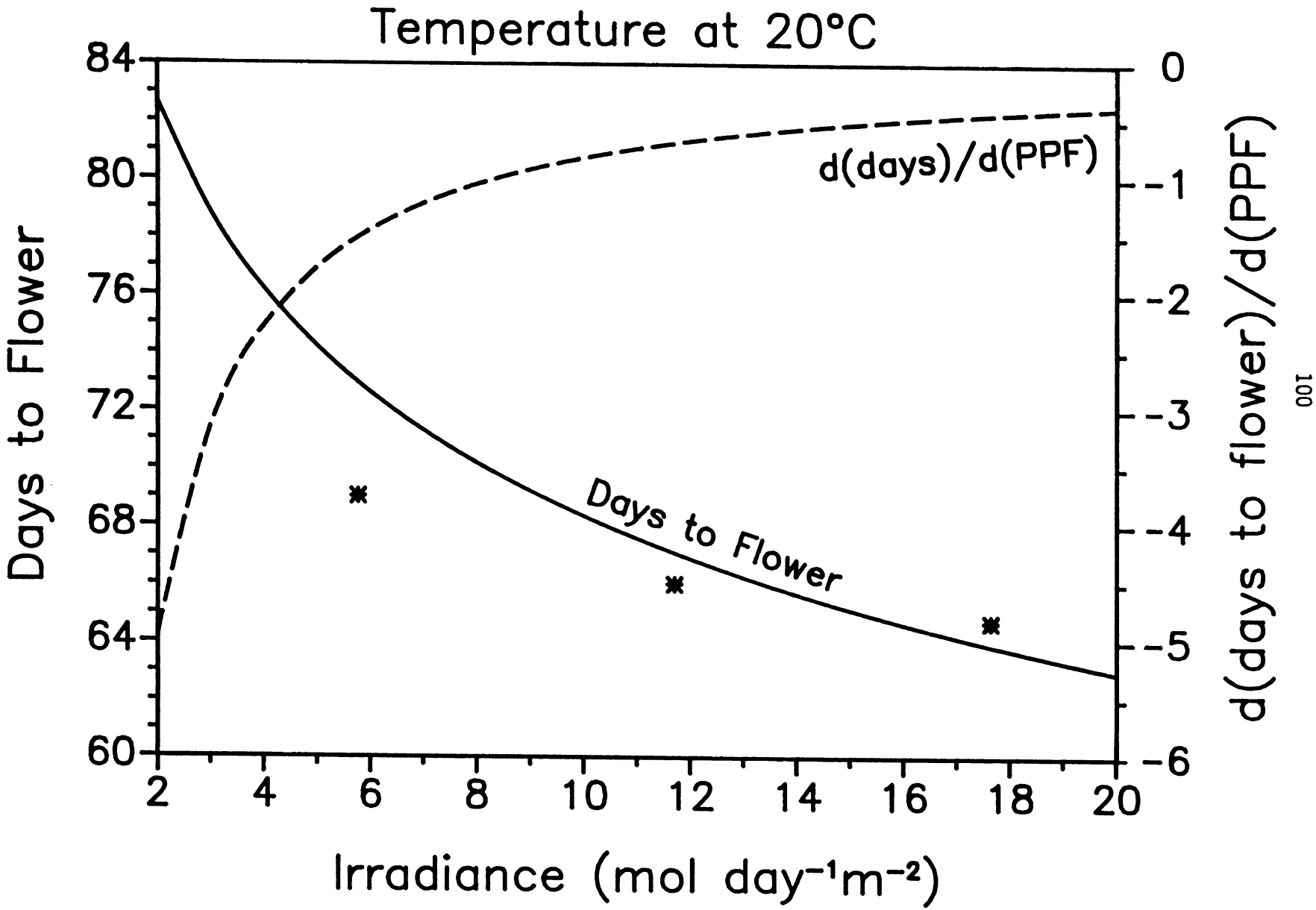

Temperature at 20°C
Days to Flower
d(days)/d(PPF)
Days to Flower
d(days to flower)/d(PPF)
Irradiance (mol day⁻¹m⁻²)
84
80
76
72
68
64
60
0
-1
-2
-3
-4
-5
-6
2
4
6
8
10
12
14
16
18
20

Figure 2. Predicted number of days from start of short days to flower as influenced by a simultaneous increase in day (DT) and night temperature (NT) at photosynthetic photon flux (PPF) levels of 5, 10 and 15 mol $day^{-1}m^{-2}$ in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne').
The functional relationship used to create this graph was:
Days to flower = $\exp(5.8915 - (0.4332 * \ln(PPF)) - (0.0179 * DT * NT) + (0.0314 * \ln(PPF) * (\text{average daily temperature})) - (0.6047 * 10^{-3} * \ln(PPF) * DT^2) - (0.6130 * 10^{-3} * \ln(PPF) * NT^2) + (0.4867 * 10^{-3} * DT * NT^2) + (0.5175 * 10^{-3} * DT^2 * NT) - (0.1410 * 10^{-4} * DT^2 * NT^2) + (0.4356 * 10^{-3} * \ln(PPF) * DT * NT))$.
(Mallows' $C_p = 10.00$, $r^2 = 0.68$)

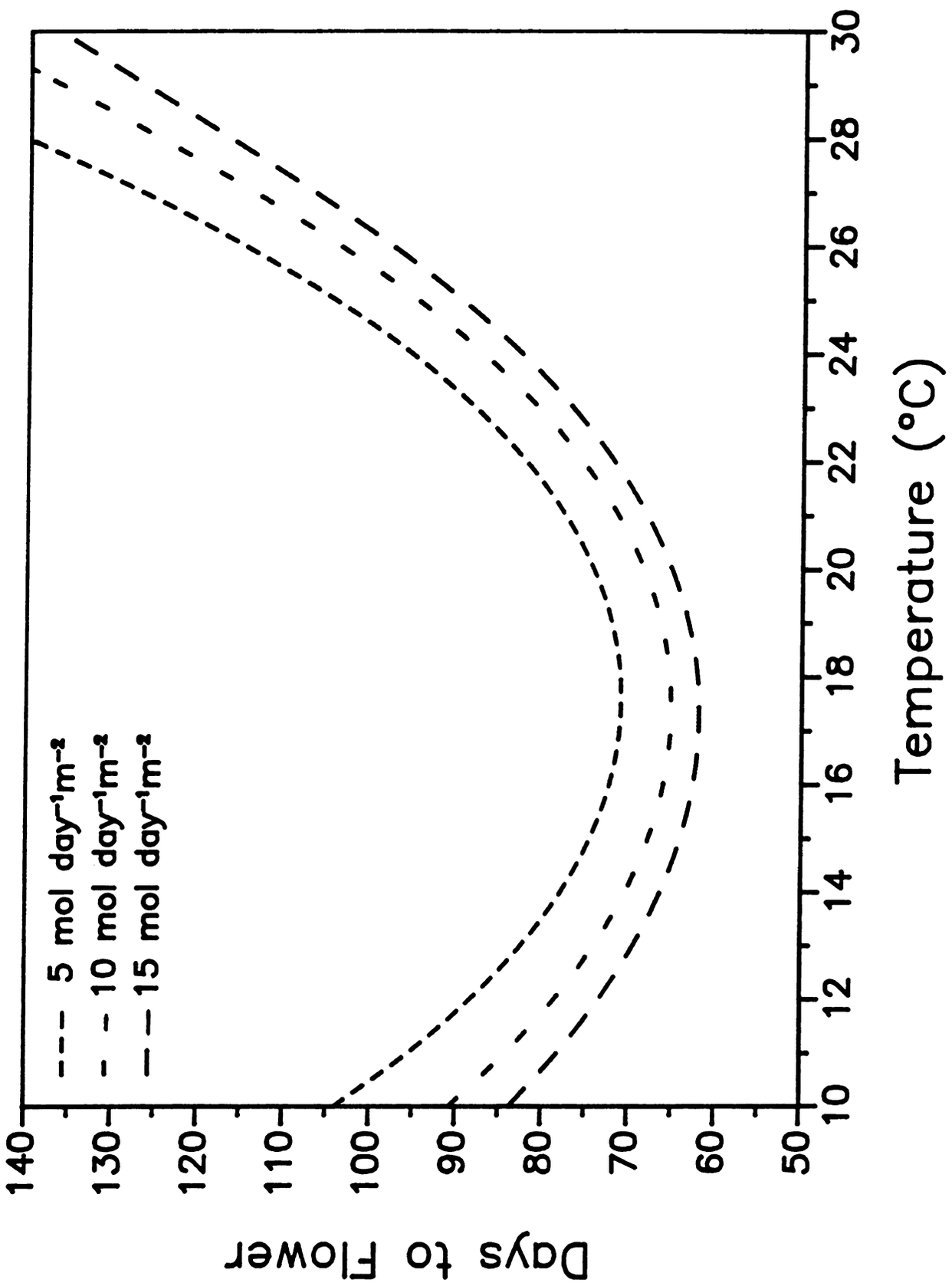

Days to Flower
Temperature (°C)
5 mol day⁻¹m⁻²
10 mol day⁻¹m⁻²
15 mol day⁻¹m⁻²
140
130
120
110
100
90
80
70
60
50
10
12
14
16
18
20
22
24
26
28
30

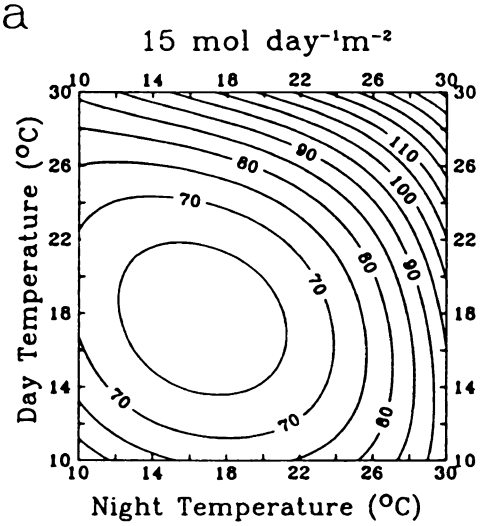
Figure 3. Days from start of short days to flower as affected by day (DT) and night temperature (NT) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') at a photosynthetic photon flux (PPF) of a) 15, b) 10, and c) 5 mol $day^{-1}m^{-2}$.

The functional relationship used to create these graphs was:

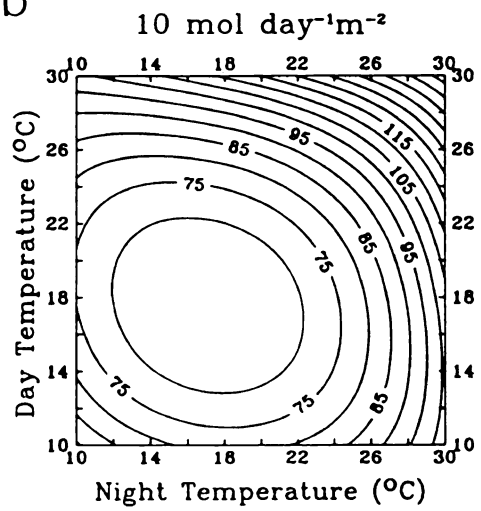
Days to flower = $\exp(5.8915 - (0.4332 * \ln(PPF)) - (0.0179 * DT * NT) + (0.0314 * \ln(PPF) * (\text{average daily temperature})) - (0.6047 * 10^{-3} * \ln(PPF) * DT^2) - (0.6130 * 10^{-3} * \ln(PPF) * NT^2) + (0.4867 * 10^{-3} * DT * NT^2) + (0.5175 * 10^{-3} * DT^2 * NT) - (0.1410 * 10^{-4} * DT^2 * NT^2) + (0.4356 * 10^{-3} * \ln(PPF) * DT * NT))$.

(Mallows' $C_p = 10.00$, $r^2 = 0.68$)

a


15 mol day⁻¹m⁻²
Day Temperature (°C)
Night Temperature (°C)
10
14
18
22
26
30
70
80
90
100
110

b


10 mol day⁻¹m⁻²
Day Temperature (°C)
Night Temperature (°C)
10
14
18
22
26
30
75
85
95
105
115

c

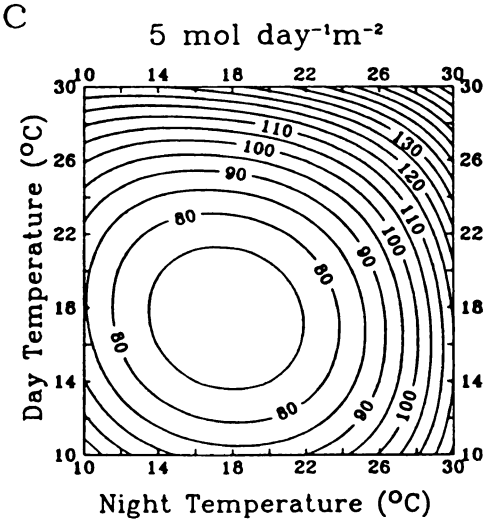

5 mol day⁻¹m⁻²
Day Temperature (°C)
Night Temperature (°C)
10
14
18
22
26
30
80
90
100
110
120
130

Figure 4. Predicted total plant flower area as influenced by a simultaneous increase in day (DT) and night temperature (NT) at photosynthetic photon flux (PPF) levels of 5, 10 and 15 mol $day^{-1}m^{-2}$ in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne').
The functional relationship used to create this graph was:
Flower area (cm^2) = $\exp(2.2318 + (1.2847 * \ln(PPF)) + (0.0829 * NT) - (0.1402 * 10^2 * \ln(PPF) * DT^2) - (0.4822 * 10^{-2} * \ln(PPF) * NT^2) - (0.0259 * (\ln(PPF))^2 * NT) + (0.1390 * 10^{-2} * (\ln(PPF))^2 * NT^2) + (0.2669 * 10^{-3} * DT * NT^2) + (0.1892 * 10^{-3} * DT^2 * NT) - (0.2057 * 10^{-4} * DT^2 * NT^2) + (0.4036 * 10^{-2} * \ln(PPF) * DT * NT))$.
(Mallows $C_p = 10.84$, $r^2 = 0.98$)

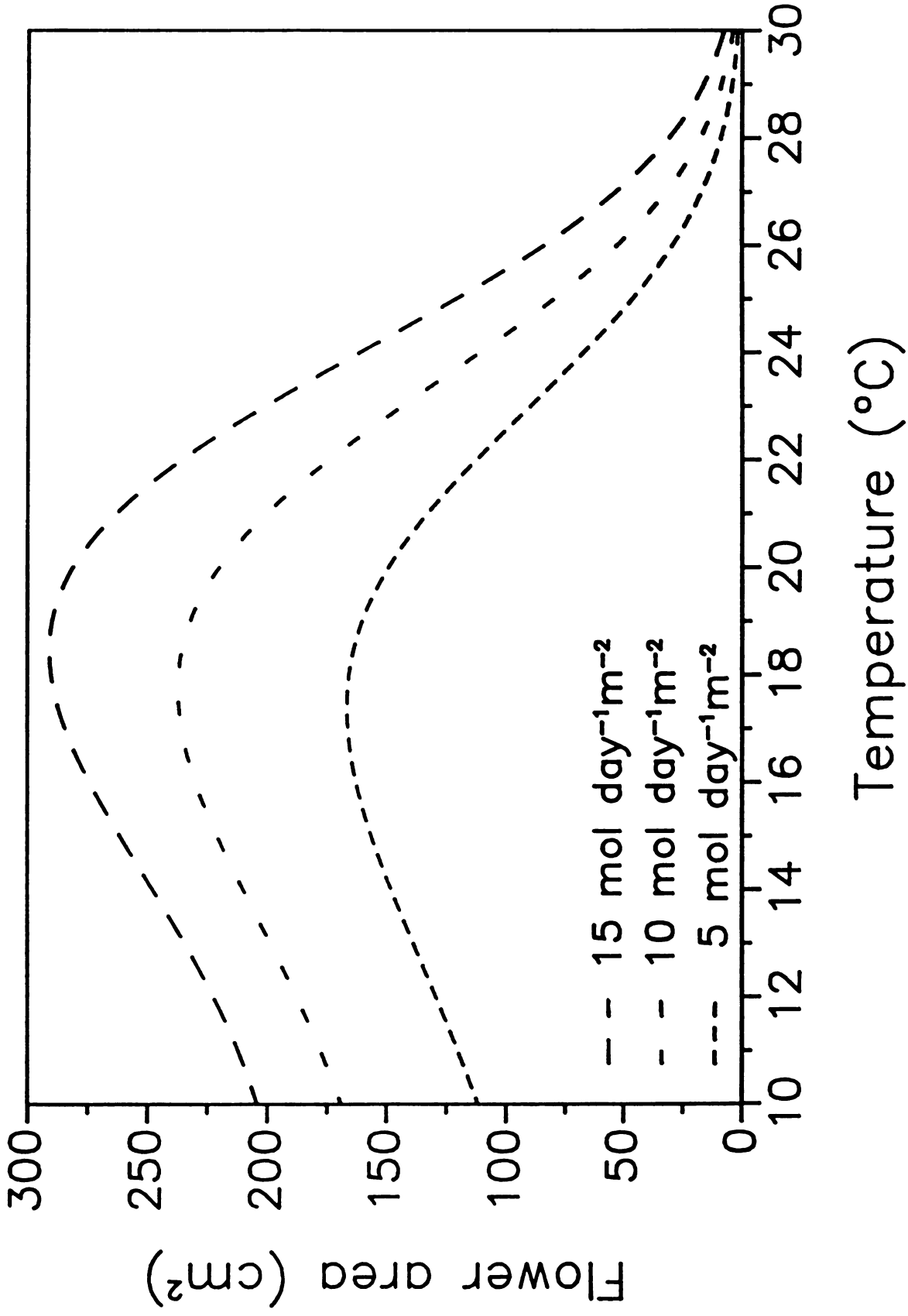

Flower area (cm²)
300
250
200
150
100
50
0
10
12
14
16
18
20
22
24
26
28
30
Temperature (°C)
15 mol day⁻¹m⁻²
10 mol day⁻¹m⁻²
5 mol day⁻¹m⁻²

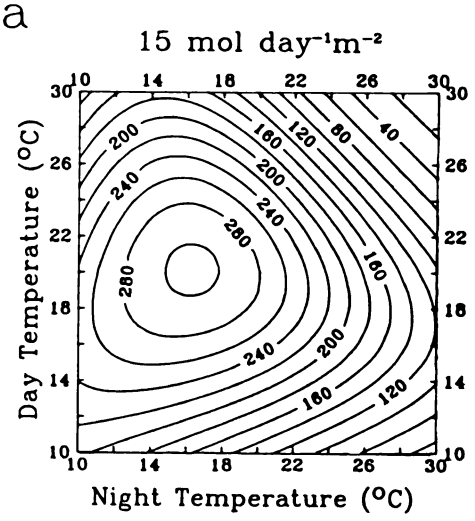
Figure 5. Total plant flower area as affected by day (DT) and night temperature (NT) in chrysanthemum (*Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne') at a photosynthetic photon flux (PPF) of a) 15, b) 10, and c) 5 mol $day^{-1}m^{-2}$.

The functional relationship used to create these graphs was:

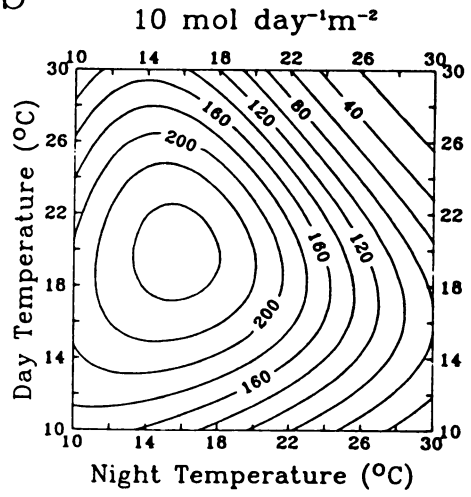
$$\text{Flower area } (cm^2) = \exp(2.2318 + (1.2847 * \ln(PPF)) + (0.0829 * NT) - (0.1402 * 10^2 * \ln(PPF) * DT^2) - (0.4822 * 10^{-2} * \ln(PPF) * NT^2) - (0.0259 * (\ln(PPF))^2 * NT) + (0.1390 * 10^{-2} * (\ln(PPF))^2 * NT^2) + (0.2669 * 10^{-3} * DT * NT^2) + (0.1892 * 10^{-3} * DT^2 * NT) - (0.2057 * 10^{-4} * DT^2 * NT^2) + (0.4036 * 10^{-2} * \ln(PPF) * DT * NT)).$$

(Mallows $C_p = 10.84$, $r^2 = 0.98$)

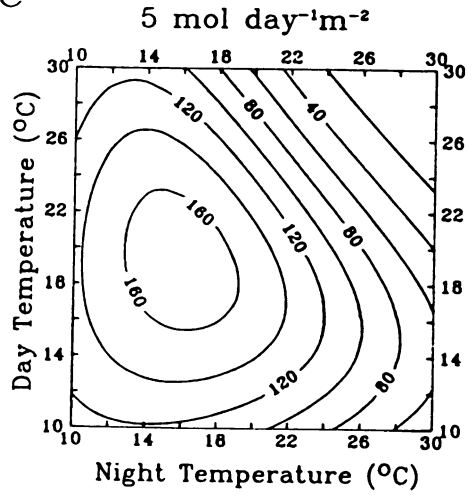
a


15 mol day⁻¹m⁻²
Day Temperature (°C)
Night Temperature (°C)
10
14
18
22
26
30
40
80
120
160
200
240
280

b


10 mol day⁻¹m⁻²
Day Temperature (°C)
Night Temperature (°C)
10
14
18
22
26
30
40
80
120
160
200

c


5 mol day⁻¹m⁻²
Day Temperature (°C)
Night Temperature (°C)
10
14
18
22
26
30
40
80
120
160

SECTION V

CHRYSANTHEMUM BIOMASS ALLOCATION PATTERNS ALONG IRRADIANCE AND TEMPERATURE GRADIENTS

Chrysanthemum Biomass Allocation Patterns Along Irradiance and Temperature Gradients[1]

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ABSTRACT

The influence of day temperature (DT), night temperature (NT) and photosynthetic photon flux (PPF) on biomass accumulation and partitioning was studied in chrysanthemum (*Dendranthema grandiflora* Tzvelev.) from start of short days to flowering. DT and NT ranged from 10 to 30 C and PPF from 1.8 to 21.6 mol $day^{-1}m^{-2}$. Total plant biomass varied from 3.6 to 17.2 g at flowering. The heaviest plants were observed in treatments with high PPF levels and high temperatures. Biomass accumulation in roots, stems, leaves and flowers showed similar trends independent of DT, NT and PPF levels when examined on a generalized time and biomass basis. Roots, stems and leaves reached a biomass maximum and then decreased in biomass as the flower developed. Biomass partitioning altered with changes in the environment. Proportion root biomass increased with increasing PPF levels while percent leaf biomass increased with decreasing PPF. Allocation to roots decreased as the DT increased, NT had only a small influence on biomass allocation within the plant. Partitioning to flowers was not strongly correlated with either PPF, DT or NT. The large plasticity of roots, stems and leaves observed may enable optimum flower development under a wide range of environmental conditions in chrysanthemum.

INTRODUCTION

Changes in partitioning patterns among plant populations of the same species may be due to genotypic differences, environmentally cued plasticity or genotypic differences in combination with some plasticity (Hickman, 1975; Douglas, 1981; Thompson and Stewart, 1981; Cartica and Quinn, 1982; Schwaegerle and Bazzaz, 1987). Characteristics such as daylength, temperature, moisture conditions and length of growing season vary among native population sites. The influence of one environmental factor on biomass allocation patterns in plants from native populations can often not be separated from the effects of other environmental gradients (Soule and Werner, 1981; Jurik, 1983; Ashmun, Brown, and Pitelka, 1985). In addition climatic conditions vary within and between seasons making the identification of environmental effects even more challenging.

The factors contributing to variation in resource allocation patterns can only be identified when auxiliary factors are kept constant. The effects of individual gradients on genotypic plasticity can be more easily interpreted when environmental conditions are controlled within and between days. This study was undertaken to quantify the response of a single genotype to 3 environmental factors (irradiance, day temperature and night temperature), and to determine the potential

plasticity of this genotype.

Dendranthema grandiflora Tzvelev. (*Chrysanthemum morifolium* Ramat.) (Anderson, 1987) which is produced and marketed as a flowering plant was chosen for this study. The cultivar 'Bright Golden Anne' was released over 20 years ago (Machin and Scopes, 1978) and has been grown extensively in commercial greenhouse production. The choice of the cultivar 'Bright Golden Anne' was based on genotypic stability and accessibility from commercial propagators.

MATERIALS AND METHODS

Rooted cuttings of *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne' were planted individually in 10 cm pots and placed in growth chambers under a photosynthetic photon flux (PPF) of 18.7 mol $day^{-1}m^{-2}$ (325 μmol $s^{-1}m^{-2}$ for 16 hr day^{-1}) at a constant temperature of 20 C for 7 days. On the seventh day, a short day (SD) photoperiod was initiated (10 hr light, 14 hr dark), plants were pinched to 6 nodes and were placed under appropriate treatment combination (Table 1) with the thermoperiod paralleling the photoperiod.

Plants were lowered as necessary to maintain the desired PPF at the canopy top. A Li-Cor LI-185B Meter and LI-190SB Quantum sensor were used to monitor PPF. The PPF was provided by cool-white fluorescent lamps and incandescent lamps with an input wattage of 80:20 respectively. Average daily temperature fluctuated $\pm$1 C from the setpoint and PPF varied $\pm$10% over the canopy.

Plants were grown in a commercial peat-lite medium (Michigan Peat Co.) and were automatically irrigated one to three times daily depending on plant size. Nutritional program 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 $\pm$ 0.2 by adjusting water pH with nitric acid.

A central composite statistical design was used to

select treatment combinations (Gardiner, Cragle and Chandler, 1976; Armitage, Carlson and Cress, 1981). The PPF levels ranged from 1.8 to 21.6 mol $day^{-1}m^{-2}$ (50 to 600 μmol $s^{-1}m^{-2}$ for 10 hr day^{-1}) and both day temperature (DT) and night temperature (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).

Data were collected on five plants the day the plants were potted, at start of SD and every 10 days thereafter. The treatments were terminated when approximately half of all flowers had reflexed their outermost petals to a horizontal position. On each sample date, leaf area, leaf number, stem length, flower diameter and dry weight of the plant parts were collected on the original and lateral shoots. Root dry weight was also determined for each plant at each sampling occasion. Leaf area was measured using a Li-Cor LI-3100 area meter with LI-3050A belt conveyer accessory. Dry weights were determined after several days of drying at 60 C.

Time and accumulated biomass in roots, stems, leaves and flowers were normalized for plants in each treatment to facilitate data analysis. The data values were transformed to values between 0 and 1 by division with the maximum value observed for each time and biomass variable. Regression analyses (Wilkenson, 1986) was performed on the

normalized values with linear, higher order terms and interaction terms of DT, NT, PPF and normalized time as independent variables. The unit for PPF used in the analyses was mol $day^{-1}m^{-2}$.

Functional relationships to determine maximum biomass during the growth from start of SD to flowering in roots, stems, leaves, and flowers were developed by stepwise regression analyses (Wilkenson, 1986). Linear, quadratic, cubic and interaction terms of DT, NT, PPF, average daily temperature and DIF (difference between DT and NT) were the independent variables available for inclusion. 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

Total plant biomass varied with changes in DT, NT and PPF (Table 1). At flowering, total plant dry matter varied from 3.6 to 17.2 g in the different treatments. Chrysanthemums grown under the five temperature combinations at 5.8 mol $day^{-1}m^{-2}$ had significantly less biomass than the same five combinations at 17.6 mol $day^{-1}m^{-2}$. Interactions between PPF and both DT and NT were also apparent. Total plant biomass increased 62% and 58% respectively as both DT and NT increased from 14 to 26 C at 5.8 and 17.6 mol $day^{-1}m^{-2}$.

Time required to complete the development from start of SD to flowering under the environmental conditions allowing for flower initiation, varied from 60 to 120 days (Table 1). Increasing the PPF level from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at 20 C resulted in 30 days faster development. High temperature (26 C) delayed the development 20 days compared to a 14 C temperature at 5.8 mol $day^{-1}m^{-2}$ and 10 days at 17.6 mol $day^{-1}m^{-2}$. There were also interactions between temperatures and PPF levels. At 26 C and 5.8 mol $day^{-1}m^{-2}$, the plants required 90 days to flowering while at 17.6 mol $day^{-1}m^{-2}$, plants flowered in 80 days. Plants failed to initiate flowers within 100 SD when either DT or NT was 30 C under low irradiance (1.8 mol $day^{-1}m^{-2}$).

Biomass accumulation in the different plant parts was first analyzed as accumulated biomass versus time on a

normalized basis. The large variation in total plant biomass and time required to reach flowering under the different environments made analyses and interpretations of environmental effects difficult. Normalized biomass accumulation was therefore analyzed with stepwise regression using environmental factors (PPF, DT and NT) and time on a normalized basis as variables available for inclusion. Stepwise regression analysis was also performed using only linear and higher order terms of time on a normalized basis as independent variables. The selection of the "best" functional relationships for biomass accumulation in each plant part were made considering the number of included variables, F-values of the equations, r^2 values and prediction adequacy determined by examination of graphs with plotted observed values for each treatment and plotted corresponding values calculated with the function under examination. Table 2 gives variable numbers, F values and r^2 values for the resulting equations. The functional relationships developed with time on a normalized basis as independent variables had less number of variables included, higher F-values, comparable r^2 values (Table 2) and similar or better prediction adequacy as the equations which included environmental variables for all plant parts. The equations with only time on a normalized basis were therefore selected to describe the biomass accumulated over time in the different plant parts (Table 3).

Biomass accumulation in roots, stems, leaves and flowers showed similar trends independent of the DT, NT and PPF levels when examined on a generalized time and biomass basis. The functional relationships are shown in Figure 1. Roots, stems and leaves reached maximum biomass at 85%, 91% and 81% of the time required for flowering. Thereafter these plant parts decreased in biomass. The flowers started biomass accumulation half through time to flower. Total plant biomass increased continuously from start of SD to flowering (Figure 2-4).

Resource allocation patterns to the various plant parts varied with DT, NT and PPF (Figure 2-7). Maximum amount of root biomass during the growth period from start of SD to flowering was correlated to interactions of PPF with DT and NT (Table 4). The proportion of total plant biomass allocated to the roots at flowering decreased as the DT increased (Table 1). Biomass allocated to the roots decreased from 12% of total biomass at 14 C temperature to 6% at 26 C temperature at a PPF level of 5.8 mol $day^{-1}m^{-2}$. The trends were similar at 17.6 mol $day^{-1}m^{-2}$, where the percentage root biomass decreased from 13% to 8%.

Stem biomass was associated with the difference between DT and NT. The selected functional relationship for maximum stem biomass included the difference between DT and NT (DIF) as a significant ($P < 0.05$) independent variable (Table 4). Plants in treatments with a constant 14 C had 27% and 30% stem biomass at PPF levels of 5.8 and 17.6 mol

day^{-1}m^{-2} (Table 2). Plants grown at the same PPF level but with a large positive DIF (DT at 26 C, NT at 14 C) had 36% and 38% of total biomass in stem tissue at flowering.

Flower initiation is morphologically delayed when chrysanthemum is grown under high temperatures. More leaves and internodes are formed prior to the transition of the vegetative meristem resulting in taller plants and greater biomass accumulation in stems (Karlsson, Heins, and Carlson, 1983; Karlsson and Heins, 1986; Whealy et al., 1987). Plants grown under 5.8 mol day^{-1}m^{-2} and 26 C constant temperature had 33% stem biomass at flowering compared to 27% at 14 C, and plants grown at 17.6 mol day^{-1}m^{-2} had 37% at 26 C and 30% at 14 C (Table 1).

Maximum leaf biomass was associated with PPF, NT and DT (Table 1). Plants grown under low PPF levels had a higher percentage leaf biomass than plants grown under high PPF levels (Table 1, Figure 2 a,b). At a constant 20 C, the leaf biomass decreased from 40% at 1.8 mol day^{-1}m^{-2} to 22% at 21.6 mol day^{-1}m^{-2} (Table 1).

More leaves were initiated per shoot at high DT and NT (26 C or above) and the percent leaf biomass increased. Leaves carried 28% and 36% biomass at flowering when the temperature increased from a constant 14 to 26 C under 5.8 mol day^{-1}m^{-2}. Similarly, as the temperature increased from 14 to 26 C at 17.6 mol day^{-1}m^{-2}, leaf biomass proportion increased from 23% to 30% (Table 1).

Flower biomass at termination of the experiment

(outermost petals had reflexed to a horizontal position) was correlated with PPF and DT (Table 4). Decreased biomass partitioning to flowers occurred at very high temperatures (30 C) or low temperature (10 C) and low irradiance (Table 1). No flowers had initiated after 100 SD at 1.8 mol $day^{-1}m^{-2}$ with either DT or NT at 30 C (Table 1). Increasing the PPF level to 21.6 mol $day^{-1}m^{-2}$ at 30 C resulted in the formation of flowers although only 7% of total biomass at flowering was allocated for flower development (Table 1).

Resource partitioning patterns over time on a normalized basis from start of SD to flowering is shown in Figure 5-7. The proportion of biomass in roots decreased over time under all environmental conditions. Percent stem biomass decreased temporarily during early development before increasing to a maximum. The stem allocation decreased during the development immediately prior to flowering. As the flowers rapidly became a larger sink, the leaf biomass proportion decreased to parallel the stem allocation pattern. The smallest proportion of leaf biomass over time occurred at flowering.

The biomass partitioning altered with changes in the environment. Figure 5 show the predicted plasticity in allocation patterns when the PPF level was increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$ at a constant temperature of 20 C. Biomass allocation to roots increased as the PPF level increased from 1.8 to 21.6 mol $day^{-1}m^{-2}$. The proportion of

biomass in roots decreased throughout the development and the influence of PPF level in determining the root proportion became less pronounced as the development continued. Low PPF levels resulted in larger resource allocation to leaves, while at high PPF levels, more biomass was partitioned to stems and flowers.

DT strongly affected the resource allocation pattern in chrysanthemum. Allocation to roots decreased as the DT increased from 10 to 30 C at a PPF level of 11.7 mol $day^{-1}m^{-2}$ and NT of 20 C (Figure 6). The decreased allocation of biomass to roots at high DT was accompanied with increased allocation to stems and leaves. Proportion flower biomass was similar over the DT range from 10 to 30 C.

NT had only a minor influence on biomass allocation. Increasing NT from 10 to 30 C when PPF was 11.7 mol $day^{-1}m^{-2}$ resulted in a small decrease in stem and flower allocation and a corresponding increase in allocation to leaves (Figure 7).

DISCUSSION

Total plant biomass accumulated varied with the environment. PPF was more important in determining total biomass accumulation than DT or NT (Table 1, Figure 2-4). High PPF conditions result in higher photosynthesis, more biomass production and heavier plants (Björkman, 1981; Charles-Edwards, Doley and Rimmington, 1986). Correlations between PPF levels and plant size have been observed in several studies of plant populations. Quinn and Hodgkinson (1983) observed a decline in shoot weight with increasing plant density in *Danthonia caespitosa*, and Schwaegerle and Bazzaz (1987) showed significant genotype-PPF level interactions in *Phlox*. The PPF level was the most important environmental factor to determine plant size, density and sexual reproduction in *Aster acuminatus* (Pitelka, Stanton, and Peckenham, 1980; Ashmun, Brown and Pitelka, 1985).

The optimum temperature for photosynthesis in chrysanthemum increased with increasing PPF level (Heins et al., 1986). The increase in total plant biomass observed when DT increased from 10 to 30 C (Table 1, Figure 3) could be a result of increased photosynthesis as the temperature approached the optimum.

Respiratory biomass losses would be expected to be lower with a low NT (Parups and Butler, 1982; Kohl and Mor, 1981). Total biomass did not increase with a decrease in

NT in this experiment (Table 1, Figure 4). Either respiration did not vary significantly with temperature or the NT influenced photosynthesis and development such that plants grown with 14 and 26 C NT had similar total biomass at flowering. The increased final biomass was not due to delayed flowering at higher temperatures as the total biomass after 60 days showed a similar relationship to that at flowering (Table 1). A suboptimal NT (12 C) reduced carbon fixation in rose plants and inhibited translocation of ^{14}C to buds on the upper part of the plant (Khayat and Zieslin, 1986). The starch concentration in the leaves increased and the photosynthetic rate was suppressed by high starch content in the chloroplasts. A similar decrease in photosynthetic rate may have occurred in chrysanthemum at 14 C NT which outweighed any increase in night respiration at high NT.

Roots, stems, leaves and flowers accumulated biomass in a similar pattern independent of the environment when the absolute values of biomass gain and developmental time were normalized to values between 0 and 1 (Figure 1). At flowering the plants were at the same morphogenetic age (Hunt, 1982) and a normalized time scale indicated stage of development rather than chronological age. Flowering occurred at a wide range of total plant biomass (Table 1) and there were no indications that a certain plant size had to be attained before flower initiation and development could take place in chrysanthemum. Plants in the 3

treatments not initiating flowers continued to accumulate biomass and grew vegetatively. Lack of flower formation was not due to a biomass shortage but unsuitable environmental conditions (Cathey, 1955).

Dry matter in roots, stems and leaves increased to a maximum and then decreased. Leaf biomass increased fast to accommodate light interception and high photosynthetic rates early. Root development accompanied the leaf development as the demands for water and nutrients increased. During early development, leaf and root growth were prioritized relative to stem growth. Increase in flower biomass was observed to start at half the morphogenetic age to flowering. At this time the stem had accumulated biomass for sufficient stem strength to support the flower. Just prior to the unfolding of the flower petals, the biomass in the other plant parts decreased. At this developmental stage the flowers acted as strong sinks for assimilates in the plant and mobilization of dry matter occurred to the flowers. Other plants have shown similar translocations and remobilizations of assimilates to fast growing plant parts (France and Thornley, 1984; Charles-Edwards, Doley and Rimmington, 1986). Flower biomass accumulation would be expected to show a similar sigmoid growth response as roots, stems and leaves if the study had been continued beyond the flowering stage.

Biomass allocation within a plant has been suggested to be determined by limiting factors in the environment

(Abrahamson and Gadgil, 1973, Lee and Cavers 1979). For instance, under water limiting conditions, more biomass would be expected to be directed to root tissue (Abrahamson and Gadgil, 1973; Jones, 1983). Although water stress was avoided in this experiment by supplying adequate amounts of water, differences in root biomass occurred. Relative root biomass increased with a large increase in PPF level (Table 1, Figure 5). The increased rate of transpiration and photosynthesis may have caused a higher demand for water (Stanghellini, 1987). Hughes and Cockshull (1971) observed similar increases in relative root biomass with increasing PPF levels for chrysanthemum. Root biomass also increased when DT was lowered (Table 1, Figure 6). Hydraulic root resistance has been found to be sensitive to low temperatures (Meidner and Sheriff, 1976). Water availability may decrease with low temperature during the day, resulting in a larger proportion biomass allocation to roots (Abrahamson and Gadgil, 1973; Jones, 1982). Plants did not respond with an increased root biomass to a low NT (Figure 7).

Internode length was shown to be correlated to the difference between DT and NT (DIF) in chrysanthemum (Erwin, 1986). A large positive DIF gave taller plants with longer internodes. These results suggested the use of DIF as a meaningful variable in the functional relationship for maximum stem biomass (Table 4). The difference in internode length on plants grown at constant 14 C and

plants grown with a large positive DIF (DT at 26 C, NT at 14 C) was 1.2 cm (70%) at 5.8 mol $day^{-1}m^{-2}$ and 1.3 cm (80%) at a PPF level of 17.6 (Karlsson and Heins, 1986). The forecasted larger biomass proportion in stems when the DT increased from 10 to 30 C at 20 NT would therefore be expected, since these plants grew taller (Figure 6). Similar increases in stem biomass partitioning have been observed when plants grew taller in a field habitate compared to a woods habitate (Gross et al., 1983). Plants in a field site will experience more fluctuations in temperature between day and night than plants in a forest site (Lee and Cavers, 1979; Jurik, 1983). Increased height growth is a better survival strategy in a field environment where the surrounding plants are of the same statue compared with a forest with surrounding plants being much taller (Abrahamson and Gadgil, 1973; Gaines et al., 1974; Gross et al., 1983). Temperature fluctuations in combination with changes in the spectral distribution of irradiance (Morgan and Smith, 1981) may be determining factors for the plastic stem elongation response.

More leaves and internodes are formed prior to flower initiation when chrysanthemum is grown at high temperatures (Karlsson, Heins and Carlson, 1983; Karlsson and Heins, 1986; Whealy et al., 1987). Under these environmental conditions, more biomass would be expected to be allocated to stems and leaves (Table 1). At a constant 26 C temperature, each shoot had 14 or 15 leaves compared to 10

or 11 leaves on plants grown in treatments with lower temperatures (Karlsson and Heins, 1986). Estimated proportion dry matter per leaf did not vary significantly for plants grown at the same PPF level but different temperatures.

More biomass is allocated to the leaves to improve the interception of irradiance under low PPF conditions. In this study, chrysanthemums grown at high irradiance and 20 C constant temperature had an average 22% leaf biomass at flowering while plants grown under low irradiance had 40% (Table 1, Figure 5). Specific leaf area (cm^2 leaf area/g leaf biomass) paralleled the allocation of biomass to leaves as PPF decreased (data not shown). Estimated biomass per leaf also increased with a decrease of PPF level from 21.6 to 1.8 mol $day^{-1}m^{-2}$. These results indicated that leaves were thinner and larger under low irradiance conditions. Lee and Cavers (1979) observed morphological adaptations to shade such as taller growth and larger, thinner leaves in three species of foxtail. Several other plant species have been observed to respond to decreasing PPF levels by changing biomass partitioning to the leaves, leaf morphology and total leaf area (Hughes and Cockshull, 1971; Abrahamson and Gadgil, 1973; Gaines et al., 1974; Abrahamson 1979; Björkman, 1981; Cartica and Quinn, 1982; Kappel and Flore, 1983; Gross et al., 1983; Ashmun, Brown and Pitelka, 1985).

Proportion biomass allocated to chrysanthemum flowers

remained the same over a wide range of environmental conditions in studies by Cockshull and Hughes (1967), and Cockshull (1982). High DT and/or NT in combination with a low PPF level (1.8 mol $day^{-1}m^{-2}$) in this study altered biomass proportion due to no flower initiation (Table 1). The deleterious effect of temperatures at the experimental extremes on flower initiation could be outweighed by high PPF and there was a trend for an increase in relative flower biomass with increasing PPF (Figure 5). There was also a trend for reduced flower allocation with high DT and NT. Flower size on plants grown in these high temperature treatments likewise decreased (Karlsson and Heins, 1986). Lee and Cavers (1979), and Pitelka, Stanton and Peckenham (1980) observed increased relative biomass partitioning to flowers of *Setaria* and *Aster acuminatus* at less shady study sites. Hume and Cavers (1981), however did not find any difference in the proportion of total biomass allocated to reproductive parts in 8 populations of *Rumex crispus*.

Partitioning of biomass to flowers was not strongly influenced by any one of the three factors PPF, DT and NT, except at the experimental extremes. It is possible that allocation to flowers in chrysanthemum is more genetically determined than allocation to other plant parts. Optimum flower development under a wide range of environmental conditions may be accomplished by the plasticity of roots, stems and leaves. Environmentally cued biomass distribution to roots, stems and leaves will result in an optimum

balance of carbohydrates, nutrients, water, etc. to the flower under prevailing limitations.

Large plasticity was observed in this study with chrysanthemum. Changes in only 3 environmental factors caused considerable variation in resource allocation patterns. More research is necessary to understand how genotypic plasticity can optimize plant competition and survival in climates with more than 3 factors and climatic variations within and between days.

In conclusion, total plant biomass and resource allocation patterns varied significantly with changes in PPF, DT and NT. Total plant biomass increased as PPF increased. Biomass allocation to roots was primarily associated with DT. Low DT resulting in more partitioning to roots. High DT and NT or a positive difference between DT and NT led to increased allocation to stems. Percent leaf biomass decreased as PPF increased. Flower biomass proportion was only strongly associated with PPF, DT or NT at experimental extremes.

LITERATURE CITED

Abrahamson, W.G. 1979. Patterns of resource allocation in wildflower populations of field and woods. Amer. J. Bot. 66:71-79.

Abrahamson, W.G. and M. Gadgil. 1973. Growth from and reproductive effort in goldenrods (*Solidago*, Compositae). Amer. Natur. 107:651-661.

Anderson, N.O. 1987. Reclassification of the genus *Chrysanthemum* L. HortScience 22:313.

Armitage, A.M., W.H. Carlson, and C.E. Cress. 1981. Determination of flowering time and vegetative habit of *Tagetes patula* through response surface techniques. J. Amer. Soc. Hort. Sci. 106:632-638.

Ashmun, J.W., R.L. Brown, and L.F. Pitelka. 1985. Biomass allocation in *Aster acuminatus*: variations within and among populations over 5 years. Can. J. Bot. 63:2035-2043.

Björkman, O. 1981. Responses to different quantum flux densities. p. 57-107. In O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler (eds.) Encyclopedia of plant physiology, Volume 12A, Physiological plant ecology I, response to the physical environment. Springer-Verlag, New York.

Cathey, H.M. 1955. A study of the effects of light and temperature upon the flowering of *Chrysanthemum morifolium* and *Tulipa gesneriana*. Ph.D. Thesis, Cornell University, Ithaca.

Cartica, R.J. and J.A. Quinn. 1982. Resource allocation and fecundity of populations of *Solidago sempervirens* along a coastal dune gradient. Bull. Torrey Bot. Club 109:299-305.

Charles-Edwards, D.A., D. Doley, and G.M. Rimmington. 1986. Modelling plant growth and development. Academic Press, Sydney.

Cockshull, K.E. 1982. Disbudding and its effect on dry matter distribution in *Chrysanthemum morifolium*. J. Hort. Sci. 57:205-207.

Cockshull, K.E and A. P. Hughes. 1967. Distribution of dry matter to flowers in *Chrysanthemum morifolium*. Nature 215:780-781.

Douglas, D.A. 1981. The balance between vegetative and sexual reproduction of *Mimulus primuloides* (Scrophulariaceae) at different altitudes in California. J. Ecol. 69:295-310.

Erwin, J.E. 1986. Environmental and physiological factors influencing the response of *Chrysanthemum morifolium* cvs. 'Bright Golden Anne' and 'Circus' to daminozide. M.S. Thesis, Michigan State University, E. Lansing.

France, J. and J.H.M. Thornley. 1984. Mathematical models in agriculture, a quantitative approach to problems in agriculture and related sciences. Butterworth & Co., London.

Gaines, M.S., K.J. Vogt, J.L. Hamrick, and J. Caldwell. 1974. Reproductive strategies and growth patterns in sunflower (Helianthus). Amer. Nat. 108:889-894.

Gardiner, D.A., R.G. Cragle, and P.T. Chandler. 1967. The response surface method as a biological research tool. Tenn. Agric. Expt. Sta. Bul. 429:25-40.

Gross, K.L., T. Berner, E. Marschall, and C. Tomcko. 1983. Patterns of resource allocation among five herbaceous perennials. Bull Torrey Bot. Club 110:345-352.

Heins, R.D., M.G Karlsson, J.A. Flore, and W.H. Carlson. 1986. Effects of photosynthetic rate maximization on chrysanthemum growth and development. J. Amer. Soc. Hort. Sci. 111:42-46.

Hickman, J.C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonace). J. Ecol. 63:689-701.

Hughes, A.P. and K.E. Cockshull. 1971. The effect of light intensity and carbon dioxide concentration on the growth of *Chrysanthemum morifolium* cv. Bright Golden Anne. Ann. Bot. 35:899-914.

Hume, L. and P.B. Cavers. 1981. Resource allocation and reproductive and life-history strategies in widespread populations of *Rumex crispus*. Can.J. Bot. 61:1276-1282.

Hunt, R. 1982. Plant growth curves, the functional approach to plant growth analysis. Edward Arnold Ltd, London.

Jurik, T.W. 1983. Reproductive effort and CO_2 dynamics of wild strawberry populations. Ecology 64:1329-1342.

Jones, H.G. 1983. Plants and microclimate, a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge.

Kappel, F. and J.A. Flore. 1983. Effects of shade on photosynthesis, specific leaf weight, leaf chlorophyll content, and morphology of young peach trees. J. Amer. Soc. Hort. Sci. 108:541-544.

Karlsson, M.G. and R.D. Heins. 1986. Response surface analysis of flowering in chrysanthemum 'Bright Golden Anne'. J. Amer. Soc. Hort. Sci. 111:253-259.

Karlsson, M., R.D. Heins, and W.H. Carlson. 1983. Development of environmental strategies based on plant growth models. Acta Hort. 147:153-160.

Khayat, E. and N. Zieslin. 1986. Effect of different night temperature regimes on the assimilation, transport and metabolism of carbon in rose plants. Physiol. Plant. 67:608-613.

Kohl, H.C. Jr. and Y. Mor. 1981. Producing pot chrysanthemums at low night temperature. J. Amer. Soc. Hort. Sci. 106:89-91.

Lee, S.M. and P.B. Cavers. 1979. The effect of shade on growth, development, and resource allocation patterns of three species of foxtail (*Setaria*). Can. J. Bot. 59:1776-1786.

Machin, B. and N. Scopes. 1978. Chrysanthemums, year-round growing. Blandford Press, Poole, Dorset.

Meidner, H. and D.W. Sheriff. 1976. Water and plants. Halsted Press, New York.

Morgan, D.C. and H. Smith. 1981. Non-photosynthetic responses of light quality. p. 109-134. In O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler (eds.) Encyclopedia of plant physiology, Volume 12A, Physiological plant ecology I, response to the physical environment. Springer-Verlag, New York.

Parups, E.V. and G. Butler. 1982. Comparative growth of chrysanthemums at different night temperatures. J. Amer. Soc. Hort. Sci. 107:600-604.

Pitelka, L.F., D.S. Stanton, M.O. Peckenham. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). Amer. J. Bot. 67:942-948.

Quinn, J.A. and K.C. Hodgkinson. 1983. Population variability in *Danthonia caespitosa* (Gramineae) in response to increasing density under three temperature regimes. Amer. J. Bot. 70:1425-1431.

Schwaegerle and F.A. Bazzaz. 1987. Differentiation among nine populations of *Phlox*: response to environmental gradients. Ecology 68:54-64.

Soule, J.D. and P.A. Werner. 1981. Patterns of resource allocation in plants with special reference to *Potentilla recta* L. Bull. Torrey Bot. Club 108:311-319.

Stanghellini, C. 1987. Transpiration of greenhouse crops, an aid to climate management. Ph.D. dissertation, Agricultural University, Wageningen, The Netherlands.

Thompson, K. and A.J.A. Stewart. 1981. The measurement and meaning of reproductive effort in plants. Am. Nat. 117:205-211.

Whealy, C.A., T.A. Nell, J.E. Barrett, and R.A. Larson. 1987. High temperature effects on growth and floral development of chrysanthemum. J. Amer. Soc. Hort. Sci. 112:464-468.

Wilkenson, L. 1986. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, IL.

Table 1. Influence of photosynthetic photon flux (PPF), day and night temperature on total biomass and resource allocation at flowering in *Dendranthema grandiflora* Tzvelev.

Environment			Days to			Biomass allocated at flowering (%)			
PPF[a]	Temp (C)		experimental	Total plant biomass (g)[c]					
mol $day^{-1}m^{-2}$	Day	Night	termination[b]	at 60 days	at flowering	Roots	Stems	Leaves	Flowers
1.8	10	10[d]	120	1.6 ± 0.08	3.8 ± 0.02	19	33	35	13
1.8	30	10[d,e]	—	—	—	—	—	—	—
1.8	20	20	90	1.9 ± 0.03	3.6 ± 0.14	8	20	40	32
1.8	10	30[d,e]	—	—	—	—	—	—	—
1.8	30	30[d,e]	—	—	—	—	—	—	—
5.8	14	14	70	4.7 ± 0.14	5.3 ± 0.10	12	27	28	33
5.8	26	14	80	4.6 ± 0.12	5.9 ± 0.09	4	36	28	32
5.8	20	20[d]	70	4.7 ± 0.06	6.2 ± 0.07	17	21	27	35
5.8	14	26	80	4.2 ± 0.10	6.6 ± 0.10	13	31	29	27
5.8	26	26	90	5.1 ± 0.09	8.6 ± 0.38	6	33	36	25
11.7	20	10	70	8.4 ± 0.09	10.7 ± 0.09	9	39	22	30
11.7	10	20	70	4.8 ± 0.06	5.9 ± 0.07	24	25	21	30
11.7	20	20	70	8.3 ± 0.14	10.0 ± 0.22	7	26	22	45
11.7	30	20	90	7.3 ± 0.21	10.6 ± 0.05	4	41	30	25
11.7	20	30	80	6.7 ± 0.13	9.3 ± 0.16	9	31	30	30
17.6	14	14	70	10.0 ± 0.25	10.9 ± 0.40	13	30	23	34
17.6	26	14	75	10.3 ± 0.19	14.3 ± 0.42	9	38	20	33
17.6	20	20[d]	70	10.1 ± 0.18	10.7 ± 0.19	20	22	20	38
17.6	14	26	70	8.6 ± 0.05	11.0 ± 0.14	12	29	25	34
17.6	26	26	80	11.8 ± 0.16	17.2 ± 0.56	8	37	30	25
21.6	10	10[d]	80	7.0 ± 0.36	10.5 ± 0.18	26	27	24	23
21.6	30	10[d]	80	8.1 ± 0.26	11.6 ± 0.38	5	51	30	14
21.6	20	20	60	15.3 ± 0.12	15.3 ± 0.12	24	24	22	30
21.6	10	30[d]	90	9.1 ± 0.21	14.6 ± 0.41	23	32	21	24
21.6	30	30[d]	120	6.4 ± 0.20	14.5 ± 0.23	14	36	43	7

[a] 10 hr irradiation day^{-1}.
[b] When ca. 50% of the flowers had reflexed their outermost petals to a horizontal position.
[c] ± SE.
[d] Treatments added to the basic central composite design.
[e] Not used in analysis due to lack of flower initiation after 100 SD.

Table 2. Number of independent variables, F-values and r^2 values for regression equations developed to study biomass accumulation over time in roots, stems, leaves and flowers of *Dendranthema grandiflora* Tzvelev. Stepwise regression analysis with linear, higher order terms and interaction terms of environmental variables (photosynthetic photon flux, day temperature and night temperature) and time on a normalized basis available for addition. Biomass was normalized to values between 0 and 1 by dividing the data values with the maximum value observed prior to analysis. All independent variables included in the equations were significant at $P < 0.05$.

Functions for biomass accumulation over time on a normalized basis	Number of independent variables	F-value of function	r^2-value of function
	Roots		
Environmental[a] and time[b] variables	5	826	0.96
Time[b] variables	3	1,398	0.95
	Stems		
Environmental[a] and time[b] variables	10	686	0.97
Time[b] variables	3	12,759	0.99
	Leaves		
Environmental[a] and time[b] variables	9	1,813	0.98
Time[b] variables	3	5,044	0.98
	Flowers		
Environmental[a] and time[b] variables	3	2,079	0.97
Time[b] variables	2	3,013	0.97

[a] Linear, higher order terms, and interaction terms of day temperature, night temperature and photosynthetic photon flux.
[b] Linear and higher order terms only of time on a normalized basis.

Table 3. Regression coefficients for functions relating normalized quantity of biomass in roots, stems, leaves and flowers over normalized time (NDAY) from start of short days to flowering in *Dendranthema grandiflora* Tzvelev. Biomass and time required for flowering were scaled to attain values between 0 and 1. (Regression variables significant at $P < 0.05$.)

Regression variable	Normalized amount of biomass in			
	Roots	Stems	Leaves	Flowers
NDAY	0.4403	0.1541	---	---
$NDAY^2$	1.9834	---	5.3947	---
$NDAY^3$	---	4.6998	-5.8463	-1.0076
$NDAY^4$	-1.5445	-3.9105	1.3252	2.0110
r^2	0.95	0.99	0.98	0.97

Table 4. Regression coefficients for functions relating maximum amount of biomass in roots, stems, leaves and flowers during the growth period from start of short days to flowering in *Dendranthema grandiflora* Tzvelev. (Regression variables significant at $P < 0.05$.)

Regression[a] variable	Maximum amount of biomass in			
	Roots	Stems	Leaves	Flowers
Constant	8.192×10^{-1}	4.360×10^{-1}	2.437	-1.818
PPF	——	——	9.133×10^{-2}	——
DT	——	——	——	2.551×10^{-1}
NT	——	——	-2.675×10^{-1}	——
DT^2	——	——	——	-8.055×10^{-3}
NT^2	——	——	5.562×10^{-3}	——
DT x PPF	-4.708×10^{-3}	1.375×10^{-2}	——	2.157×10^{-2}
DT x NT	——	——	5.152×10^{-3}	——
NT x PPF^2	8.680×10^{-4}	——	——	——
DT^2x PPF^2	——	-9.800×10^{-6}	——	-2.619×10^{-5}
NT^2x PPF^2	-1.891×10^{-5}	——	——	——
DIF^2	——	3.027×10^{-3}	——	——
r^2	0.84	0.82	0.89	0.88

[a] PPF=photosynthetic photon flux, DT=day temperature, NT=night temperature, DIF= difference between DT and NT.

Figure 1. Relative biomass accumulation in roots, leaves, stems and flowers plotted against relative time from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev.

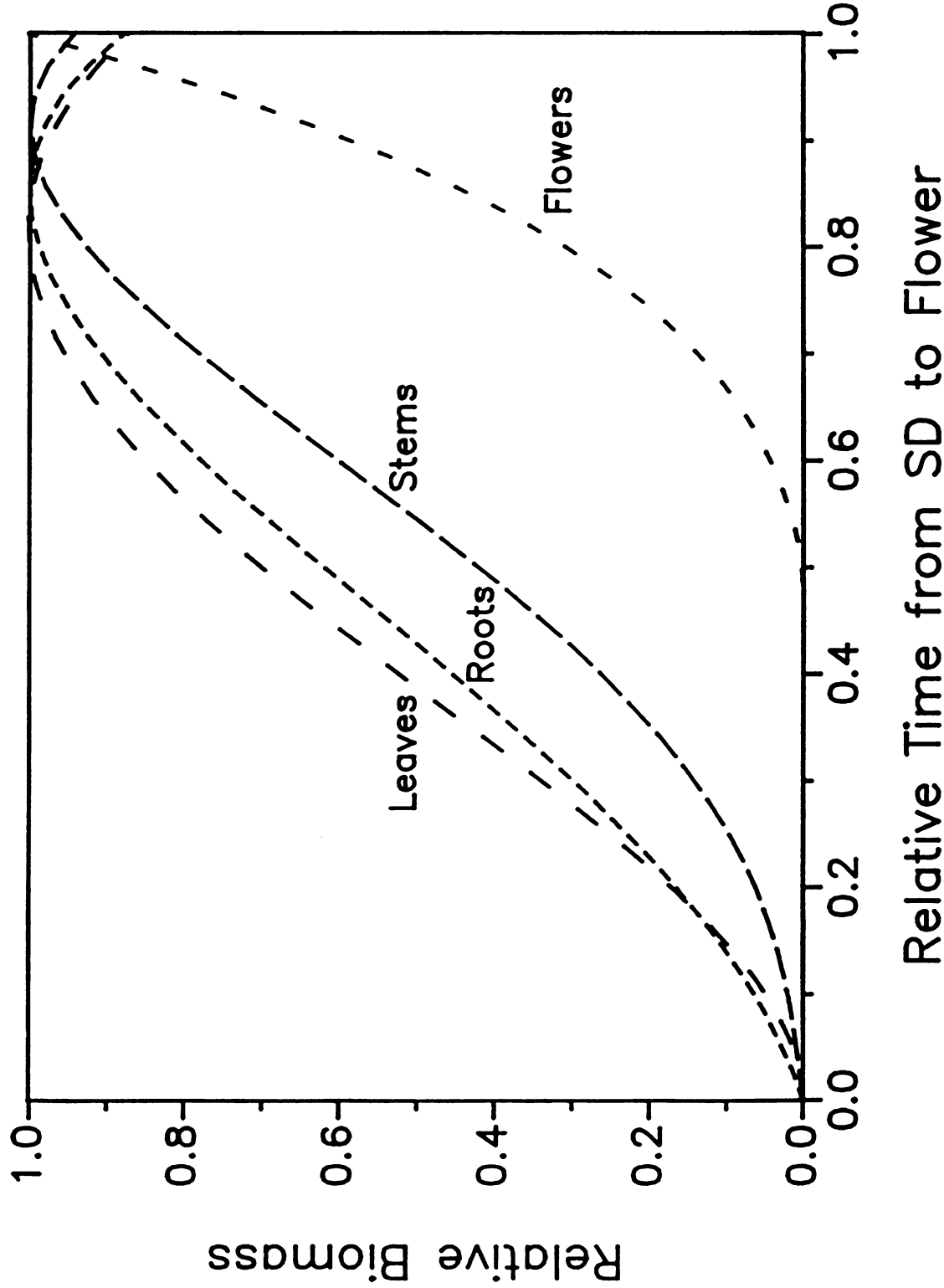
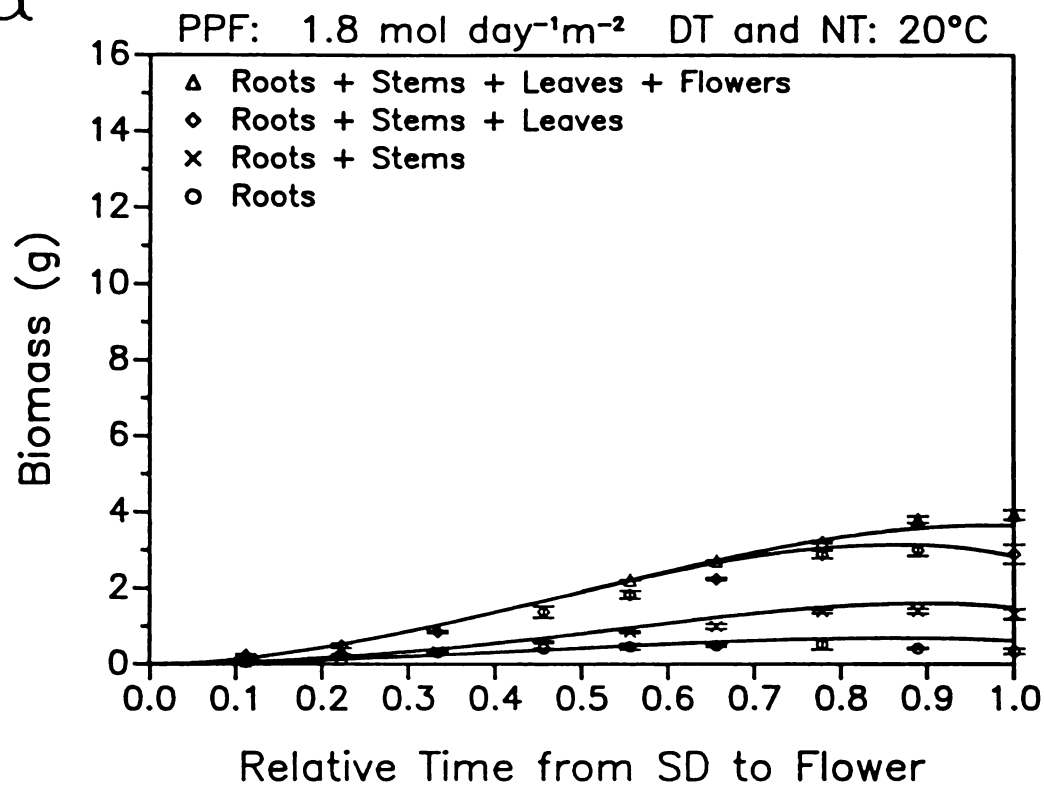

Relative Biomass
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Relative Time from SD to Flower
Flowers
Stems
Roots
Leaves

Figure 2. Gain of biomass in roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. Biomass in the different plant parts was estimated by developed functions. Root biomass, stem biomass added to root biomass, leaf biomass added to root and stem biomass and flower biomass added to root, stem and leaf biomass were plotted to show accumulated plant biomass. Observed values are plotted with standard deviations.

a) Photosynthetic photon flux (PPF) of 1.8 mol $day^{-1}m^{-2}$ with day temperature (DT) and night temperature (NT) at 20 C. Observed time to flower was 90 days.

b) PPF level of 21.6 mol $day^{-1}m^{-2}$ with DT and NT at 20 C. Observed time to flower was 60 days.

a


PPF: 1.8 mol day⁻¹m⁻² DT and NT: 20°C
Roots + Stems + Leaves + Flowers
Roots + Stems + Leaves
Roots + Stems
Roots
Biomass (g)
0
2
4
6
8
10
12
14
16
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

b

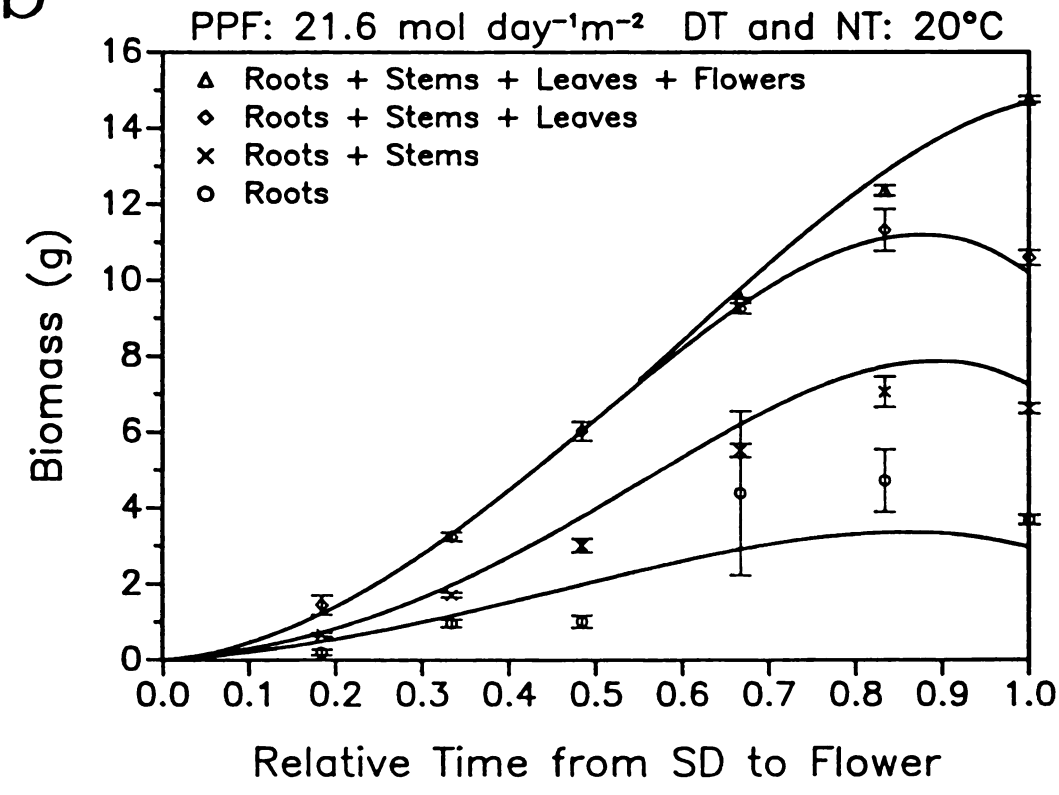
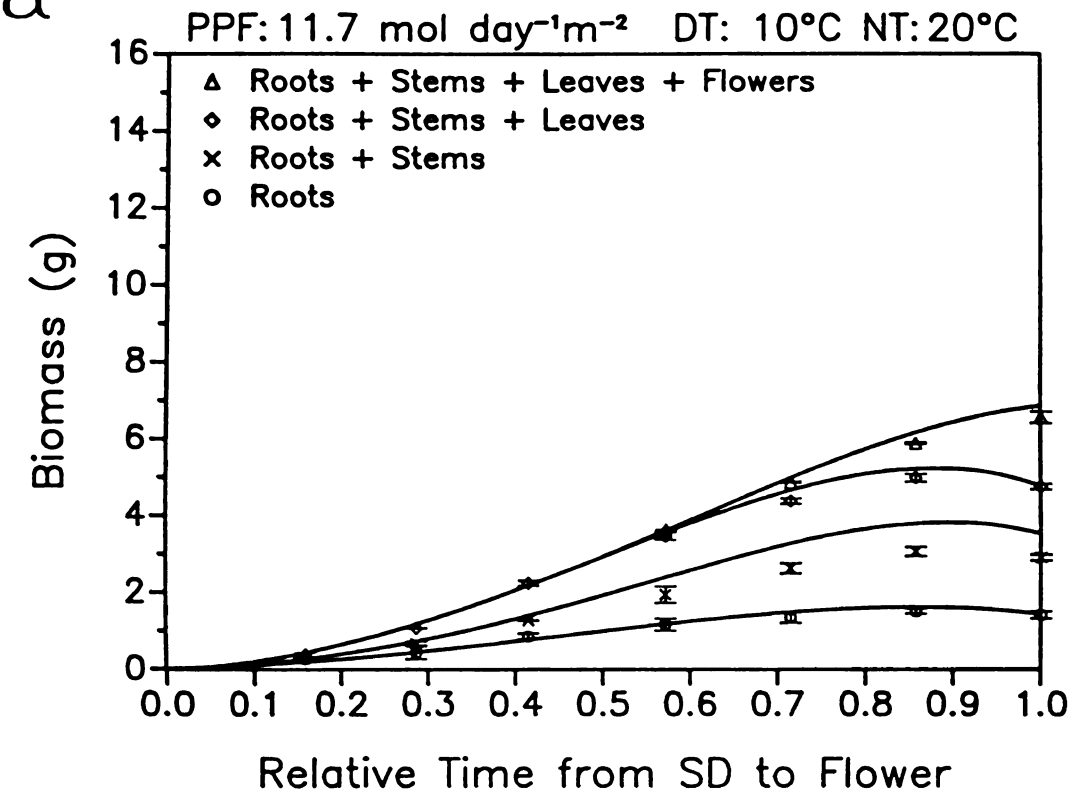

PPF: 21.6 mol day⁻¹m⁻² DT and NT: 20°C
Roots + Stems + Leaves + Flowers
Roots + Stems + Leaves
Roots + Stems
Roots
Biomass (g)
0
2
4
6
8
10
12
14
16
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

Figure 3. Gain of biomass in roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. Biomass in the different plant parts was estimated by developed functions. Root biomass, stem biomass added to root biomass, leaf biomass added to root and stem biomass and flower biomass added to root, stem and leaf biomass were plotted to show accumulated plant biomass. Observed values are plotted with standard deviations.

a) Day temperature (DT) at 10 C with night temperature (NT) at 20 C and photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days.

b) DT at 30 C with NT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 90 days.

a


PPF: 11.7 mol day⁻¹m⁻² DT: 10°C NT: 20°C
Roots + Stems + Leaves + Flowers
Roots + Stems + Leaves
Roots + Stems
Roots
Biomass (g)
0
2
4
6
8
10
12
14
16
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

b

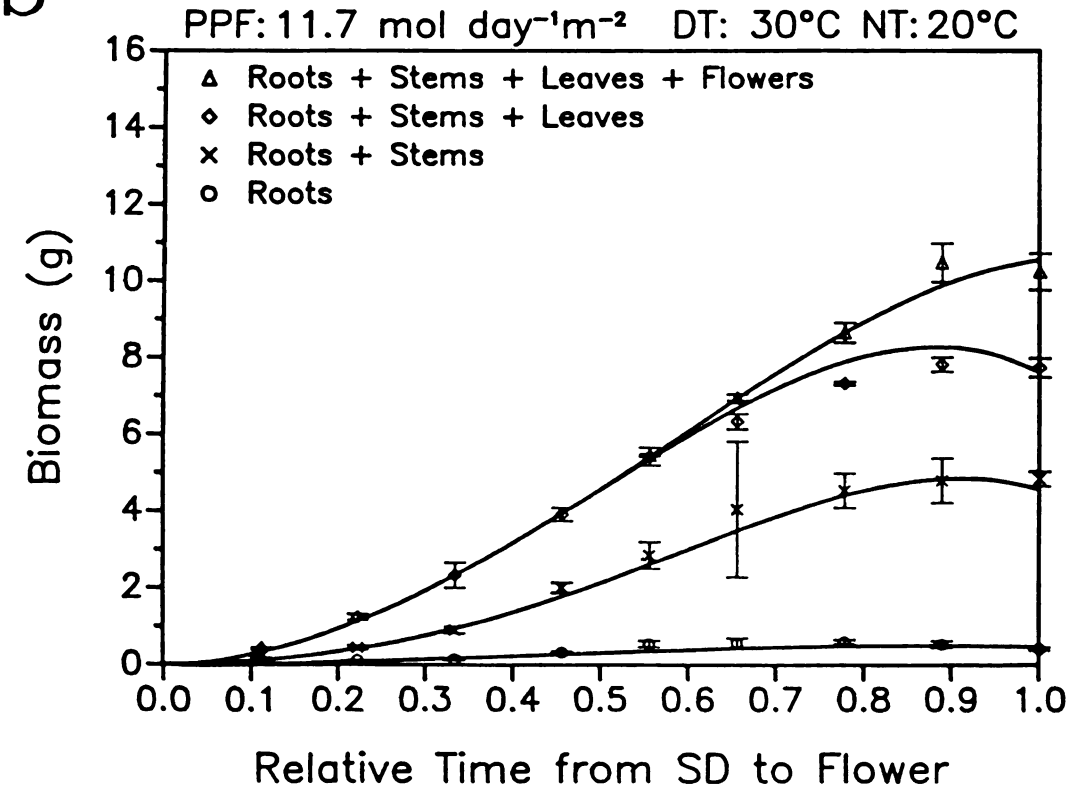
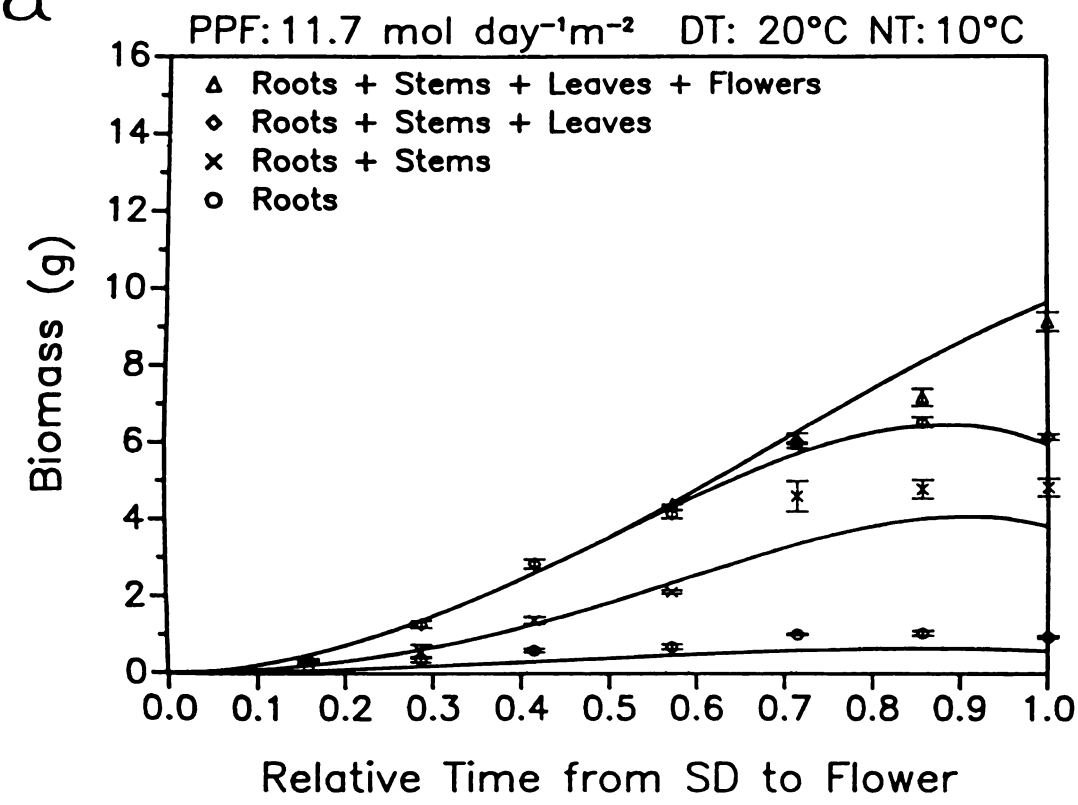

PPF: 11.7 mol day⁻¹m⁻² DT: 30°C NT: 20°C
Roots + Stems + Leaves + Flowers
Roots + Stems + Leaves
Roots + Stems
Roots
Biomass (g)
0
2
4
6
8
10
12
14
16
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

Figure 4. Gain of biomass in roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. Biomass in the different plant parts was estimated by developed functions. Root biomass, stem biomass added to root biomass, leaf biomass added to root and stem biomass and flower biomass added to root, stem and leaf biomass were plotted to show accumulated plant biomass. Observed values are plotted with standard deviations.

a) Night temperature (NT) at 10 C with day temperature (DT) at 20 C and photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days.

b) NT at 30 C with DT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 80 days.

a


PPF: 11.7 mol day⁻¹m⁻² DT: 20°C NT: 10°C
Roots + Stems + Leaves + Flowers
Roots + Stems + Leaves
Roots + Stems
Roots
Biomass (g)
0
2
4
6
8
10
12
14
16
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

b

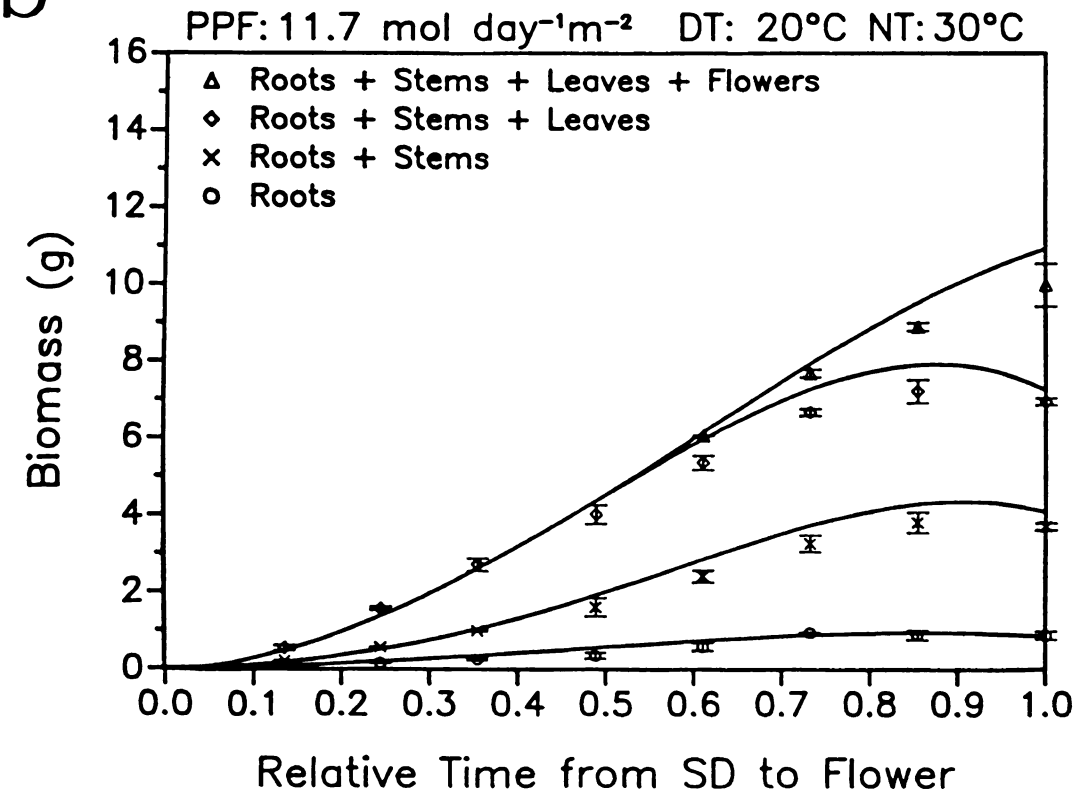
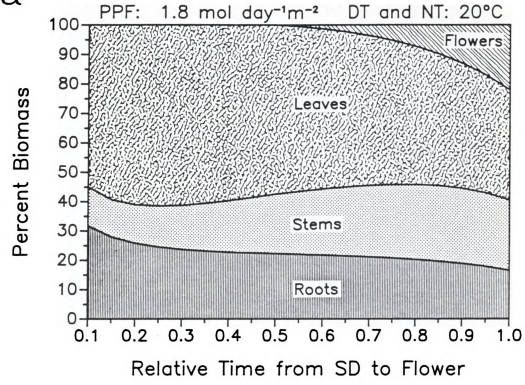

PPF: 11.7 mol day⁻¹m⁻² DT: 20°C NT: 30°C
Roots + Stems + Leaves + Flowers
Roots + Stems + Leaves
Roots + Stems
Roots
Biomass (g)
0
2
4
6
8
10
12
14
16
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

Figure 5. Estimated biomass allocation to roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. using developed functional relationships.

a) Photosynthetic photon flux (PPF) of 1.8 mol $day^{-1}m^{-2}$ with day temperature (DT) and night temperature (NT) at 20 C. Observed time to flower was 90 days and observed total plant dry matter at flowering was 3.6 g.

b) PPF level of 21.6 mol $day^{-1}m^{-2}$ with DT and NT at 20 C. Observed time to flower was 60 days and observed total plant dry matter at flowering was 15.3 g.

a


PPF: 1.8 mol day⁻¹m⁻² DT and NT: 20°C
Flowers
Leaves
Stems
Roots
Percent Biomass
100
90
80
70
60
50
40
30
20
10
0
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

b

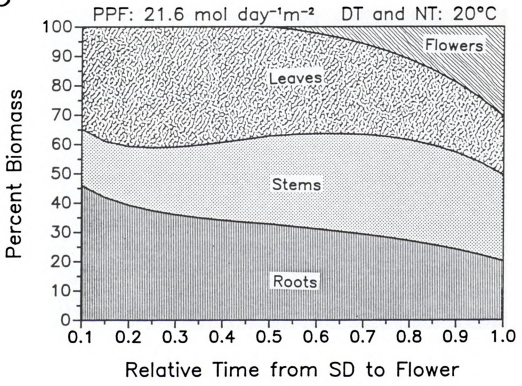
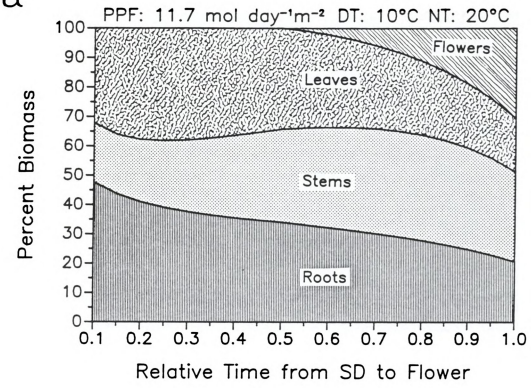

PPF: 21.6 mol day⁻¹m⁻² DT and NT: 20°C
Flowers
Leaves
Stems
Roots
Percent Biomass
100
90
80
70
60
50
40
30
20
10
0
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Relative Time from SD to Flower

Figure 6. Estimated biomass allocation to roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. using developed functional relationships.

a) Day temperature (DT) at 10 C with night temperature (NT) at 20 C and photosynthetic photon flux (PPF) of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days and observed total plant dry matter at flowering was 5.9 g.

b) DT at 30 C with NT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 90 days and observed total plant dry matter at flowering was 10.6 g.

a


PPF: 11.7 mol day⁻¹m⁻² DT: 10°C NT: 20°C
Flowers
Leaves
Stems
Roots
Percent Biomass
Relative Time from SD to Flower

b

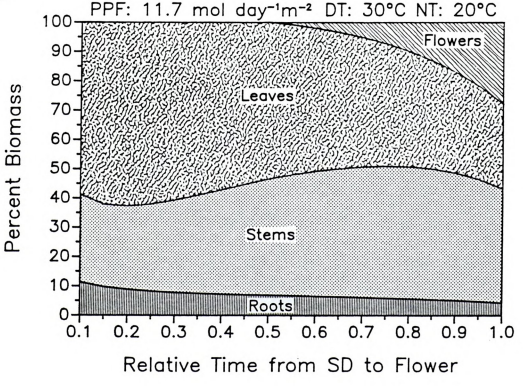
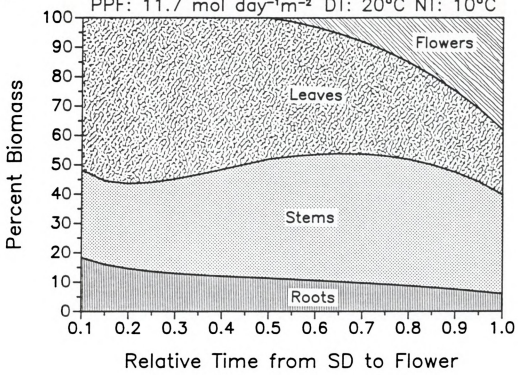

PPF: 11.7 mol day⁻¹m⁻² DT: 30°C NT: 20°C
Flowers
Leaves
Stems
Roots
Percent Biomass
Relative Time from SD to Flower

Figure 7. Estimated biomass allocation to roots, stems, leaves and flowers over time expressed in relative units from start of short days (SD) to flowering in *Dendranthema grandiflora* Tzvelev. using developed functional relationships.

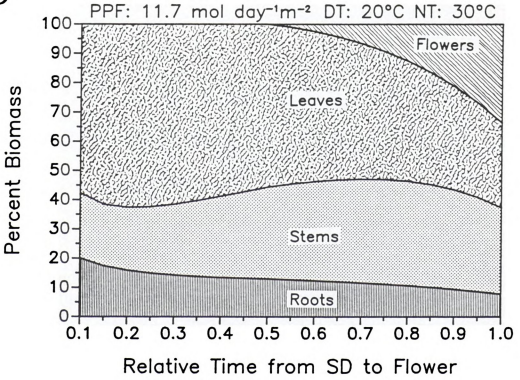
a) Night temperature (NT) at 10 C with day temperature (DT) at 20 C and photosynthetic photon flux of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 70 days and observed total plant dry matter at flowering was 5.9 g.

b) NT at 30 C with DT at 20 C and PPF level of 11.7 mol $day^{-1}m^{-2}$. Observed time to flower was 80 days and observed total plant dry matter at flowering was 9.3 g.

a


PPF: 11.7 mol day⁻¹m⁻² DT: 20°C NT: 10°C
Flowers
Leaves
Stems
Roots
Percent Biomass
Relative Time from SD to Flower

b


PPF: 11.7 mol day⁻¹m⁻² DT: 20°C NT: 30°C
Flowers
Leaves
Stems
Roots
Percent Biomass
Relative Time from SD to Flower