THESIS

This is to certify that the

thesis entitled

INFLUENCE OF TEMPERATURE AND IRRADIANCE ON GROWTH AND DEVELOPMENT OF CHRYSANTHEMUM MORIFOLIUM 'BRIGHT GOLDEN ANNE'

presented by

Meriam G. Karlsson

has been accepted towards fulfillment
of the requirements for

M.S. degree in Horticulture

Royal D. Heins

Major professor

Date April 19, 1984

INFLUENCE OF TEMPERATURE AND IRRADIANCE ON GROWTH AND DEVELOPMENT OF *CHRYSANTHEMUM MORIFOLIUM* 'BRIGHT GOLDEN ANNE'.

By

Meriam G. Karlsson

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Horticulture

1984

ABSTRACT

INFLUENCE OF TEMPERATURE AND IRRADIANCE ON GROWTH AND DEVELOPMENT OF CHRYSANTHEMUM MORIFOLIUM 'BRIGHT GOLDEN ANNE'.

By

Meriam G. Karlsson

Chrysanthemum morifolium 'Bright Golden Anne' plants were grown under 15 combinations of Quantum Flux Density (QFD), day temperature, and night temperature in a central composite statistical design. Functional relationships between these three environmental factors and subsequent growth were developed. This type of knowledge is necessary for development of growth optimization models. At 20° C temperature, time to flower decreased 30 days when QFD was increased from 50 to 600 μmol $s^{-1}m^{-2}$. Increasing day or night temperature from 14° to 26° delayed flowering. Shoot length increased linearly with day temperature. Total flower area increased as QFD increased or night temperature decreased. Final dry weight at flowering ranged from 4.1 g to 18 g. As QFD increased, partitioning to the roots and leaves decreased while partitioning to the stems and flowers increased. High day temperature increased partitioning to the stems but decreased partitioning to the roots.

ACKNOWLEDGMENTS

I would like to thank all those who in different ways have helped me throughout this study.

Gratitude is extended to my major professor Dr. Royal D. Heins for help, encouragement and support.

Appreciation also goes to the members of my guidance committee: Drs. W. Carlson, C. Cress and J. Flore for their direction and assistance.

A special thank you to Mrs. S. Kilyanek for help with data analysis and to Mrs. L. Kent for assistance in the typograhical completion of this thesis.

Financial support for this study was provided in part by grants from Fred C. Gloeckner Foundation, the American Florists Endowment, and the US Department of Agriculture Small Business Innovation Research program (grant no. 83SBIR-8-0001) in collaboration with Oglevee Computer Systems.

Guidance Committee:

The paper format was adopted for this thesis in accordance with departmental and university regulations. Section I is to be submitted to the Journal of the American Society for Horticultural Science; and Section II to the Journal of Horticultural Science.

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LITERATURE REVIEW

Literature from two different areas has been reviewed. Plant growth analysis is discussed in the first part and the influence of the environment, primarily irradiance and temperature on growth and development of Chrysanthemum morifolium Ramat. is the topic for the last part of this literature review.

Plant Growth Analysis

Various procedures are used to compare plant growth and development. Many of the procedures used in growth analysis were first studied and defined at the beginning of this century as rates and ratios (30,31,70); these calculated estimators of population parameters will be called statistics in this review (63). When the statistics are estimated as a mean value over the time period between data collection, the calculation method is referred to as the classical approach to growth analysis. When the statistics are derived from fitting mathematical functions to the raw data (40,42), the calculation method is referred to as the functional approach.

Several statistics are described below and some typical values are presented in Table 1. The classical and the functional approaches are then discussed followed by mathematical functions typically used in the functional approach.

Statistics of Growth Analysis

Growth can be described as a function of time:

$$W = f(t) \tag{1}$$

where W is total plant dry weight at time t (16,30,40,42,59). The absolute growth rate (G) is given by the derivative of this function:

$$G = dW/dt \tag{2}$$

Absolute growth rate has often been observed to be approximately proportional to the size of the plant (15,16,59). Therefore absolute growth rate isn't necessarily the best way to describe a plant's physiological performance. Dry matter gain per unit plant weight is another way to express the production efficiency. This statistic is called the relative growth rate (RGR) and is the absolute growth rate divided by the existing weight (6,9,15,16,30,31,40,42,59):

$$RGR = (dW/dt) \times (1/W) \tag{3}$$

Also since, by definition,

$$d(\ln W)/dt = (dW/dt) \times (1/W) \tag{4}$$

the first derivative of any total dry weight function expressed as the natural logarithm of total dry weight automatically gives RGR. The mean

relative growth rate ($\overline{RGR}$) between two times (T_1 and T_2) can be expressed:

$$\overline{RGR} = (\ln W_2 - \ln W_1) / (T_2 - T_1) \quad (5)$$

Equation 3 gives instantaneous values of RGR. Hunt (42) has shown that RGR often changes smoothly over time and this drift can often be followed by deriving mean relative growth rates between harvest intervals. As the harvest intervals become shorter the mean relative growth rate gives better and better estimates of instantaneous RGR.

The RGR is useful for growth rate comparisons between experiments and species. But this method implies that all parts of the plant are equally efficient in producing new dry matter. In most plants the leaves are the main site for photosynthesis and Briggs et al. (10) found that the weekly increase in total plant dry weight per unit leaf area for a particular species and set of environmental conditions is rather constant throughout plant development. The net weight gain per unit leaf area seems to be an appropiate index for plant assimilation efficiency. This weight gain has been called Unit Leaf Rate (ULR) (10) and the instantaneous value can be expressed:

$$ULR = (1/L_A) \times (dW/dt) \quad (6)$$

where L_A is the plant total leaf area (9,16,30,40,42). Sometimes the ULR is called Net Assimilation Rate (NAR) (30,40,42,67,70). Before the term ULR was introduced by Briggs et al. (9) the only existing name for

this statistic was the German word 'Assimilationenergie' and since NAR can be confused with the term apparent assimilation, which relates to the photoreduction of carbon dioxide, the term ULR is preferred (30).

The Leaf Area Ratio (LAR) is the ratio between leaf area and total dry weight:

$$LAR = L_A/W \tag{7}$$

LAR can be broken into two parts, specific leaf area (SLA) and leaf weight ratio (LWR). SLA is the leaf area divided by leaf weight (L_A/L_W) and is a measurement of leaf density or relative leaf thickness (42). Plant 'leafiness' can either be expressed on an area/weight basis (SLA) or on a weight/weight basis (L_W/W) as in LWR (42).

The RGR can be expressed with the help of ULR and LAR (9,16,30,40,42):

$$(1/W) \times (dW/dT) = ((1/L_A) \times (dW/dT)) \times (L_A/W) \tag{8}$$

$$RGR = ULR \times LAR$$

In some experimental analysis the relationship between shoot dry weight and root dry weight is of interest. The statistics are simple ratios (16,42):

$$R_W/S_W \quad \text{or} \quad S_W/R_W \tag{9}$$

ULR is not appropiate when a population of plants is studied.

This is because spacing between plants must be taken into account and measurements of 'leafiness' in relation to land area gives more information about a whole crops potential productivity. This ratio between total leaf area and the occupied land area (P) is called leaf area index (LAI) (30,42)

$$LAI = L_A/P \tag{10}$$

Only the most common ratios and rates in plant growth analysis have been discussed here but many others have been defined (16,30,42). Some statistic values observed in plant growth analysis are presented in Table 1.

Classical Approach to Growth Analysis

The ratios and rates mentioned above were traditionally calculated from the raw data without further attempts to find underlying mathematical functions (16). This procedure of calculation on raw data is referred to as the classical approach to plant growth analysis. The main advantage of the classical approach is the ease with which rates and ratios can be calculated. However assumptions must often be made. For example, when calculating mean values of quantities like ULR, weight and leaf area are assumed to be linearly related over the time period (30,40,42,67). This isn't necessarily the case for fast growing plants or long harvest intervals (40).

While frequent sampling is necessary for the functional approach, the classical method can be used with a small number of sampling periods (40,42,67). Since plant dry weight measurements are

Table 1. Observed values for absolute growth rate, relative growth rate, unit leaf rate, leaf area ratio, shoot-root ratio and leaf area index.

Statistic	Calculation method	Range of typical values	Unit	Species	References
Absolute growth rate	$\frac{dw}{dt}$	0.01	g day^{-1}	Holcus lanata	Hunt (1978)
		1.9		Maize	Hunt (1978)
		0.01 - 10.26		Helianthus annuus	Evans (1972)
		0.12 - 0.38		Helianthus debilis	Evans (1972)
Relative growth rate	$\frac{dw}{dt} \cdot \frac{1}{w}$	0.06 - 0.16	day^{-1}	Phalaris tuberosa	Williams (1946)
		0.09 - 0.13		Impatiens parviflora	Evans (1972)
		0.088 - 0.20		Helianthus annuus	Evans (1972)
		0.262 - 0.482		Pigweed	Potter, Jones (1977)
		0.39		Poa annuus	Hunt (1978)
Unit leaf rate	$\frac{1}{L_A} \cdot \frac{dw}{dt}$	5.6 - 10.2	g $m^{-2}day^{-1}$	Chrysanthemum morifolium	Hughes (1973b)
		2.07 - 4.72		Impatiens parviflora	Evans (1972)
		8.47		Helianthus annuus	Hunt (1978)
		9.77		Apple	Maggs (1960)
		-21.4 - 17.9		Maize	Briggs et al. (1920b)
Leaf area rate	$\frac{L_A}{w}$	0 - 0.004	$m^2 g^{-1}$	Callistephus chinensis	Evans (1972)
		0.0044		Pinus sylvestris	Hunt (1978)
		0.0006 - 0.022		Maize	Briggs et al (1920a)
		0.0177		Helianthus annuus	Hunt (1978)
		0.01 - 0.02		Chrysanthemum morifolium	Hughes (1973b)
Shoot-root ratio	$\frac{S_w}{R_w}$	2.03 - 2.36	--	Helianthus annuus	Evans (1972)
		3 - 5		Impatiens parviflora	Evans (1972)
		4.17 - 6.17		Helianthus debilis	Evans (1972)
		0.48		Sugarbeet	Milthorpe,Moorby (1979)
Leaf area index	$\frac{L_A}{P}$	0 - 3	--	Sugarbeet	Hunt (1982)
		0 - 8		Wheat	Hunt (1982)
		0.2 - 8.84		Wheat	Austin et al. (1980)
		2.2 - 12.6		Chrysanthemum morifolium	Acock et al. (1978)

destructive, a plant can only be sampled once. This problem has been handled for years in the classical approach by pairing plants. The largest plant in harvest one is paired with the largest plant in harvest two etc. (16,30,40,42). Differences between plants are reduced with this method and the experimental error is primarily random.

Rates estimated using the classical approach are sensitive to sampling errors and environmental variations. Therefore the overall trend might be hard to interpret (16). Curve fitting as described below in the functional approach often makes it easier to follow both the development of the plant and the statistics of interest (15,16,40,42,59).

Functional Approach to Growth Analysis

Fitting functions to experimental data using regression analysis is referred to as the functional approach to plant growth analysis (16,28).

Three statistical requirements must be fulfilled for regression analysis to be valid when fitting functions to growth data. The independent variable (X) should be measured without errors, the distribution of measured Y values at each X should be normal, and the variance of Y at each X should be uniform and not change throughout the analysis (28,42). Time is usually the independent variable and can be virtually measured without errors. But the second and third requirements for regression analysis sometimes cause problems. The conventional method to satisfy the last two requirements is to transform the data (28) by taking the natural logarithm (base e) of each datum point. Transformation using any other base would be equally

efficient to fulfill the statistical requirements (42).

The functional approach has many advantages and computers have made the method possible to use. Complicated mathematical equations once avoided can now be quickly and accurately calculated (40,41,42). Experimental data contain random errors and a fitted function generally smooths these variations to give a growth curve free from large fluctuations (16,42). Each point on the curve contains information from all sampling occasions (40,41,42) and the model with the information condensed into a few parameters often become more important to the experimenter than the data from which it was derived (42).

Available Functions

The two types of functions mainly used in the functional approach to plant growth analysis are polynomial functions and asymptotic functions.

Polynomial functions have been extensively used in plant growth analysis. This is not due to any biological significance, but rather that they are a simple kind of mathematical function (15). Polynomial functions which have linear parameters or parameters which can be transformed to a linear form can be fitted to data by exact and well defined multiple regression techniques (28,63).

A polynomial has the form:

$$y = a + b_1x + b_2x^2 + \ldots + b_nx^n \qquad (11)$$

The coefficients 'a, b_1 . . . b_n' are estimated in the regression

analysis, and the highest power of the independent variable determine the name of the polynomial (15,16,42,59).

The first order polynomial or 'linear regression' have the following form when applied to total plant dry weight (15,16,42).

$$W = a + bT \tag{12}$$

To fulfill the statistical requirements mentioned earlier concerning regression, transformation before curve fitting to natural logarithms is often done. The first order polynomial in exponential form will be:

$$\ln W = a + bT \tag{13}$$

The absolute growth rate (dW/dT) is given by the derivative of equation 12 (42,59):

$$G = dW/dT = b \tag{14}$$

If the natural logarithm is used as in equation 13 the derivative calculates RGR:

$$b = RGR = (d(\ln W))/dT = (1/W) \times (dW/dT) \tag{15}$$

Coefficient 'a' implies the size of the growing system at the time chosen to be zero, and 'b' is the rate of increase in W (absolute

growth) or ln W (RGR). A constantly increasing W will be the result of a positive 'b' value and decreasing W with a negative 'b' value. When 'b' is zero, W will be equal to 'a', see Figure 1a.

The first order polynomials are appropiate functions when growth occurs by equal cell division at regular intervals. But meristematic tissues cannot keep on dividing for long time periods without cell differentiation. The use of first order polynomials is therefore limited to short periods of growth in young plants or parts of plants (42).

The second order polynomial has the form:

$$W \text{ (or } \ln W) = a + b_1T + b_2T^2 \qquad (16)$$

As in the first order polynomial the derivative of equation 16 will give the absolute growth rate when applied to untransformed data and RGR for transformed data.

$$dW/dT \text{ (or } (1/W) \times (dW/dT)) = b_1 + 2b_2T \qquad (17)$$

Coefficient 'a' is the size when T equals zero, 'b_1' represent growth rate at time zero and 'b_2' the amount of curvature or rate of change of the growth rate (42). The second derivative of equation 16 is:

$$d^2W/dT^2 = 2\ b_2 \qquad (18)$$

and this stands for acceleration or the rate of change of the rate of

change of W. A sample of second order curves is shown in Figure 1b.

The second order polynomial is a growth curve where the growth rate always will be a first order function (Figure 1b). This might be a limitation, since no inflections in the growth data can be illustrated. But it is a simple growth curve and good fits are often obtained for at least parts of a growing process (42).

An increase from second to third order polynomial will give the following equation:

$$W \text{ (or } \ln W) = a + b_1T + b_2T^2 + b_3T^3 \qquad (19)$$

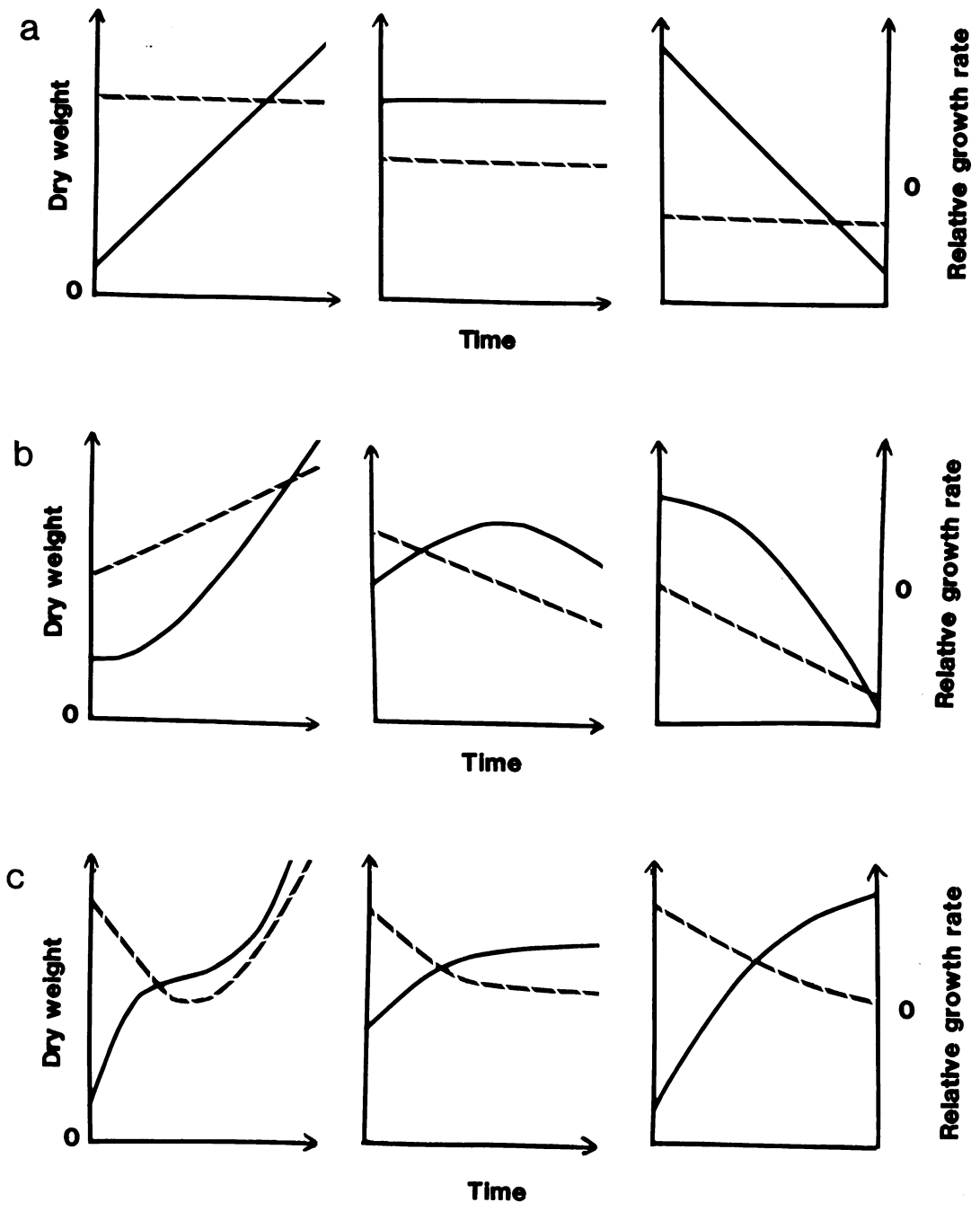
The growth rates of this function are given by

$$dW/dT \text{ (or } (1/W) \times (dW/dT)) = b_1 + 2b_2T + 3b_3T^2 \qquad (20)$$

The cofficient 'a' is as in all polynomials the starting size of the system (42). Growth rate at time zero is given by the coefficient 'b_1'. A third order polynomial can take many different shapes and a few examples are shown in Figure 1c. This polynomial can be considered as a function for relationships which curve in one direction or change curvilinearity over time (42).

Polynomials with higher order than three have great flexibility and can describe many biological processes; however the coefficients don't have any biological significance and the functions are just empirical equations. This is one limitation for use of higher order polynomials. Another possible limitation is the size of the computer

Figure 1. Examples of polynomial curves showing the progression of dry weight (———) and relative growth rate (-———-); a) first order polynomials; b) second order polynomials; and c) third order polynomials.


a
Dry weight
0
Time
0
Relative growth rate
b
Dry weight
0
Time
0
Relative growth rate
c
Dry weight
0
Time
0
Relative growth rate

facility. As the number of coefficients increases, the coefficient's numerical value usually decrease and more memory space is required for precision. There also is a risk for overfitting with higher order polynomials, since a function exactly fitting every point can be developed (16,42). From a growth analysis stand point this is not desirable. No 'smoothing' of the data has been done and the overall trend cannot readily be seen (40,42).

Asymptotic functions are nonlinear in the parameters by means of multiplication, division or exponentiation with each other (16,28,42). Because of the nonlinear nature there is no direct method for parameter estimations. Arbitrary starting values are usually assigned to all or some of the parameters and with this starting equation the best possible statistics are calculated through several iterations. Good calculating facilities are necessary for fitting of nonlinear functions and for many years this has been a limiting factor. Only during recent years with the development of high capacity computers have the asymptotic functions become reasonable to use in growth analysis (16,28,40,41,42).

When equation 15 is integrated the result is the so called exponential equation (42,59):

$$W = a\, e^{bT} \qquad (21)$$

where coefficient 'a' is the initial system size at the beginning of the study and 'b' is the rate of increase in growth (42,59).

The monomolecular function was developed to illustrate the progression of a first order chemical reaction (29,42,48,59). With the

notations used here for growth analysis the monomolecular function has the form (42):

$$W \text{ (or } \ln W) = a(1 - be^{-cT}) \qquad (22)$$

This function is constantly increasing from the point 'a(1-b)' at time zero (28) and has no point of inflection (28,42) as shown in Figure 2a. Coefficient 'a' is the asymptotic value which determines the range of the dependent axis, 'b' is a measure of where the intercept will occur and coefficient 'c' is a rate constant controlling the spread along the independent axis (42,59).

From equation 22 the rate of growth is given by the derivative (42):

$$dW/dT = abc\ e^{-cT} \qquad (23)$$

and

$$1/W \times dW/dT = (bc\ e^{-cT}) \ / \ (1 - b\ e^{-cT}) \qquad (24)$$

The growth rate is proportional to the amount of growth yet to occur (28,42,48,59) and is continuously decreasing (59) see Figure 2a.

The monomolecular growth function has primarily been used for fitting data from later parts of plant growth (28,59).

A growth function where the rate of growth is proportional to the present size and tc some assumed final size is called the <u>logistic</u>

equation (28,29,59), since the original use of this function was for an autocatalytic monomolecular reaction the name autocatalytic is sometimes used (28,29,42,58,59).

The form of the logistic function is:

$$W \text{ (or } \ln W) = a/(1 + b\, e^{-cT}) \qquad (25)$$

The growth curve is S-shaped with an inflection at the point $W = a/2$ (16,29,59). This inflection point divides the curve into two parts which have different directions but otherwise are identical (59). At time zero W is 'a/(1+b)' and the function is asymptotic to $W = 0$ and $W = a$ (29,42,48,59). The constants 'a', 'b' and 'c' have the same biological significance as in the monomolecular function (42,48,59). Growth rate or the slope can be calculated from the derivative of equation 25:

$$dW/dT = (abc\, e^{-cT}) \;/\; (1 + b\, e^{-cT})^2 \qquad (26)$$

and

$$1/W \times dW/dT = (bc\, e^{-cT}) \;/\; (1 + b\, e^{-cT}) \qquad (27)$$

The logistic function is a relatively simple asymptotic function and it often gives a good fit to growth data. Because of this the logistic function has been popular in plant growth analysis (42,59). Figure 2b illustrates the logistic function and its slope.

A third growth function with three coefficients often used is the Gomperz function. The three coefficients are arranged in a double exponent (16,28,29,42,58,59):

$$W \text{ (or } \ln W) = a\, e^{-be^{-cT}} \qquad (28)$$

The final size 'a' is approached asymptotically and W equals zero when $T = -\infty$ (59). At the size 'a/e' (0.3679 a) the point of inflection occurs (28,29,42,59). Many growth data have their maximal growth rates somewhere between 'a/3' and 'a/2', and the Gomperz function will reproduce these growth processes well (59). As in the monomolecular and the logistic functions coefficient 'b' is a measure of initial system size and 'c' is a rate constant (59).

Derivation of equation 28 gives the rate of growth (42):

$$dW/dT = abc\, e^{-cT-b\, e^{-cT}} \qquad (29)$$

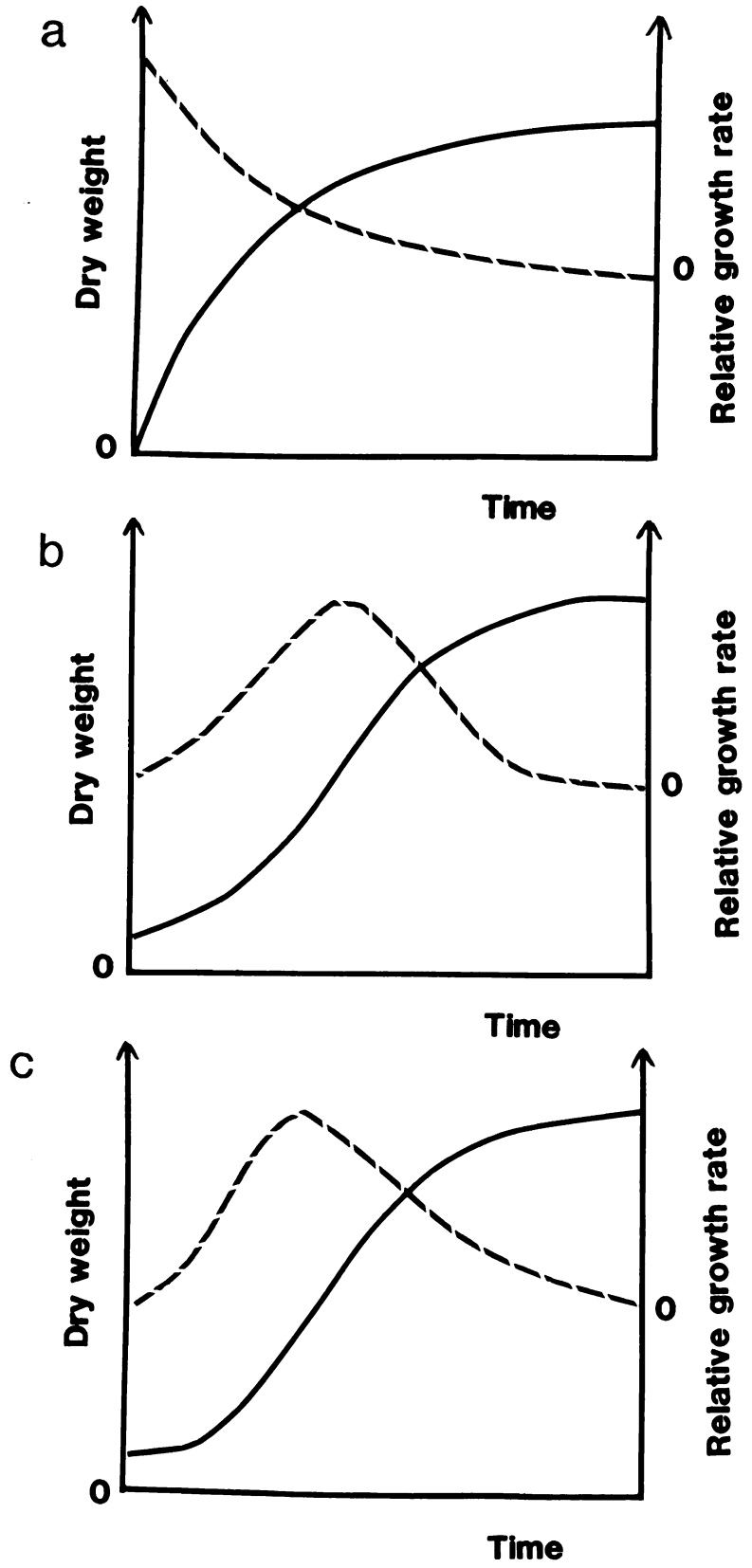
and

$$1/W \times dW/dT = bc\, e^{-cT} \qquad (30)$$

The Gomperz function was developed for work with animals and population studies (16,28,29,59). In plant growth analysis it has often been adapted to growth of parts of plants, especially to leaf growth data (42,58,59). Figure 2c gives a graphical representation of equation 28, 29 and 30.

The Richards function is a four parameter function and was

Figure 2. Examples of nonlinear functions showing the progression of dry weight (———) and relative growth rate (— — —); a) monomolecular function; b) logistic function; c) Gomperz function.


a
Dry weight
0
0
Relative growth rate
Time
b
Dry weight
0
0
Relative growth rate
Time
c
Dry weight
0
0
Relative growth rate
Time

introduced by F.J. Richards in 1959 (28,42,58,59). Its form is shown in equation 31 and the derivatives in equation 32 and 33.

$$W \text{ (or } \ln W) = a(1 \pm e^{(b-cT)})^{-1/d} \tag{31}$$

$$dW/dT = (ac\, e^{(b-cT)}/d)\ ((1 \pm e^{(b-cT)})^{-(1/d+1)}) \tag{32}$$

$$1/W \times dW/dT = (c\, e^{(-b-cT)}) \ /\ (d(1 \pm e^{(b-cT)}) \tag{33}$$

Two examples of Richards function can be seen in Figure 3.

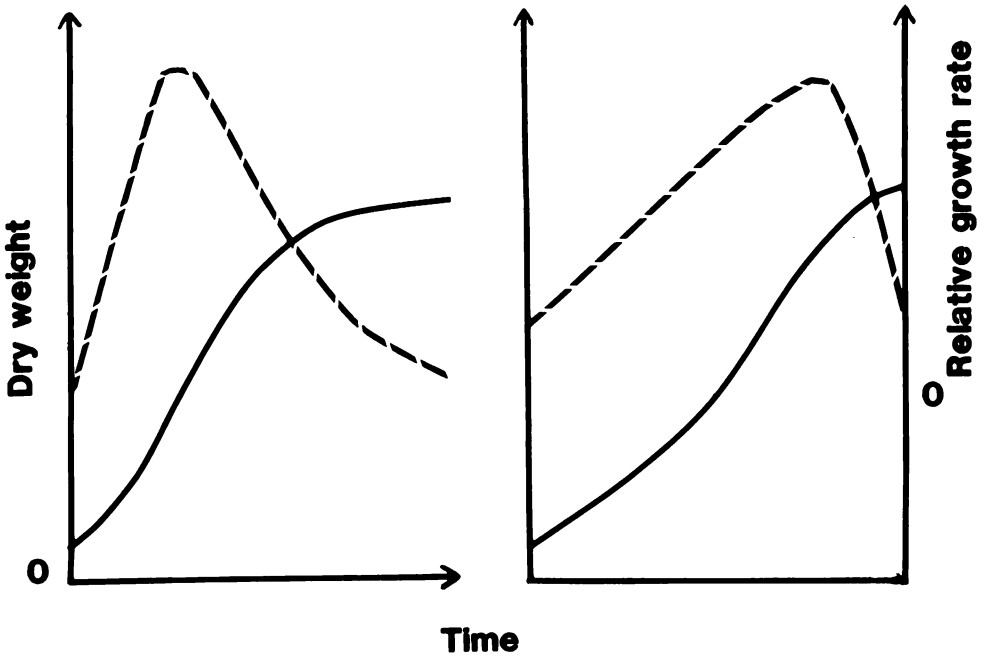
The Richards function was derived from a function developed by von Bertalanffy (16,28,29,58,59). This Bertalanffy function was first used to describe metabolic rates in animals (5) and has the form (5,28):

$$W = (a^{1-m} - b\, e^{cT})^{1/1-m} \tag{34}$$

Because of some theoretical considerations about animal growth von Bertalanffy put limitations on the values 'm' could take (5,16,28). Richards (58) however, pointed out that Bertalanffy function can be useful in growth analysis when 'm' is assigned values of a wider range than originally used (16,28,58,59).

Some values for 'm' are of special interest. When m = 0 Bertalanffy function reduces to the monomolecular function, when m = 2 the function will be the logistic function, when m = 1 the equation cannot be solved, but when m $\rightarrow$ 1 the result will be the Gomperz function (28,58,59). The curve shape will continuously change from

Figure 3. Two examples of Richards curve showing the progression of dry weight (———) and relative growth rate (·—·—·).


Dry weight
0
Time
0
Relative growth rate

monomolecular into Gomperz form when the 'm' value goes from 0 to 1, and from Gomperz into autocatalytic form when 'm' increases from 1 to 2 (59), see Figure 4. Where the inflection point is on the growth curve depends on the size of 'm'. Larger values of 'm' will move the inflection point to the later parts of growth development. In Richards function (equation 31) the coefficient 'd' controls where the inflection point will occur on the growth curve (42). The other coefficients have the same biological significance as in the three earlier mentioned growth functions used in nonlinear growth analysis.

Richards function has lately become popular in growth analysis. It gives a good fit to many plant growth data, especially when parts of plants are studied. In whole plant studies however the first and the last part of the development sometimes cause problems, since Richards function doesn't seem to reproduce the growth pattern well at these developmental stages (42). Another problem, which might be encountered is the increased difficulty of estimating and finding starting values for four instead of three coefficients.

Tables 2 and 3 are a summary of some characteristics for the growth functions discussed here.

The term modeling is now frequently used for studies applying the functional approach to data analysis. Thornley (65) described a model as a set of mathematical equations, which quantitatively represent the assumptions made about a studied system. When equations are fitted to experimental data the model is empirical. This type of modeling is most suitable as a first approach to a problem. It might be possible with this model as a basis, to look at the mechanism behind the responses and make a so called mechanistic model (65).

Figure 4. Shape of the Bertalanffy function when m = 2 (the logistic function); m = 1 (the Gomperz function) and when m = 0 (the monomolecular function).

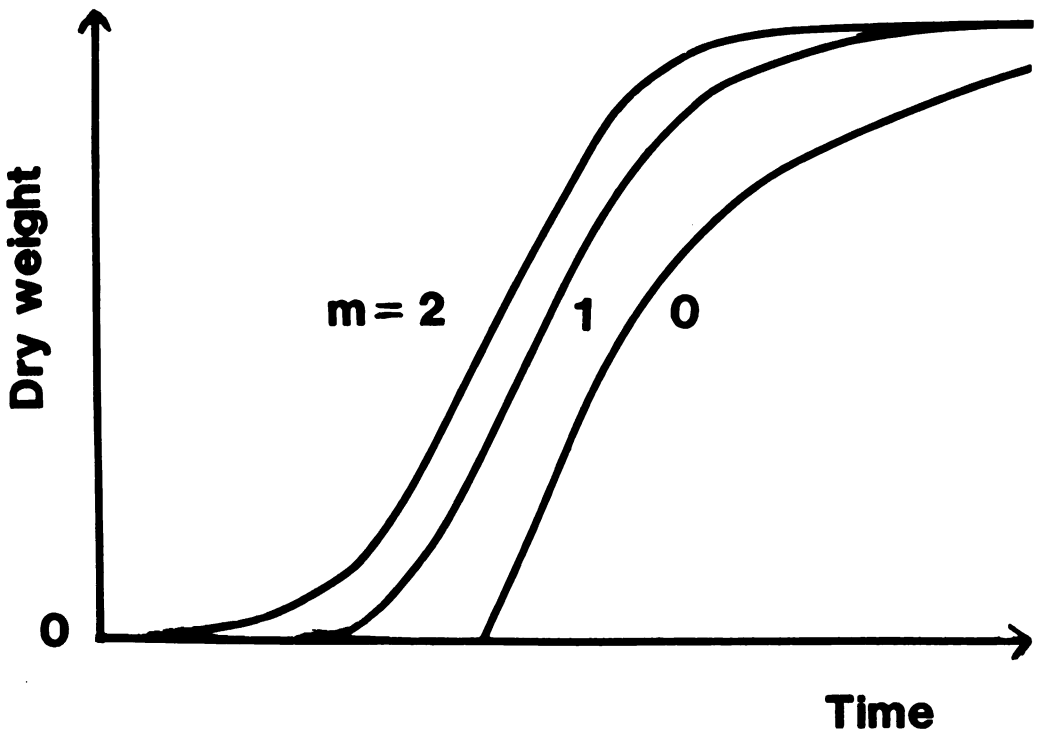

Dry weight
m = 2
1
0
0
Time

Table 2. Characteristics of the monomolecular, logistic, Gomperz and Richard's functions.

Function	Equation	Value of W at t = 0	Value of W at t = ∞	Inflection point in W
Monomolecular	$W = a(1-be^{-cT})$	$a(1-b)$	a	none
Logistic	$W = a/(1+be^{-cT})$	$a/(1+b)$	a	$\frac{a}{2}$
Gomperz	$W = ae^{-be^{-cT}}$	ae^{-b}	a	$\frac{a}{e}$
Richards	$W = a(1\pm e^{(b-cT)})^{-1/d}$	$a(1\pm e)^{-1/d}$	a	variable

Table 3. Characteristics of the monomolecular, logistic, Gompers and Richard's functions.

Function	Absolute growth rate		Relative growth rate	
	untransformed data	transformed[z] data	untransformed data	transformed[z] data
Monomolecular	$abce^{-cT}$	$abce^{(a(1-be^{-cT})-cT)}$	$\frac{bce^{-cT}}{1-be^{-cT}}$	$abce^{-cT}$
Logistic	$\frac{abce^{-cT}}{(1+be^{-cT})^2}$	$\frac{abce^{(a/(1+be^{-cT})-cT}}{(1+be^{-cT})^2}$	$\frac{bce^{-cT}}{1+be^{-cT}}$	$\frac{abce^{-cT}}{(1+be^{-cT})^2}$
Gompers	$abce^{-cT-be^{-cT}}$	$abce^{(ae^{-be^{-cT}}-be^{-cT}-cT)}$	bce^{-cT}	$abce^{-cT-be^{-cT}}$
Richards	$\frac{ace^{b-cT}}{d}.(1\pm e^{b-cT})^{-(1/d+1)}$	$\frac{ace^{b-cT}}{d}.(1\pm e^{b-cT})^{(1/d+1)}.e^{(a(1\pm e^{b-cT})^{-1/d}}$	$\frac{ce^{b-cT}}{d(1\pm e^{b-cT})}$	$\frac{ace^{b-cT}}{d}.(1\pm e^{b-cT})^{-(1/d+1)}$

[z] log base e

The main problem with a functional approach is to decide which function is most suitable to use for the growth analysis in question (16,40,42,67). Classical estimated parameters often give an indication of the overall growth trends and the form of the underlying growth functions can be distinguished easier (30,42). A combination of classical and functional methods is necessary for successful growth analysis.

Influence of Irradiance and Temperature on the Development of Chrysanthemum morifolim Ramat.

Chrysanthemum morifolium Ramat. is one of the most important crops grown in commercial greenhouses today (2). This review, will emphasize how irradiance and temperature influence the growth and development of chrysanthemums grown as pot plants. The influence of irradiance and daylength on time to flower and plant appearance (height, number of leaves and flowers, flower diameter etc.) will be described, followed by the influence of different day and night temperatures on time of development and final plant appearance. Partitioning of dry matter will be discussed in the last part of the literature review.

Introduction

Chrysanthemum morifolium Ramat. has been classified as a short day (SD) plant (14,24,62). The critical photoperiod was reported in 1939 to be 14 1/2 hours (9 1/2 hours darkness) (54). Later Post (55) discovered that 14 1/2 hours was the critical photoperiod for flower bud initiation and that the critical photoperiod for development of the flower buds was 13 1/2 hours (10 1/2 hours darkness). The time necessary for flower development after start of short days varies with cultivar; cultivars are classified into response groups based on the number of weeks from start of SD to flower (46). Response groups vary from 6 weeks to 15 weeks (3).

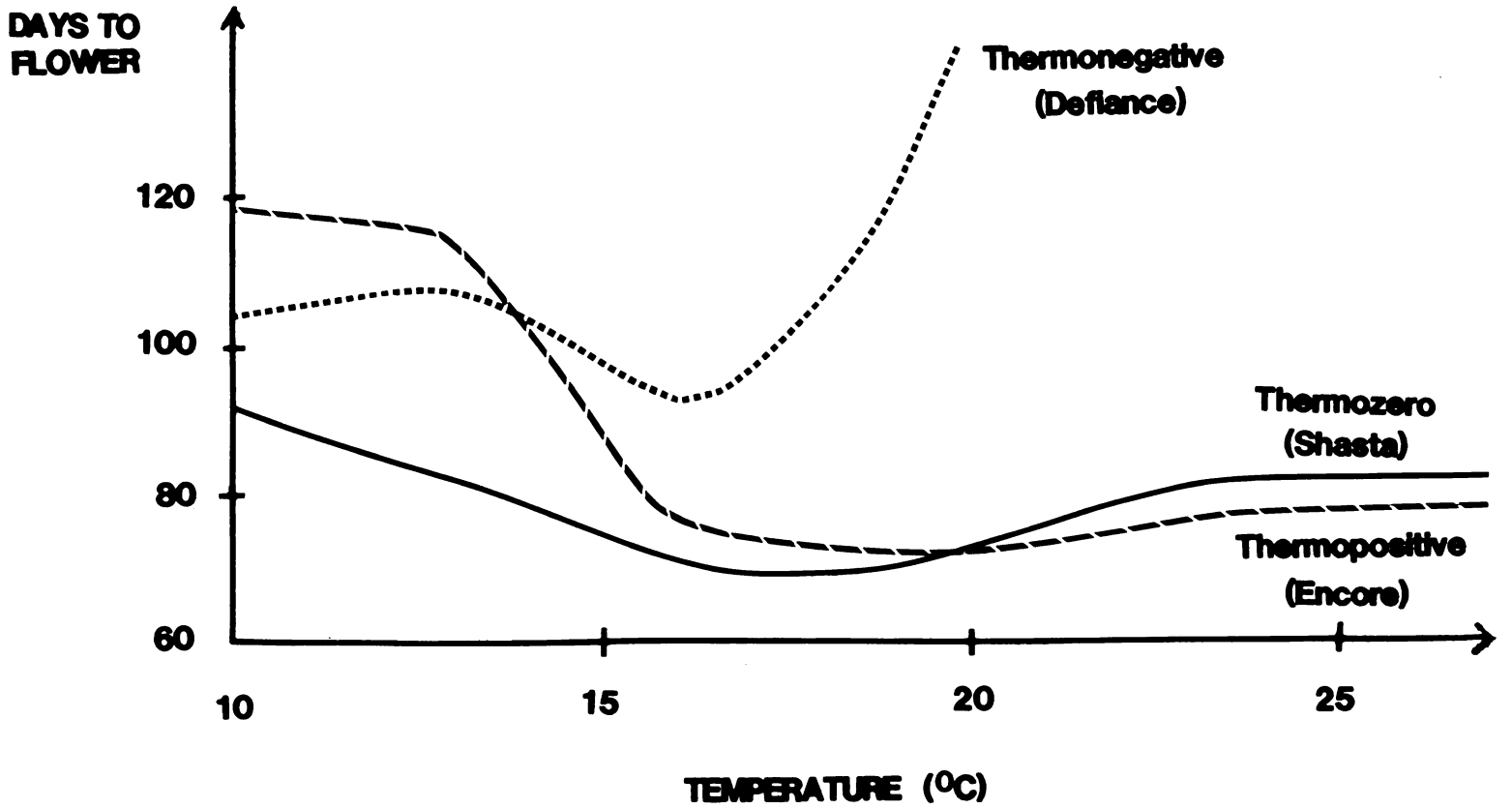
Doorenbos and Kofranek (27) found flower initiation to initially occur at the same rate after the start of SD in early (9 weeks) and late cultivars (14 weeks) but subsequent flower development was slower in the late varieties. Critical daylength was shorter for late cultivars than early cultivars (32). Langhans (46) published the critical daylengths for different response groups after data by Cathey (15) (Table 4).

Flower development in chrysanthemum is affected by both photoperiod and temperature. In 6 to 7 week response group cultivars, temperature seemed to be the dominating factor, while daylength was more important for the development of a longer response group (47). Cathey (12) divided chrysanthemums into three different groups based on their response to temperature. Cultivars that flowered in a temperature range of 10° to 27° with the fastest development at 16° and only slight delay at 10° and 27° were called thermozero cultivars. When a minimum temperature of 16° was necessary for initiation of flower buds, the cultivars were called thermopositive. In this group temperatures below 16° inhibited initiation and development of flower buds. The third group was called thermonegative, since temperatures above 16° inhibited flowering. Flower buds in this group were initiated at higher temperatures but failed to develop. Figure 5 shows the response of temperature on time to flowering for a thermozero, a thermonegative and a thermopositive cultivar. When the cultivar Lilian Doty was grown at 13°, 17° and 21°, SD only induced flowering under 21°. The plants remained vegetative at the lower temperatures even with SD (60). Post and Lacey (56) showed that high temperatures during SD also can delay flowering. It appears that bud initiation and development under SD is

Table 4. Critical photoperiod for flower bud initiation and flower bud development of 5 varieties of chrysanthemums grown at a 16°C temperature (from Langhans, 1964 after data from Cathey, 1954).

Variety	Response group	Critical photoperiod (hrs)	
		Flower bud initiation	Flower bud development
White Wonder	6	16	13 3/4
Pristine	8	15 1/4	12
Encore	10	14 1/2	12
Fortune	12	13	12
Snow	15	11	10

Figure 5. Number of days from start of short days to flower for a thermopositive, thermonegative and thermozero variety planted in early January from stock plants kept at 16°. The plants were grown in a night temperature range from 10 to 27°. (Redrawn from Machin and Scope 1978 after data from Cathey 1954a).


DAYS TO FLOWER
120
100
80
60
10
15
20
25
TEMPERATURE (°C)
Thermonegative (Defiance)
Thermozero (Shasta)
Thermopositive (Encore)

dependent on temperature and optimum temperature varies with cultivar (47).

A partially differentiated shoot apex where complete development is arrested is called a crown bud (14). This kind of bud has strap-shaped leaves beneath it, while a normal terminal bud has lobed leaves below it (14). Flowering is often described with criteria like number of developed leaves, number of days to visible bud or days to anthesis and a measure for vegetative growth often used is internode length (14).

Irradiance

Schwabe (62) found that the time required for flower bud initiation and time to flower under short days to be affected by seasonal changes in Quantum Flux Density (QFD). As irradiance increased, the transition to reproductive development as indicated by earlier appearance of flower buds and less number of leaves below the bud, began earlier even though all plants were under short days (19,62). Hughes (34) experimenting with different daylengths and irradiance found vegetative growth to be primarily dependent on total daily irradiance, irrespective of photoperiod (8 or 12 hour). Fastest flower development occured under the conditions of highest irradiance (95 J $cm^{-2}d^{-1}$) and 8 hours daylength. This irradiance corresponds to 150 µmol $s^{-1}m^{-2}$ during the 8 hours light span. An almost linear relationship between total dry weight and irradiance at constant daylength was observed (34).

The cultivar 'Bright Golden Anne' flowered after 70 short days

when grown under either 125 or 250 J cm^{-2} 8-hr d^{-1} (200 or 400 µmol $s^{-1}m^{-2}$ for 8 hours) (36). At 31 and 63 J cm^{-2} 8-hr d^{-1} (50 and 100 µmol $s^{-1}m^{-2}$ for 8 hours) flowering occured after 94 and 87 short days respectively. Cockshull and Hughes (23) concluded that an irradiance of 125 J cm^{-2} for 8 hours per day (200 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}), was adequate for normal flower development.

Transferring plants from an irradiance of 63 to 125 J cm^{-2} d^{-1} (from ca. 100 to 200 µmol $s^{-1}m^{-2}$ on an 8 hour basis) during the first two weeks of short days hasten flower initiation and decreased time to flowering compared to plants grown continuously at 63 J $cm^{-2}d^{-1}$ (24). The effect on flower development was greatest when the high irradiance was provided at the beginning of short days; two weeks at 125 J $cm^{-2}d^{-1}$ (ca. 200 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}) were more efficient (faster flower initiation and development) than one week. A low irradiance (31 J $cm^{-2}d^{-1}$, corresponding to ca. 50 µmol $s^{-1}m^{-2}$ for 8 hr d^{-1}) after the two initial weeks at 125 J cm^{-2} d^{-1} for 8 hr d^{-1} did not stop further development of flowers but the final flower quality was poor (retarded floret initiation and a large variability in flower development) due to the low average irradiance of 47 J $cm^{-2}d^{-1}$ (75 µmol $s^{-1}m^{-2}$ for 8 hr d^{-1}) during the whole short day period (24). Plants grown continuously at 63 J $cm^{-2}d^{-1}$ had a more variable development than plants under 125 J $cm^{-2}d^{-1}$ (24,36). Cockshull and Hughes (23) showed this increased variability to be due to variable flower initiation under the lower light at the beginning of short days. Chrysanthemums under a constant irradiance of 125 J $cm^{-2}d^{-1}$ developed similar to plants receiving the same total irradiance but given alternately as 31 and 219 J $cm^{-2}d^{-1}$ (50 and 350 µmol $s^{-1}m^{-2}$ for 8

hr d^{-1}) (24). This similarity is not surprising as the reaction of light in photosynthesis is primarily photochemical (50). The amount of photosynthetically active quanta absorbed will determine photosynthesis and the dry matter production would be expected to be similar at the same average QFD (50).

Stepped irradiance was studied by Hughes and Cockshull (37) in an effort to resemble diurnal irradiation with higher intensities at noon and lower intensities at the beginning and end of a day. Morphology and growth in the range from 31 to 250 J $cm^{-2}d^{-1}$ (50 to 400 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}) was found to be a function of total daily irradiance rather than to changing irradiance during the day.

Schawbe (62) concluded that the seasonal differences in time to flower was correlated with changes in irradiance. However no seasonal changes in leaf number were observed. When Cockshull and Hughes (24) grew plants under 63 and 125 J cm^{-2} d^{-1} (100 and 200 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}) they found a higher leaf number at the lower irradiance. Similar results have been reported by Hughes and Cockshull (36); 15 leaves were formed at 31 J cm^{-2} d^{-1} (50 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}), 10 at 63 J cm^{-2} d^{-1} (100 µmol $s^{-1}m^{-2}$) and 7-8 leaves at 125 and 250 J cm^{-2} d^{-1} (200 and 400 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}). The shoot height was shorter in the highest and the lowest irradiance (15.8 - 21.7 cm) than in the middle two irradiance levels (16.6 - 27.4 cm)(36).

Supplemental lighting of flowering pot plants during low light conditions often result in improved quality (11). Lighting at 5 W ft^{-2} for 10 hr d^{-1} (270 µmol $s^{-1}m^{-2}$, 10 hr d^{-1}) of 6-inch pot chrysanthemums during dark winter months resulted in plants with increased flower

number (up to 5 flowers/plant), dry weight (2-4 grams/plant) and stem diameter. An increase in plant height (13 - 39 % depending on cultivar) also occured under the increased irradiance (11).

Even under continuous long days, chrysanthemums will eventually initiate flower buds. The number of leaves initiated under long day conditions varied both with variety and time of year (17,47). However when the cultivars were ranked by leaf number, their relative positions were always the same as shown in Table 5. Flower initiation in long days was related to an ageing process of the apical meristem (17,18,47). The time necessary for this process was influenced by environmental factors. Cockshull (19) found that under continuous irradiance (24 hours a day) fewer leaves were initiated at 120 W m^{-2} (550 µmol $s^{-1}m^{-2}$) in the cultivars 'Polaris' and 'Bright Golden Anne' prior to flower bud initiation than on plants grown under 7.5 W m^{-2} (35 µmol $s^{-1}m^{-2}$). Above 60 W m^{-2} (280 µmol $s^{-1}m^{-2}$) the leaf number approached a minimum and the rate of leaf initiation increased with irradiance reaching a maximum above 60 W m^{-2}. Temperatures in the range 16 to 28^{o} had little effect on time to flower initiation in continuous light (17,18).

Cockshull and Hughes (23) found the number of initiated florets per flower to be higher when plants were grown at 375 J $cm^{-2}d^{-1}$ (600 µmol $s^{-1}m^{-2}$ for 8 hr h^{-1}), than when grown at 31 J $cm^{-2}d^{-1}$ (50 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}). The irradiance level between the 15th to 21st short days was the most important in influencing floret number.

Total dry weight increase was approximately proportional to increasing irradiance up to 125 J $cm^{-2}d^{-1}$ (200 µmol $s^{-1}m^{-2}$ for 8 hr d^{-1}), while a linear effect of irradiance in the range 63 to 250

Table 5. Numbers of leaves and bracts initiated before the flower on five cultivars of chrysanthemum grown in long days (Natural daylength plus 5 h night break). (After Cockshull, 1974).

Cultivar	Date of Planting			Average
	6.13.73	10.10.73	5.29.74	
Tuneful	45.3	90.3	56.9	64.2
Gold Crystal	44.0	69.2	49.5	54.2
Polaris	33.5	56.1	40.8	43.5
Bluechip	29.9	48.4	33.8	35.4
Bright Golden Anne	20.3	34.3	18.4	24.3

J $cm^{-2}d^{-1}$ (100 to 400 μmol $s^{-1}m^{-2}$, 8 hr d^{-1}) on flower dry weight was observed (24,37,38,39). Carbon dioxide enrichment had a greater effect on flower dry weight than on total dry weight. Hughes and Cockshull (36) explained this to faster flower development and greater partitioning of dry matter to the flowers.

Lowering irradiance (from 375 to 125 J $cm^{-2}d^{-1}$ or from 125 to 31 J $cm^{-2}d^{-1}$) during any stage of the short day period generally reduced both total and flower dry weight (23). Higher irradiance (125 or 375 J $cm^{-2}d^{-1}$) during the first four weeks of short days didn't result in any detectable increased total dry weight at time of flowering if plants were shifted to a lower irradiance during the final 6 weeks of development. Transfers after five weeks of short days to higher irradiance from lower irradiance levels produced a significant increase in total dry weight. After five weeks maximum leaf area had developed and a higher irradiance could be used more efficiently by the plants to produce dry matter (23).

Only a small difference in total dry weight production has been detected when the same total irradiance (in a range up to 250 J $cm^{-2}d^{-1}$) was given during a day, irrespective of daily timing (34). For example, the average daily irradiance could be given in a rising and falling diurnal cycle (37); by alternating days at high and low irradiance (24) or by exposing plants to different irradiance with inversely compensating daylengths (34).

There did not appear to be a requirement for a certain leaf number or area before flower initiation could occur (23). However flower initiation was delayed under low irradiance (31 and 63 J cm^{-2} 8-hr d^{-1}), and the number of leaves formed often was larger

compared to plants grown under 250 J cm^{-2} 8-hr d^{-1}). Total leaf area per plant was similar for all light treatments and maximum leaf area was developed by the end of six to seven weeks of short days (23). Hughes and Cockshull (36) found a smaller total leaf area under low irradiance (31 J cm^{-2} 8-hr d^{-1}) and CO_2 concentration (325 µl l^{-1}), than under 125 J cm^{-2} 8-hr d^{-1} and 900 µl l^{-1} CO_2. The higher irradiance and CO_2 combinations generally had a larger leaf area, but no consistent pattern could be distinguished.

Unit Leaf Rate (ULR) increased with increasing irradiance (31 - 250 J cm^{-2} 8-hr d^{-1}) and CO_2 levels (325 - 600 µl l^{-1}) from 0.08 to 0.5 mg cm^{-2} d^{-1} when the plants were 20 days old (36). When this experiment was repeated with plants initially smaller, the ULR was higher for corresponding combinations of irradiance and CO_2. A downward trend for ULR occurs on growing and developing plants since intraplant shading increases as the plant gets larger (36). Leaf Area Ratio (LAR) decreased with increasing light and flower development (36).

The Relative Growth Rate (RGR) when the plants were 40 days old decreased from 0.042 d^{-1} under a 12 hour photoperiod with a high irradiance (33 J $m^{-2}s^{-1}$, corresponding to ca. 150 µmol $s^{-1}m^{-2}$ for 12 hr d^{-1}) to 0.035 d^{-1} under an 8 hour photoperiod with a low irradiance (22 J $m^{-2}s^{-1}$ or 100 µmol $s^{-1}m^{-2}$, 8 hr d^{-1}) (34). Under the same conditions, LAR increased from 90 to 160 cm^2g^{-1} (0.0009 - 0.016 m^2g^{-1}), while ULR decreased from 0.39 to 0.2 mg $cm^{-2}d^{-1}$ (3.9 - 2 g $m^{-2}d^{-1}$) (34).

Plants grown in daylengths of 8 or 12 hours didn't show any difference in specific respiration rates (34). However, there was a

decrease over the dark period and the overall period of development. Based on total dry weight, mature flowers were found to have the same respiration rate as the rest of the plant (34).

Hughes and Tsjuita (39) found Leaf Weight Ratio (LWR) to be relatively unaffected by irradiance. However Hughes and Cockshull (36) found that LWR was greater on chrysanthemums grown under low irradiances (31 - 63 J cm^{-2} 8-hr d^{-1}) than at higher irradiances (125 - 250 J cm^{-2} 8-hr d^{-1}).

Temperature

A night temperature of 27° hasten bud formation and plants had a lower percentage of blind shoots (shoots failing to form flower buds) than when plants were exposed to a night temperature of 10° C (54). A combination of low night and high day temperature (10° and 21°C) produced more flower buds than the reciprocal combination (21° night and 10° day temperature). Under low irradiances and high temperature conditions the initiation of flower buds was poorer (more blind shoots) than under higher irradiances (54).

The cultivar 'Sea Gull' formed flower buds under night temperatures from 16° to 32°, but at an average night temperature of 32° C the buds failed to develop into flowers. At 30° C, flowering was delayed 11 days compared to plants grown under cooler night temperatures (33).

Cathey (12) studied temperature effects on bud initiation and flower development in chrysanthemum. His results showed delayed bud initiation at temperatures either above or below 16° C. The longer the

high or low temperatures were maintained during bud initiation the greater the delay (12).

Samman and Langhans (61) found low night temperature during the initiation phase to give the greatest delay in flower development with a maximum delay at 4.5°. Similar results have been reported by Vince (68). Low night temperature (4.5° - 10°) during initiation until the bud was visible delayed flowering up to 100 days and at the lowest temperature (4.5°) most cultivars failed to flower. Low night temperature (4.5° - 10°) after the visible bud stage had little or no effect on flower development. However an interaction between night temperature and light intensity was observed. A reduced QFD (1/3 of average natural daylight during fall and winter in England) during the short day period delayed flowering considerably.

Several cultivars were investigated in a Dutch study to find optimum night temperature for flower development (43). The best development occured at night temperatures between 17° and 21° C. Cathey (13) reported 16° to be the best temperature for growth of chrysanthemums. The difference in results may be due to cultivar differences or the difference in latitude between the two places where the experiments were conducted (Holland at 52° north and Ithaca, New York at 43° north) (43). At Ithaca the experiment started in January and was conducted under natural days, in Holland short days (15 hours dark) were provided with black cloth.

At a temperature combination of 22° day and 18° night, chrysanthemums flowered in the least number of days. An increase or decrease in either day or night temperature from this combination increased the time necessary for flower development (7).

The cultivars 'Polaris' and 'Bright Golden Anne' initiated flowers between 10° and 28° C under continuous light (24 hours a day). The fastest bud initiation occurred in the temperature range 16° to 22°. But only at the two lowest temperatures (10° and 16°) did the initiated buds develop into flowers (19).

Chrysanthemums grown under so called split night temperatures (10 hours light at 22° followed by 4 hours dark at 16° and 10 hours dark at 10°, compared to 10 hours light at 22° and 14 hours dark at 16°) showed an average 4 days delay in flowering compared to 'normal' night temperature of 16°. The averaged temperature (for 24 hours) in this experiment with split night temperatures was 11.8° and at 'normal' temperatures 18.5° (53).

A temperature regime with night temperatures of 17° for the first half of the dark period (8 hours); 10° for the remaining 8 hours and a day temperature at 22° resulted in a 3 day delay in time to flowering (52).

Flowering was delayed when night temperatures were reduced for 7 1/2 hours from a constant 16° (8). As the low temperature duration (down to 10° C) increased from 6 to 10 1/2 hours during the night flowering delay increased from 4 to 11 days.

Lowering night temperature from 16° to 13° C delayed flowering 3 to 8 days in experiments by Tsujita et al. (66). The delay was due to retarded flower bud development rather than delayed flower initiation.

Cathey (13) concluded that "the temperature during the dark period was 3.3 times more effective in hastening flowering than temperature during the light period" and that "the averaging of night

and day temperature or mean temperature was not correlated with flowering time". Cockshull et al. (25) pointed out that the way Cathey (13) calculated mean temperature by averaging day and night temperatures without taking the number of hours these temperatures were kept into consideration was misleading and made a recalculation of the result presented by Cathey (13). The new values showed that average temperature was important for flower development and that night temperature didn't have any special influence on time to flower by itself. Flower development in experiments conducted by Cockshull et al. (25) was correlated with average temperature with time to bud appearance decreasing from 42 to 26 short days as temperature increased from 10° to 20°. Kohl and Thigpen (44) grew plants at night temperatures of 15.6° and 5.6°. Under the lower night temperature the development was 25 days slower. Just lowering the night temperature to 5.6° C for the first 21 days of short days resulted in flowering 6 days later than when grown at 15.6° C throughout. Night temperatures at 15.6° C for the first 3 weeks under short days and the remaining period at 5.6° caused a delay of 16 days (44). Zieslin and Kohl (72) achieved similar results with continuous night temperatures of 5.5° and 16.5°, however the delay in development was even larger (35 days) at 5.5°.

Night temperatures lower than 16° during flower bud initiation increased the leaf number and stem length. The cultivar 'Shasta' initiated on average 10 more leaves at 2° night temperature than at 16° C and the stem length increased ca. 25 cm. Day temperature was kept at a minimum of 21° C (61).

A decrease in night temperature from 16° to 10° during the period from the start of short days until buds became visible gave an

increase in leaf number with 6 leaves (68).

Mean internode length was longer under night temperatures of 15.6° than 10° C; the average length was 1.9 cm and 1.2 cm respectively. Day temperature was held at a minimum of 15.6°, but maximum temperature was uncontrolled and varied with time of year (69). When plants were transferred from 15.6° to 10° C, the third internode from the last leaf was expanding at time of temperature change and showed a significant reduction in length compared to when grown continuously at 15.6° C; the third and the sixth internode showed significantly increases in length when night temperature was changed from 10° to 15.6° C and the response was comparable to plants grown at 15.6° C throughout (69).

Bonaminio and Larson (8) compared number of nodes on plants grown in an environment of 16° constant night temperature or when the temperature was reduced to 10° for part of the night. No difference in the number was found, but the plants under reduced night temperature grew taller.

Internode length on plants grown in a climatic environment with different day and night temperatures was not the same as when a constant temperature corresponding to the average of the different day and night temperatures was used (25). At a lower day temperature the internode length was shorter and Cockshull et al. (25) stated "the main influence on internode extension was exerted by the day temperature, although this effect was accentuated in some cultivars if the following night temperature was low".

Height of plants at 21° - 23° day temperature and 10° night

temperature was found by Tawagen and Hassan (64) to be shorter than plants under 16° C night temperature. Bonaminio and Larson (7) reported similar results for chrysanthemums grown under day/night temperatures of 30°/26° C and 18°/14° C. However, when Kohl and Mor (45) kept chrysanthemums under a day temperature of 21°-27° C and night temperatures of 5° and 15.6° C, the plants under the lower night temperature grew taller.

Several cultivars showed an increase in stem length when the temperature during part of the night was lowered from 15.5° to 10° C. This trend was even more accentuated when plants were provided supplemental light (ca. 40 μmol $s^{-1}m^{-2}$) during cloudy days. In this study day temperature was kept at 18° on cloudy days and at 22° on sunny days (52).

The number of flowers per plant decreased with decreasing night temperature (from 27° to 10°), but the average flower diameter increased by ca. 1 cm from 3.8 to 4.7 cm (54). Cathey (13) found that high night temperature produced flowers with more petals. Chrysanthemums grown at 10° had 6 flowers per plant, while a temperature of 16° resulted in 12 flowers per plant (64). Several researchers (68,52,45) found an increased number of flowers at lower night temperatures.

Increases in flower diameter with a decreased night temperature have been reported by Bonaminio and Larson (8) and Tsujita et al. (66). The night temperature after visible bud appeared to be most important for flower size with an optimum temperature at 10° C. An even lower temperature at 4° C produced larger flowers, but the quality was "somewhat inferior" (68). For fast and high quality production of

chrysanthemum Vince (68) recommended 16° night temperature up to visible bud followed by 10° - 13°.

Increased leaf area under decreased temperatures has been found in several experiments (7,8,53). The rate of leaf emergence however, was faster as temperature increased (25).

Several growth statistics (relative growth rate, unit leaf rate, leaf area, plant dry weight and leaf dry weight) were larger when the temperature was lowered for parts of the night from 'normal' night temperature (53). Leaf Area Ratio and Leaf Weight Ratio decreased and Specific Leaf Area didn't show any difference between the higher and the lower night temperatures (53). Respitory dry weight losses in plants are temperature dependent. A decrease in temperature should decrease the respiration rate and reduce dry weight losses. The increased RGR supported this theory (45,53).

Kohl and Thigpen (44) showed that the rate of dry weight gain could be the same if the Leaf Area Index was adjusted according to growth. The critical LAI in this experiment was found to be 2.7 - 3.0. If the LAI was kept at or above the critical value there was no difference in dry weight accumulation at 5.6° and 15.6° C. The efficiency with which the plants utilized provided Photosynthetically Active Radiation (PAR) was shown by Kohl and Mor (45) to be better at a night temperature of 5.6° rather than 15.6° C. This greater efficiency was explained to be due to a lower respiration during low night temperatures (45).

Partitioning of Dry Matter

The percentage dry matter partitioned to the leaves stayed the same (about 46%) when chrysanthemums were grown vegetatively for 5 - 6 weeks at 20° C under different irradiances in the range from 1.9 to 9.2 MJ m^{-2} d^{-1} (300 - 1470 μmol $s^{-1}m^{-2}$, 8 hr lightspan d^{-1}). At a higher temperature (30°) the percentage partitioned to the leaves increased. The leaf area, however increased with lower irradiances and higher temperatures (1).

Cockshull and Hughes (21) studied flower weight ratios (the weight of the flower divided by the total plant dry weight) in plants grown under different environments. They found that the heaviest plants always had the highest flower weight ratio. The proportion of the total dry matter going into the flowers was highly correlated with stage of flower development and the number of flowers per plant didn't seem to significantly influence the partitioning pattern. To improve flower weight and quality, either an overall increase in plant dry weight or a decrease in number of flowers per plant seemed to be necessary. Cockshull (20) and Cockshull and Hughes (21) have pointed out the importance of early disbudding to produce larger flowers.

As the flowers developed, they increasingly became the primary sink for dry weight accumulation and the weight of vegetative parts became relatively constant. But when all flowers were removed dry matter was diverted into other parts of the plant, primarily the roots and to some extent the leaves. The extension of stems stopped when the flower buds were taken away, although the accumulation of dry matter continued in the stem and the weight per unit stem increased. From this

experiment Cockshull and Hughes (22) suggested that there was no severe depression in the rate of dry matter production per unit leaf area when the primary sink was taken away in chrysanthemums.

Woodson and Boodley (71) found that stems and petiols attained their maximum dry weight before the 8th week of growth when the fast flower development started in the cultivar 'Gt.#4 Indianapolis White'. The leaves however, continued to accumulate dry matter during flower development. The temperature in the greenhouse was kept at 24° day and 18° night, black cloth was used to provide a photoperiod of 15 hours dark and the plants were grown single stem. Under these conditions at least, the photosynthetic capacity seemed to exceed the demand from the sinks in this variety (71).

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LITERATURE CITED

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SECTION I

INFLUENCE OF QUANTUM FLUX DENSITY AND TEMPERATURE ON FLOWERING TIME AND PLANT QUALITY OF *CHRYSANTHEMUM MORIFOLIUM* RAMAT. 'BRIGHT GOLDEN ANNE'.

Influence of Quantum Flux Density and Temperature on Flowering Time and Plant Quality of Chrysanthemum morifolium Ramat. 'Bright Golden Anne'.

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Additional index words. central composite design, modeling

Abstract. Chrysanthemum morifolium 'Bright Golden Anne' plants were grown under 15 combinations of Quantum Flux Density (QFD), day temperature, and night temperature in a central composite design. The influence of these environmental factors on flowering time and plant quality is reported both quantitatively and qualitatively. Time to flower depended on both irradiance and the interaction between day and

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Received for publication _____. Michigan Agricultural Experiment Station No. _____. This project was supported in part by grants from the Fred C. Gloeckner Foundation, the American Florists Endowment, and the US Department of Agriculture Small Business Innovation Research program (grant no. 83SBIR-8-0001) in collaboration with Oglevee Computer Systems. Chrysanthemum cuttings were donated by Yoder Brothers, Inc., Barberton, OH. The cost of publishing this paper was defrayed in part by the payment of page charges. Under portal regulation, this paper therefore must be hereby marked advertisement solely to indicate this fact.

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night temperature. At a constant 20° C temperature, time to flower decreased from 90 to 60 days when QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$. Increasing either day or night temperature from 14° to 26° delayed flowering. High temperature delay was compensated for in part by increased QFD. Regression analysis showed shoot length to increase linearly as day temperature increased. Low night temperature accentuated the day temperature response. Total flower area increased as QFD increased or as night temperature decreased.

Introduction

While the influence of environmental factors on growth and development in many greenhouse crops has been extensively studied, few experiments have addressed several environmental factors simultaneously. Simultaneous evaluation of several environmental factors is important when determining the functional relationship between the environment and plant response. Commercially available computer systems for greenhouse climate control allow environmental control to be interactive. For example, temperature and CO_2 concentration can be controlled based on Quantum Flux Density (QFD) in the greenhouse (16). However to use this type of computer control system, one must know the functional relationship between environmental factors and subsequent growth and development of a particular plant.

Both time to flower and plant quality are the primary factors of concern in commercial production of chrysanthemums. While an extensive body of literature exists on Chrysanthemum morifolium Ramat., we are unaware of any information describing the functional

relationships between chrysanthemum growth and the environmental factors of day temperature, night temperature and QFD. This paper adresses this problem by describing such functions.

Materials and Methods

Rooted cuttings of Chrysanthemum morifolium 'Bright Golden Anne' were planted individually in 10 cm pots and placed in growth chambers (Sherer-Gillete, Marshall, Michigan) under a QFD of 325 µmol $s^{-1}m^{-2}$ (16 hr d^{-1}) at a constant temperature of 20° C for seven days. On the seventh day after potting, short day (SD) photoperiod was initiated (10 hr light, 16 hr dark) and plants were pinched to six nodes and placed under appropriate treatment combinations (Table 1) with the thermoperiod following the photoperiod. Daminozide was applied 7 and 14 days after the start of SD at 2500 mg l^{-1}. Ten days after the start of SD, lateral shoot number was reduced to 3 per plant. Lateral flower buds were removed when they had reached a stage where removal would not damage the apical flower bud.

Shelves were lowered as necessary to maintain the desired QFD at the canopy top; QFD was measured with a Li-Cor LI-185B Meter and LI-190SB Quantum sensor. The QFD was provided by cool-white flourescent lamps (GE, F48T12, CW 1500) and incandescent lamps (GE, 40 W, 120 V) with an input wattage of 80:20 respectively. Average daily temperature fluctuated ± 1° C from the setpoint and QFD varied ± 10%.

Plants were grown in a peat-lite medium (VSP, Michigan Peat Co.) and were automatically irrigated one to three times daily depending on plant size and environmental conditions using an

individual emitter in each pot. Nutrition consisted of 200 mg l^{-1} N and K at every watering provided by ammonium nitrate, potassium nitrate and nitric acid (used to adjust water pH to 6.0). Necessary leaching occurred at each watering to prevent salt accumulation.

A central composite statistical design (1,15,22) was used. Ranges for the three factors were 50 to 600 μmol $s^{-1}m^{-2}$ for QFD and 10 - 30° C for both day and night temperature (Table 1). Regression analysis was computed using the SPSS subprogram 'Regression' (25).

Data were collected on five plants the day the plants were potted, at start of SD and every 10 days thereafter. Time to flower was determined as the day when half the flowers in the population had reflexed their outermost petals to a horizontal position. The QFD was measured at the canopy top and recorded when a plant was sampled. On each sample date, leaf area, leaf number, stem length, flower diameter and dry weight of these plant parts were collected on the original and three lateral shoots. Root dry weight was also determined for each plant at each sampling occasion.

Only data on time to flower and final stem length, leaf number and flower size are reported in this paper. The remaining data will be published elsewhere (21). Treatments will be referred to with three numbers corresponding to QFD, day temperature, and night temperature, e.g. 50-20-20 is the first treatment in Table 1.

Results and Discussion

Time to flower depended on both irradiance and the interaction between day and night temperature (Table 2, Figure 1). A second order

equation to predict time to flower was developed (Table 3). The simple r values (Table 4) indicated QFD to be the main factor promoting early flowering. Simple r is the estimated first-order correlation between the dependent variable and the independent variable (25). At a constant 20° C day and night temperature, time to flower decreased from 90 to 60 days as QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$ (Table 2); at 325 μmol $s^{-1}m^{-2}$, flowering occured in 70 days. The delay under 50 μmol $s^{-1}m^{-2}$ appears to be due to slowed development and not delayed initiation as flowering shoots in all three treatments had similar node numbers. This contrasts to work by others (10,11,12,18,27) which showed hastened flower initiation under high irradiance conditions. A possible explanation for this difference is that all plants in our experiment received one week of long days (LD) at 325 μmol $s^{-1}m^{-2}$ (16 hr d^{-1}) prior to the start of the treatment environments. Since most plants can be grown successfully under 50 W m^{-2} (ca. 250 μmol $s^{-1}m^{-2}$) in growth chambers (2,9,28) 325 μmol $s^{-1}m^{-2}$ is a very acceptable QFD. In that research (10,11,12,18,27), plants were given the same QFD during both the LD and SD periods. Therefore sufficient carbohydrate reserves may have accumulated during the LD period in our experiment to allow rapid flower initiation even under the low QFD treatments while carbohydrate levels may have limited rapid flower initiation in the previously reported low irradiance treatments (10,11,12,18,27).

The simple r values (Table 4) also indicated that both increasing day or night temperature within the experimental range delayed flowering. Treatment combinations with higher day than night temperature showed greater flowering delay than the reciprocal combinations (325-30-20 vs. 325-20-30 and 490-26-14 vs. 490-14-26). The

high temperature delay was compensated for in part by increased QFD. Under 160 μmol $s^{-1}m^{-2}$ and a day and night temperature of 26°, flowering occurred after 90 days; an increase in the QFD to 490 μmol $s^{-1}m^{-2}$ decreased flowering time by 10 days.

While high (above 30°) and low (4.5 - 10°) night temperatures were found to delay flowering initiation (14,26,30), Cockshull et al. (13) reported the average daily temperature to be the factor controlling rate of plant development rather than the specific day or night temperature. The average temperature relationship did not hold in this experiment. Plants flowered in 70 days with average temperatures varying from 14° to 21° C (Table 2).

Considering that shoots had similar node numbers (9-11 nodes) under a wide diversity of environments (Table 2), it appears no treatment environment specifically accelerated flower initiation but rather adverse environments delayed initiation. For example, plants in three treatments had significantly higher node numbers combined with delayed flowering; all three treatments are characterized by high temperature conditions (160-26-26, 325-30-20, and 490-26-26). High temperatures have been found to delay flower initiation and flowering in chrysanthemum (8,30).

The response to QFD and temperature explain why time to flower in chrysanthemum does not vary significantly on a year around basis. In the winter, while greenhouse temperature control is good, irradiance limits the rate of development (Figure 1a). In the summer, irradiance is not limiting but greenhouse temperature regularly exceeds 20°. As day or night temperature exceeds 20°, flowering is delayed (Figure 1c).

Therefore time to flower in the chrysanthemum on a year around basis is controlled by the relationship between greenhouse temperature and the QFD from solar radiation. Flowering time can only be minimized under conditions of high QFD and an acceptable temperature control.

Irrespective of night temperature or QFD, plants grown in combinations with a high day temperature (above 20°) were tall with stem lengths about 30 cm. Plants grown at 14° day temperatures had an average stem length of 16 cm. Simple r values confirm these observations (Table 4). A plot of the regression equation predicts stem length to increase in a linear fashion as day temperature increases (Figure 2). Low night temperatures accentuate the day temperature response. Cockshull et al. (13) also reported day temperature to be the main environmental factor controlling height in chrysanthemum. They reported high day temperature caused stem elongation independent of what the night temperature was, although a low night temperature appeared to accentuate the effect of day temperature.

While the number of leaves per shoot increased on plants grown under constant high temperature (26°), the average internode length did not increase compared to plants grown at 20° temperature. On plants grown under high day and low night temperatures (160-26-14, 490-26-14 and 325-20-10), the opposite response occurred; no change in leaf number but average internode length increased (Table 2).

Flower size is important for plant quality, but since people perceive the total flower area per plant rather than the diameter of individual flowers, total flower area was calculated. Simple r values (Table 4) indicate increasing QFD or decreasing night temperature to be the primary factors positively affecting flower area. As QFD increased

from 160 to 490 μmol $s^{-1}m^{-2}$ and night temperature decreased from 26° to 14°, total flower area increased from 34 cm^2 to 304 cm^2, almost a 10-fold increase (Table 2). The response to increasing QFD by itself or decreasing temperature by itself increased flower area, but to a smaller extent. The response to low night temperature has been reported before (4,29,30). Flower area was also reduced by high day temperature, especially in combinations with high night temperature (Figure 3).

Part of the increased flower area per plant under higher QFD was due to increased uniformity of flower size on all three shoots (Table 2). While flower diameter varied from 1.2 to 7.4 cm on plants grown under 50-20-20, flower size only varied from 9.7 to 11.7 cm on plants grown under 600-20-20. Increased uniformity has been one of the primary advantages cited when plants received supplemental irradiation under low QFD conditions in greenhouses (11,23,24).

In summary, increasing day temperature from 10° to 30° increased stem length, increased time to flower, and decreased flower area. Increasing night temperature from 10° to 30° slightly decreased stem length, increased time to flower, and greatly decreased flower area. Increasing QFD from 50 to 600 μmol $s^{-1}m^{-2}$ had no effect on stem length, but decreased time to flower, and increased flower area. High day temperature interacts with night temperature to further delay flowering and decrease flower area while a low night temperature interacts with high day temperature to increase stem length.

While many of the influences of QFD and temperature on Chrysanthemum morifolium flower time and plant quality have been previous reported, we believe this is the first time that all these

factors have been simultaneously reported both quantitatively and qualitatively. The real significance of this type of research lies in its ability to predict plant response under environmental conditions not specifically tested. For example, Table 5 shows the predicted time to flower, final stem length, and flower area per plant on plants grown under 4 different environmental conditions. The first two environments represent production under winter conditions in a northern U.S. greenhouse with and without supplemental irradiation at 75 μmol $s^{-1}m^{-2}$ for 10 hr d^{-1} (ca. 575 fc from high pressure sodium lamps). The last two environments represent summer production in a greenhouse at different temperatures.

The supplemental irradiation during winter is predicted to decrease time to flower by 3 days, have no effect on shoot length, and increase flower area by 20%. Publications on the use of supplemental lighting have shown similar responses (5,6,7,17,19). In the summer, decreasing day and night temperature is predicted to decrease time to flower by 10 days, decrease stem length 3 cm, and increase flower area by 90%. The direction and relative magnitude is expected (3,4,8,14,20,29,30,31).

The major limitation to this research is that plants were maintained under constant conditions throughout the development and this work represents one cultivar 'Bright Golden Anne'. Future work must be directed at determining the functional response to a changing environment, the vegetative growth period and to other cultivars.

Table 1. Actual and coded values for treatment combinations used in the central composite design.

Treatment number	QFD (μmol $s^{-1}m^{-2}$)	Temperature (^{o}C)		Coded values		
		Day	Night	QFD	DT	NT
1	50	20	20	-1.68	0	0
2	160	14	14	- 1	- 1	- 1
3	160	26	14	- 1	1	- 1
4	160	14	26	- 1	- 1	1
5	160	26	26	- 1	1	1
6	325	20	20	0	0	0
7	325	10	20	0	-1.68	0
8	325	30	20	0	1.68	0
9	325	20	10	0	0	-1.68
10	325	20	30	0	0	1.68
11	490	14	14	1	- 1	- 1
12	490	26	14	1	1	- 1
13	490	14	26	1	- 1	1
14	490	26	26	1	1	1
15	600	20	20	1.68	0	0

Table 2. Influence of QFD, day temperature and night temperature on growth and development of Chrysanthemum morifolium 'Bright Golden Anne'

Environment												
QFD	Temp (°C)		Average daily temp(°C)	Time to flower[z] (days)	Avg shoot length (cm)	Avg No. Leaves per shoot	Internode length[y] (cm)	Flower diameter (cm)			Total plant flower area (cm^2)	Relative flower area per plant
($\mu mols^{-1}m^{-2}$)	Day	Night						Shoot 1	Shoot 2	Shoot 3		
50	20	20	20.0	90	17	11	1.7	7.4	9.0	1.2	108	39
160	14	14	14.0	70	16	10	1.6	11.5	8.4	4.5	175	63
160	26	14	19.0	80	31	11	3.1	6.4	8.8	4.8	111	40
160	14	26	21.0	80	17	11	1.7	6.6	5.1	3.4	64	23
160	26	26	26.0	90	29	15	1.9	4.6	3.9	2.6	34	12
325	20	20	20.0	70	21	10	2.1	11.7	10.8	10.5	286	
325	20	20	20.0	70	23	11	2.2	12.2	11.6	10.0	301	100
325	20	20	20.0	70	22	10	2.2	11.8	11.8	5.6	243	
325	10	20	15.8	70	10	9	1.0	8.6	7.5	5.8	129	47
325	30	20	24.2	90	28	14	2.0	4.9	6.0	4.8	65	23
325	20	10	14.2	70	30	10	3.1	12.4	9.9	8.7	257	93
325	20	30	25.8	80	18	11	1.7	5.4	6.1	3.4	61	22
490	14	14	14.0	70	16	11	1.4	11.9	11.9	10.2	304	110
490	26	14	19.0	75	31	10	3.1	11.6	11.9	9.7	291	105
490	14	26	21.0	70	16	12	1.4	8.1	8.6	5.5	133	48
490	26	26	26.0	80	31	14	2.2	6.6	6.9	7.0	110	40
600	20	20	20.0	60	17	10	1.7	11.7	11.3	9.7	282	102

[z]From start of SD to 50% of the flowers had reflexed the outermost petals to a horizontal position.

[y]Shoot 2.

Table 3. Regression coefficients for time to flower, shoot length and flower area per plant in Chrysanthemum morifolium 'Bright Golden Anne'.

Regression[z] coefficient	Time to flower (r^2 = .89)	Shoot length (r^2 = .89)	Flower area per plant (r^2 = .88)
Constant	112.070	18.011	-422.150
QFD	- .247E-1	.144E-1	.826
DT	-2.947	1.33	39.413
NT	-1.69	-2.06	19.218
$(QFD)^2$	.708E-4	- .364E-4	- .375E-3
$(DT)^2$	.918E-1	- .453E-2	-1.182
$(NT)^2$	.573E-1	.504E-1	- .631
QFD x DT	- .113E-2	.394E-3	.842E-2
QFD x NT	- .168E-2	.592E-4	- .202E-1
DT x NT	.243E-1	- .106E-1	.111

[z]QFD = Quantum Flux Density; DT = Day temperature; NT = Night temperature

Table 4. Simple r values for time to flower, shoot length and flower area per plant in Chrysanthemum morifolium 'Bright Golden Anne'.

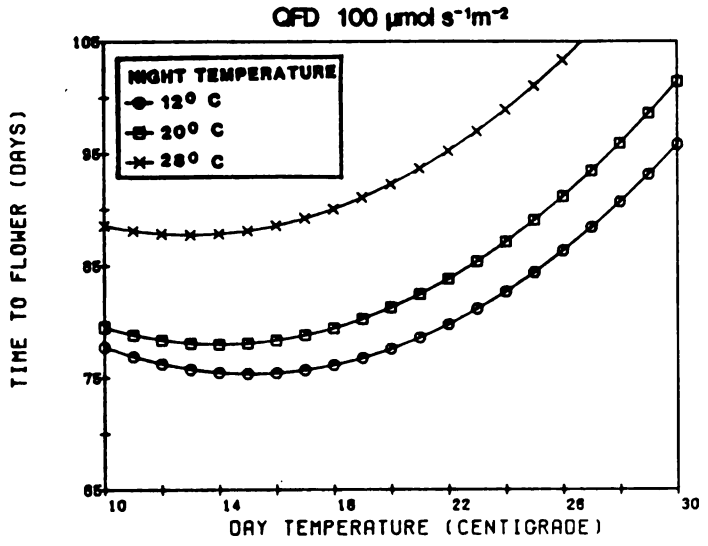
Regression[z] coefficient	Simple r		
	Time to flower	Shoot length	Flower area
QFD	-.58	-.01	.57
DT	.53	.87	-.17
NT	.35	-.19	-.62
$(QFD)^2$	-.56	-.04	.57
$(DT)^2$	.57	.86	-.21
$(NT)^2$	.36	-.15	-.63
QFD x DT	-.24	.45	.40
QFD x NT	-.34	-.10	.13
DT x NT	.63	.47	-.55

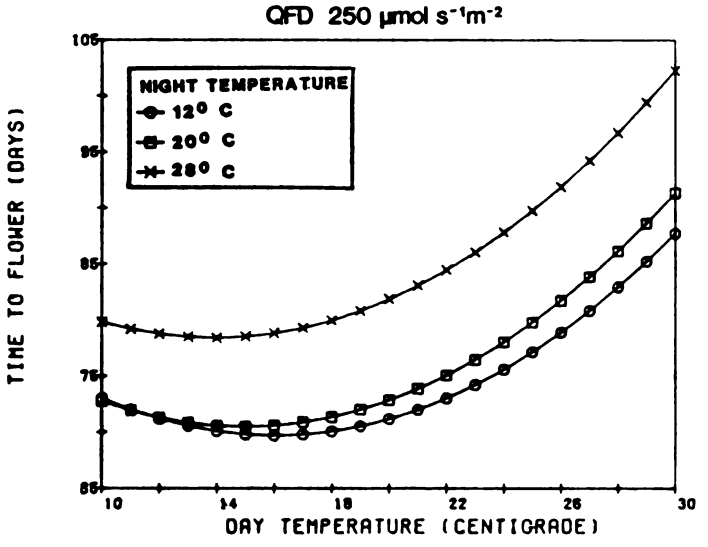
[z]QFD = Quantum Flux Density; DT = Day temperature; NT = Night temperature

Table 5. Time to flower, final shoot length and flower area predicted for Chrysanthemum morifolium 'Bright Golden Anne' grown under four different environments.

Environment			Predicted		
QFD ($\mu mols^{-1}m^{-2}$)	Temp (^oC) Day	Night	Time to flower (days)	Shoot length (cm)	Flower area (cm^2)
175	20	16	74.4	22.3	180.8
250	20	16	71.1	22.9	219.2
400	28	22	81.0	29.1	127.5
400	24	18	71.3	26.2	238.3

Figure 1. Predicted time to flower as effected by day temperature, night temperature, and QFD for Chrysanthemum morifolium 'Bright Golden Anne', at a) 100 µmol $s^{-1}m^{-2}$; b) 250 µmol $s^{-1}m^{-2}$; and c) 400 µmol $s^{-1}m^{-2}$.


QFD 100 µmol s⁻¹m⁻²
NIGHT TEMPERATURE
12° C
20° C
28° C
TIME TO FLOWER (DAYS)
105
95
85
75
65
10
14
18
22
26
30
DAY TEMPERATURE (CENTIGRADE)


QFD 250 µmol s⁻¹m⁻²
NIGHT TEMPERATURE
12° C
20° C
28° C
TIME TO FLOWER (DAYS)
105
95
85
75
65
10
14
18
22
26
30
DAY TEMPERATURE (CENTIGRADE)

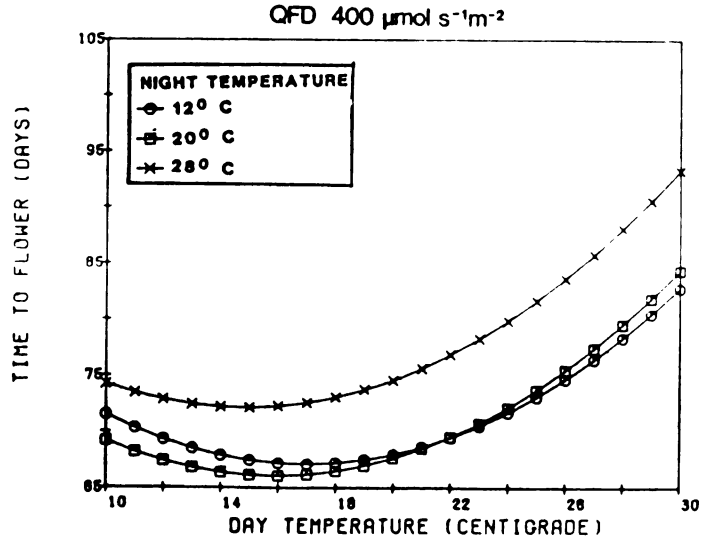

QFD 400 µmol s⁻¹m⁻²
NIGHT TEMPERATURE
12° C
20° C
28° C
TIME TO FLOWER (DAYS)
105
95
85
75
65
10
14
18
22
26
30
DAY TEMPERATURE (CENTIGRADE)

Figure 2. Predicted final shoot length as effected by day temperature and night temperature for Chrysanthemum morifolium 'Bright Golden Anne' at 325 μmol $s^{-1}m^{-2}$.

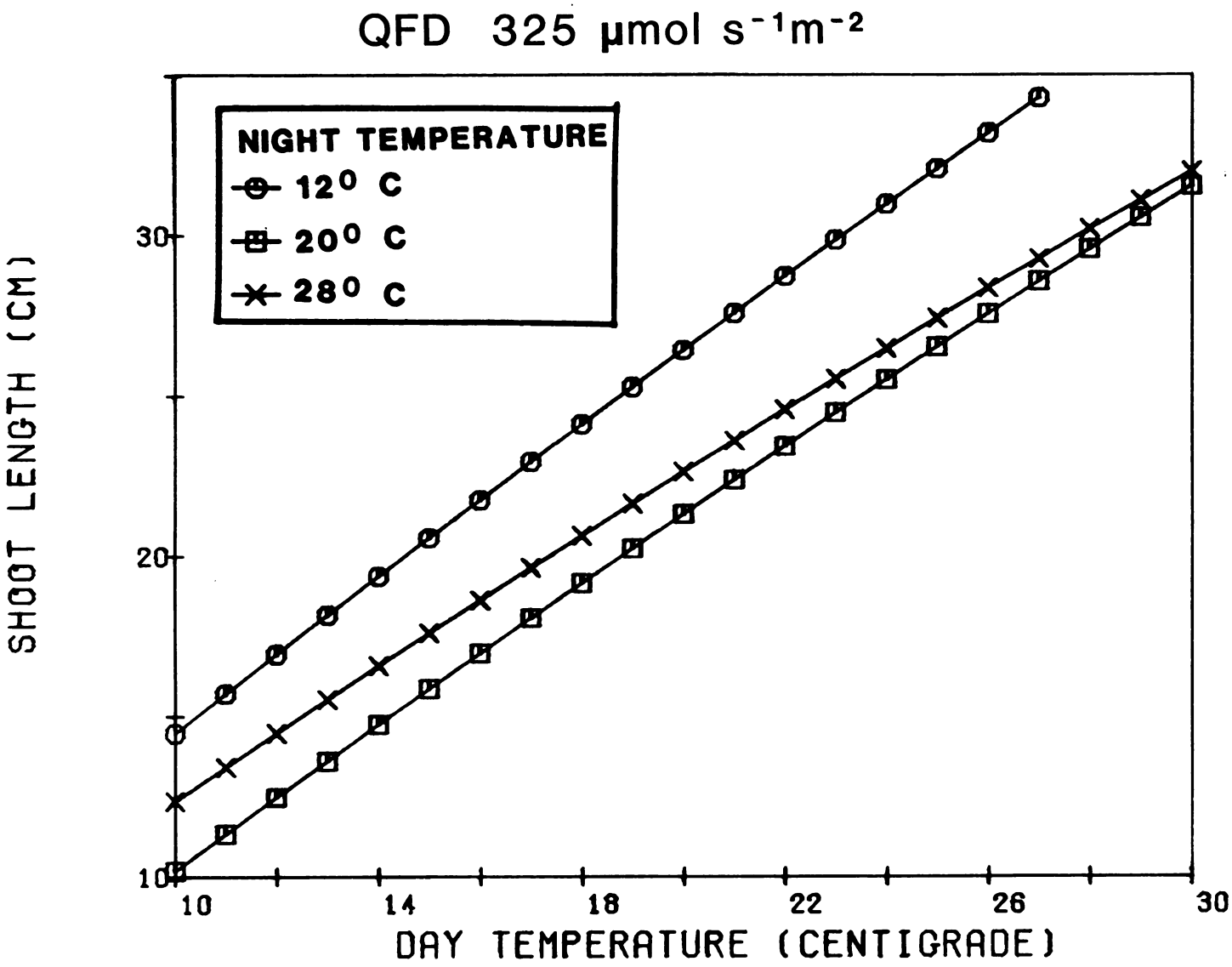
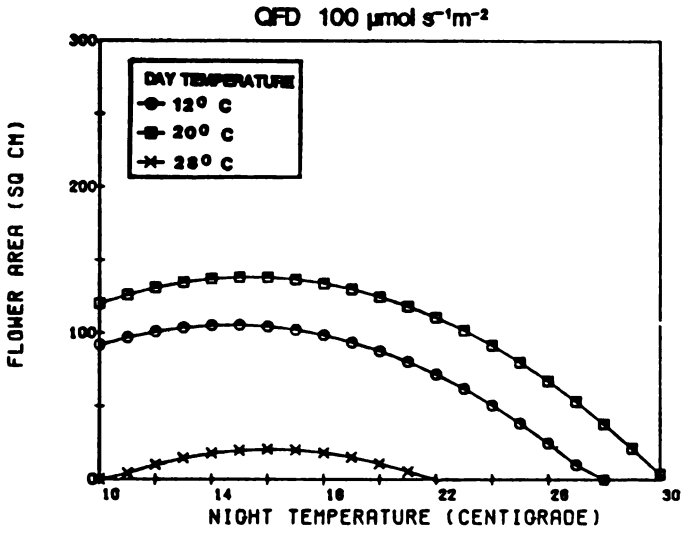
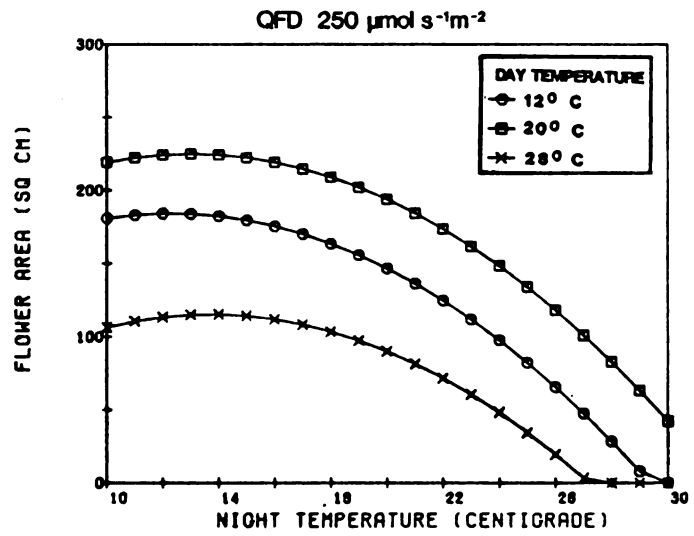
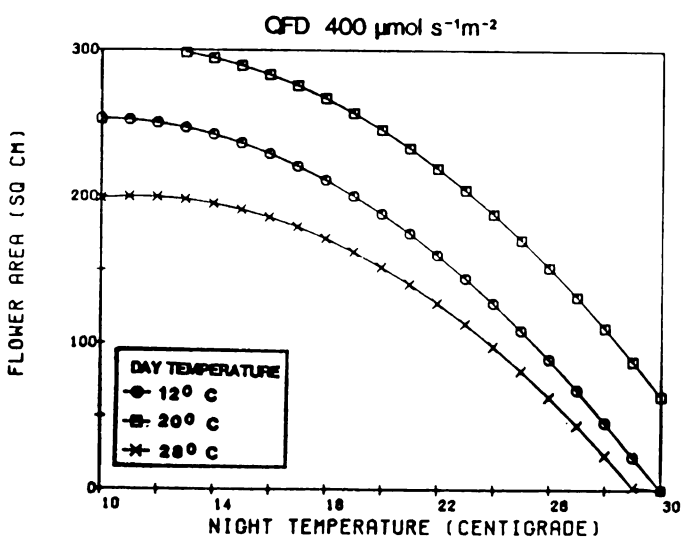

QFD 325 µmol s⁻¹m⁻²
NIGHT TEMPERATURE
12⁰ C
20⁰ C
28⁰ C
SHOOT LENGTH (CM)
30
20
10
10
14
18
22
26
30
DAY TEMPERATURE (CENTIGRADE)

Figure 3. Predicted flower area per plant as effected by day temperature, night temperature and QFD for Chrysanthemum morifolium 'Bright Golden Anne', at a) 100 μmol $s^{-1}m^{-2}$; b) 250 μmol $s^{-1}m^{-2}$; and c) 400 μmol $s^{-1}m^{-2}$.


QFD 100 µmol s⁻¹m⁻²
DAY TEMPERATURE
12° C
20° C
28° C
FLOWER AREA (SQ CM)
300
200
100
0
10
14
18
22
26
30
NIGHT TEMPERATURE (CENTIGRADE)


QFD 250 µmol s⁻¹m⁻²
DAY TEMPERATURE
12° C
20° C
28° C
FLOWER AREA (SQ CM)
300
200
100
0
10
14
18
22
26
30
NIGHT TEMPERATURE (CENTIGRADE)


QFD 400 µmol s⁻¹m⁻²
DAY TEMPERATURE
12° C
20° C
28° C
FLOWER AREA (SQ CM)
300
200
100
0
10
14
18
22
26
30
NIGHT TEMPERATURE (CENTIGRADE)

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LITERATURE CITED

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SECTION II

INFLUENCE OF QUANTUM FLUX DENSITY AND TEMPERATURE ON DRY WEIGHT ACCUMULATION AND PARTITIONING IN *CHRYSANTHEMUM MORIFOLIUM* RAMAT. 'BRIGHT GOLDEN ANNE'.

Influence of quantum flux density and temperature on dry weight accumulation and partitioning in Chrysanthemum morifolium Ramat. 'Bright Golden Anne'.

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Department of Horticulture, Michigan State University,

East Lansing, MI 48823

SUMMARY

Chrysanthemum morifolium 'Bright Golden Anne' plants were grown under 15 combinations of Quantum Flux Density (QFD), day temperature, and night temperature in a central composite design. The influence of these environmental factors on total plant dry weight and partitioning to roots, leaves, stems, and flowers is reported quantitatively and qualitatively. Final total dry weight was primarily influenced by the interaction between QFD and day and night temperature. At flowering final dry weight varied from 4.1 g on plants grown under 50 μmol $s^{-1}m^{-2}$ and 20° C day and night temperature to 18 g on plants grown under

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Received for publication _____. Michigan Agricultural Experimental Station No. _____. This project was supported in part by grants from the Fred C. Gloeckner Foundation, the American Florists Endowment, and the US Department of Agriculture Small Business Innovation Research program (grant no. 83SBIR-8-0001) in collaboration with Oglevee Computer Systems. Chrysanthemum cuttings were donated by Yoder Brothers, Inc., Barberton, OH.

[1]Research Assistant and Associate Professor respectively.

490 μmol $s^{-1}m^{-2}$ and 26° day and night temperature. Partitioning to roots, stems, leaves and flowers was primarily influenced by QFD or day temperature. As QFD increased, partitioning to the roots and leaves decreased; partitioning to the stems and flowers however increased. Increasing day temperature promoted partitioning to the stems but decreased partitioning to the roots. Actual flower dry weight was correlated with total dry weight (r^2 = .77).

INTRODUCTION

While many studies have shown environmental factors to influence the partitioning pattern and total amount of dry matter accumulated in plants (e.g. Bula, et al. 1959, Cockshull and Hughes, 1967, Hammer and Langhans, 1976, Hughes and Cockshull, 1969, Merritt and Kohl, 1983), few have addressed the functional relationship between the environment and partitioning (Armitage, et al. 1981, Hammer and Langhans, 1976). A knowledge of the functional relationships is necessary if the advantage of computerized environmental control in greenhouses is to be realized. This advantage includes the ability to control the environment for optimized plant growth or to minimize production costs based on such factors as solar radiation and stage of plant development. Since little information is known on the functional relationship between partitioning in chrysanthemum and the environment, this study was undertaken to develop such information so growth optimization models can be developed.

MATERIAL AND METHODS

Rooted cuttings of Chrysanthemum morifolium 'Bright Golden Anne' were planted individually in 10 cm pots and placed in growth chambers (Sherer-Gillete, Marshall, Michigan) under a Quantum Flux Density (QFD) of 325 μmol $s^{-1}m^{-2}$ (16 hr d^{-1}) at a constant temperature of 20° for seven days. On the seventh day after potting, short day (SD) photoperiod was initiated (10 hr light, 16 hr dark) and plants were pinched to six nodes and placed under appropriate treatment combinations (Table 1) with the thermoperiod following the photoperiod. Daminozide was applied 7 and 14 days after the start of SD at 2500 mg l^{-1}. Ten days after the start of SD, lateral shoot number was reduced to 3 per plant. Lateral flower buds were removed when they had reached a stage where removal would not damage the apical bud.

Shelves were lowered as necessary to maintain the desired QFD at the canopy top; QFD was measured with a Li-Cor LI-185B Meter and LI-190SB Quantum sensor. The QFD was provided by cool-white flourescent lamps (GE, F48T12, CW 1500) and incandescent lamps (GE, 40 W, 120 V) with an input wattage of 80:20 respectively. Average daily temperature fluctuated 1° C from the setpoint and QFD varied 10%.

Plants were grown in a peat-lite medium (VSP, Michigan Peat Co.) and were automatically irrigated one to three times daily depending on plant size and environmental conditions using an individual emitter in each pot. Nutrition consisted of 200 mg l^{-1} N and K at every watering provided with ammonium nitrate, potassium nitrate and nitric acid (used to adjust water pH to 6.0). Necessary leaching occurred at each watering to prevent salt accumulation.

A central composite statistical design (Gardiner, et al. 1976, Armitage, et al. 1981, Karlsson, et al. 1983) was used. Ranges for the three factors were 50 to 600 μmol $s^{-1}m^{-2}$ for QFD and 10 - 30° C for both day and night temperature (Table 1). Regression analysis was computed using the SPSS subprogram 'Regression' (Nie, et al. 1975). Simple r values are presented to show the relationship between each environmental factor and the dependent variables.

Data were collected on five plants the day the plants were potted, at start of short day and every 10 days thereafter. Time to flower was determined as the day when half the flowers in the population had reflexed their outermost petals to a horizontal position. The QFD was measured at the canopy top and recorded when a plant was sampled. On each sample date, leaf area, leaf number, stem length, flower diameter and dry weight of these plant parts were collected on the original and three 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 conveyor accessory. Dry weights were determined after 3 days drying at 50° C.

Only data on leaf area and dry weights are reported in this paper. The remaining data will be published elsewhere (Karlsson and Heins, 1984). Treatments will be referred to with three numbers corresponding to QFD, day temperature, and night temperature, e.g 50-20-20 is the first treatment in Table 1.

RESULTS AND DISCUSSION

Final total plant dry weight (DW) was primarily influenced by QFD (Table 2, Figure 1). Under a constant temperature of 20°, total accumulated DW increased from 4.1 grams to 15.3 grams as QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$. Chrysanthemums grown under the four temperature combinations at 160 μmol $s^{-1}m^{-2}$ had less total DW than plants grown under the same four combinations at 490 μmol $s^{-1}m^{-2}$. In addition to the response to QFD, simple r values indicated a strong positive interaction between QFD and day and night temperature. As day temperature and night temperature increased from 14° to 26° at 160 or 490 μmol $s^{-1}m^{-2}$, total DW increased 62% and 55% respectively. A plot (Figure 1) of the regression equation (Table 3) graphically demonstrates the relationship between QFD and day temperature. The increased final DW was not due to delayed flowering under higher temperatures as the total DW after 60 SD showed a similar relationship to that at flowering (Table 2). Similar responses to QFD and day temperature were reported by Armitage, et al. (1981) for marigolds. They did not report any response to night temperature however.

Parups and Butler (1982) reported increased plant DW when the night temperature was lowered for part of the night from the 'normal' night temperature of 16°. Respiratory losses were expected to be less with the low night temperature (Parups and Butler, 1982, Kohl and Mor, 1981). Either respiration at night did not vary significantly with temperature in this experiment or the 26° night temperature promoted photosynthesis as plants from treatments 490-14-14 and 490-14-26 flowered in the same number of days (Table 2) and had a similar final

DW (11.6 vs 11.8 g). Alternatively the photosynthetic rate during the day might have increased proportional to any increased night respiration on the 490-14-26 plants.

Root DW increased with increasing QFD and decreased with increasing day temperature (Table 2). As QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$ at a constant 20° C, root DW increased from 0.4 g to 3.6 g per plant, and as day temperature increased from 10° to 30° C at 325 μmol $s^{-1}m^{-2}$ and 20° night temperature, root DW decreased from 1.5 to 0.5 g per plant. Similar responses to QFD have been reported by Rhykerd, et al. (1960) and Bula, et al. (1959) for alfalfa and red clover, and by Hughes and Cockshull, (1971) for chrysanthemum.

Simple r values (Table 2) indicated partitioning to the roots to be primarily influenced by day temperature. Under a QFD of 160 μmol $s^{-1}m^{-2}$ and 14° day temperature (160-14-14; 160-14-26), total DW partitioned to the roots on average was 14%. Increasing day temperature from 14° to 26° (160-26-14; 160-26-26) decreased partitioning to ca. 7% of the total DW (Table 2). Similarly, at 325 μmol $s^{-1}m^{-2}$ and 20° night temperature, percent root DW decreased from 23% to 5% as temperature increased from 10° to 30°. A plot of the regression equation (Table 3) shows the relationship between percent root DW and day temperature (Figure 2). These results contrast with Acock, et al. (1981) who reported the proportion of DW partitioned to chrysanthemum roots increased with temperature in the range from 20° to 30°. However, their experiment was on vegetative plants and terminated after 35 days while our data were collected on plants at flowering (60 to 90 days after the start of SD depending on treatment).

Stem DW was influenced by QFD, day temperature, and by their interaction. Stem DW increased from 0.8 to 3.7 g per plant as QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$ at 20° and from 1.7 to 4.5 g as day temperature increased from 10° to 30° at 20° night temperature and 325 μmol $s^{-1}m^{-2}$. Day temperature and QFD interacted synergistically in that greatest stem DW occurred on plants grown under 490 μmol $s^{-1}m^{-2}$ and 26° day temperature.

Partitioning to the stem was primarily controlled by day temperature (Table 2, Figure 3). Average percent stem DW under 14° day temperature was 29%, but 36% under 26° day temperature. Increased partitioning to the stem as day temperature increased was accompanied by a significant increase in stem length. At 14° day temperature, average stem length was 16 cm while at 26°, average stem length was 30 cm (Karlsson and Heins, 1984). The increased partitioning to the stems as day temperature increased was not reported by Acock, et al. (1979). Over a day temperature range of 10° to 30° and a 20° night temperature, they reported partitioning to decrease from 45% to 36%. Their plants however, were kept vegetative and ours were reproductive, which may have altered the response to day temperature.

Day temperature, night temperature and QFD influenced leaf DW. As QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$, leaf DW increased from 1.8 to 3.6 g. Increasing day and night temperature from 14° to 26° at 160 μmol $s^{-1}m^{-2}$ increased leaf DW from 1.9 to 3.6 g; increasing the QFD to 490 μmol $s^{-1}m^{-2}$ at 26° further increased DW to 5.8 g.

While leaf DW increased as all three environmental factors increased, the percent of total DW partitioned to the leaves was primarily influenced by QFD (Table 2, Figure 4). The highest DW

proportion in the leaves (44%) was found under the lowest QFD (50 μmol $s^{-1}m^{-2}$) and the lowest proportion (24%) at the highest QFD (600 μmol $s^{-1}m^{-2}$). Specific leaf area (cm^2/g) paralleled the partitioning of DW to the leaves as QFD increased, indicating leaves were thinner under low irradiance conditions. This has been reported previously for several species (Björkman, 1981), e.g. for Impatiens parviflora (Evans and Hughes, 1961), Helianthus annuus and Lathyrus maritimus (Blackman and Black, 1959), and for chrysanthemum (Hughes and Cockshull, 1971).

Flower DW was primarily influenced by QFD. As QFD increased from 50 to 600 μmol $s^{-1}m^{-2}$, flower DW increased four-fold from 1.1 to 4.4 g per plant. While QFD strongly influenced flower DW, the DW partitioning to the flower was not strongly influenced by any one factor (Table 2). Partitioning to the flowers decreased as day temperature either increased or decreased to the experimental extremes (Figure 5). Partitioning to the flowers was further reduced when high day temperature was combined with high night temperature. Total flower area per plant under these treatments also decreased (Karlsson and Heins, 1984).

Partitioning to chrysanthemum flowers has been reported to remain the same over a wide range of environmental conditions in studies reported by Cockshull and Hughes, 1967, and Cockshull, 1982. Also, plants with the highest total DW were reported to have the heaviest flowers. A linear regression of flower DW with total DW in this experiment showed the same correlation ($r^2 = .77$).

The real significance of this type of research lies in its ability to predict plant response under a wide range of environmental

conditions. For example, Table 4 shows the predicted total plant dry weight and percent DW partitioning to the different plant organs at flowering in plants grown under four different environmental conditions. The first two environments represent production under winter conditions in a northern U.S. greenhouse with and without supplemental irradiation at 75 μmol $s^{-1}m^{-2}$ for 10 hr d^{-1} (ca. 575 fc from high pressure sodium lamps). The last two environments represent summer production in a greenhouse at different temperatures.

The supplemental irradiation during the winter is predicted to increase total plant DW by 23%. Possibly even more important is how this increased DW is partitioned. Combining the change in partitioning with the increase in DW results in actual stem and flower DW increases of 27% and 33%. These increases translate into higher quality plants. Increased stem stength and flower size have been reported on plants grown under supplemental irradiation (Carpenter, 1975 and 1976, Hicklenton and McRae, 1984, and Hughes and Tsujita, 1981).

In the summer, lowering the temperature is predicted to decrease total DW by 14%. However, partitioning is again modified. Partitioning is increased to the flowers and decreased to the stems with decreasing temperature. The decrease in partitioning to the stem is also associated with decreased stem length (Karlsson and Heins, 1984), a desirable horticultural characteristic.

Further research is required to define optimum ratios between root, stem, leaf, and flower DW. In addition, future research must be directed at determining the functional response of the plant to a changing environment. One can envision environmental control to optimize the development of roots, stems, leaves, or flowers at

different developmental stages. It is not known however, when root or leaf growth should be optimized during development to produce a plant of a desired quality. Until such information is determined, environmental control strategies are limited to information obtained from final DW partitioning at flowering.

Table 1. Actual and coded values for treatment combinations used in the central composite design.

Treatment number	QFD (μmol $s^{-1}m^{-2}$)	Temperature (^{o}C)		Coded values		
		Day	Night	QFD	DT	NT
1	50	20	20	-1.68	0	0
2	160	14	14	- 1	- 1	- 1
3	160	26	14	- 1	1	- 1
4	160	14	26	- 1	- 1	1
5	160	26	26	- 1	1	1
6	325	20	20	0	0	0
7	325	10	20	0	-1.68	0
8	325	30	20	0	1.68	0
9	325	20	10	0	0	-1.68
10	325	20	30	0	0	1.68
11	490	14	14	1	- 1	- 1
12	490	26	14	1	1	- 1
13	490	14	26	1	- 1	1
14	490	26	26	1	1	1
15	600	20	20	1.68	0	0

Table 2. Influence of QFD, day and night temperature, on final dry weight accumulation and partitioning in Chrysanthemum morifolium 'Bright Golden Anne'

Environment			Dry weight[z] (g)				Total plant dry weight (g)		Days to Flower	Percent dry weight[z]			
QFD ($\mu mols^{-1}m^{-2}$)	Temp (°C) Day	Night	Roots	Stems	Leaves	Flowers	at 60 days[y]	at flowering		Roots	Stems	Leaves	Flowers
50	20	20	0.4	0.8	1.8	1.1	2.4	4.1	90	9	21	44	26
160	14	14	0.8	1.5	1.9	1.6	5.3	5.8	70	13	26	33	28
160	26	14	0.4	2.5	2.1	1.9	5.3	6.9	80	6	36	31	27
160	14	26	1.1	2.2	2.2	1.9	4.9	7.4	80	15	30	31	25
160	26	26	0.6	3.0	3.6	2.2	6.1	9.4	90	7	32	38	23
325	20	20	1.3	2.9	2.8	4.4	9.2	11.4	70	11	25	25	39
325	20	20	1.1	2.4	2.9	3.4	8.3	9.8	70	11	24	30	35
325	10	20	1.5	1.7	1.7	1.8	5.5	6.7	70	23	25	25	27
325	30	20	0.5	4.5	3.6	2.5	8.5	11.1	90	5	41	32	22
325	20	10	1.0	4.6	2.9	3.1	8.4	11.6	70	9	40	25	26
325	20	30	0.9	3.1	3.3	2.8	7.4	10.1	80	9	31	33	27
490	14	14	1.5	3.4	3.0	3.7	11.1	11.6	70	13	30	26	31
490	26	14	1.3	5.3	3.2	4.5	11.7	14.3	75	9	37	23	31
490	14	26	1.4	3.4	3.2	3.8	9.5	11.8	70	12	29	27	32
490	26	26	1.5	6.7	5.8	4.0	12.3	18.0	80	8	37	33	22
600	20	20	3.6	3.7	3.6	4.4	15.3	15.3	60	22	25	24	29
Regression coefficient							Simple r values						
QFD			.83	.67	.57	.87	.95	.85	.58	.35	.17	-.73	.30
DT			-.36	.54	.53	.18	.20	.10	.53	-.69	.62	.22	-.31
NT			.08	.00	.38	.00	-.05	.37	.35	.02	-.19	.36	-.22
$(QFD)^2$			.82	.63	.55	.81	.94	.83	-.56	.39	.09	-.65	.25
$(DT)^2$			-.36	.54	.52	.16	.18	.35	.57	-.68	.66	.21	-.36
$(NT)^2$			.08	.04	.39	.02	-.05	.12	.36	-.02	-.12	.35	-.25
QFD x DT			.55	.87	.76	.82	.90	.92	-.24	-.03	.47	-.51	.07
QFD x NT			.73	.57	.70	.72	.79	.77	-.34	.30	.04	-.41	.13
DT X NT			-.19	.39	.68	.12	.12	.34	.63	-.48	.29	.45	-.40

[z]at flowering

[y]60 days from the start of short days

Table 3. Regression coefficients for percent root, stem, leaf, and flower dry weights and final total dry weight in Chrysanthemum morifolium 'Bright Golden Anne'

Regression[z] coefficient	Percent root dry_2 weight (r^2 = .73)	Percent stem dry_2 weight (r^2 = .92)	Percent leaf dry_2 weight (r^2 = .89)	Percent flower dry_2 weight (r^2 = .80)	Final total dry_2 weight (r^2 = .92)
Constant	14.341	85.281	67.174	-66.795	14.380
QFD	- .284E-1	.968E-2	- .900E-1	.109	.389E-3
DT	-1.161	-2.572	-1.052	4.784	- .270
NT	1.748	-4.202	-1.596	4.050	- .868
$(QFD)^2$	.374E-4	- .178E-4	.913E-4	- .111E-3	.481E-5
$(DT)^2$	.779E-2	.857E-1	.732E-2	- .101	- .141E-2
$(NT)^2$	- .400E-1	.111	.102E-1	- .816E-1	- .152E-1
QFD x DT	.889E-3	.594E-3	- .768E-3	- .715E-3	.753E-3
QFD x NT	- .111E-3	- .177E-3	.912E-3	- .633E-3	.918E-4
DT x NT	- .372E-2	- .198E-1	.618E-1	- .383E-1	.159E-1

[z]QFD = Quantum Flux Density; DT = Day temperature; NT = Night temperature

Table 4. Predicted final total dry weight and proportions partitioned to roots, stems, leaves and flowers for Chrysanthemum morifolium 'Bright Golden Anne'

Environment			Predicted				
QFD ($\mu mols^{-1}m^{-2}$)	Temp (^oC) Day	Night	Root dry weight (%)	Stem dry weight (%)	Leaf dry weight (%)	Flower dry weight (%)	Total plant dry weight (g)
175	20	16	11.6	25.9	31.9	30.7	6.6
250	20	16	11.8	26.9	28.1	33.2	8.1
400	28	22	10.8	36.5	27.8	24.9	14.0
400	24	18	12.3	31.0	24.1	32.6	12.1

Figure 1. Predicted final plant dry weight as effected by day temperature and QFD for Chrysanthemum morifolium 'Bright Golden Anne' at 20° night temperature.

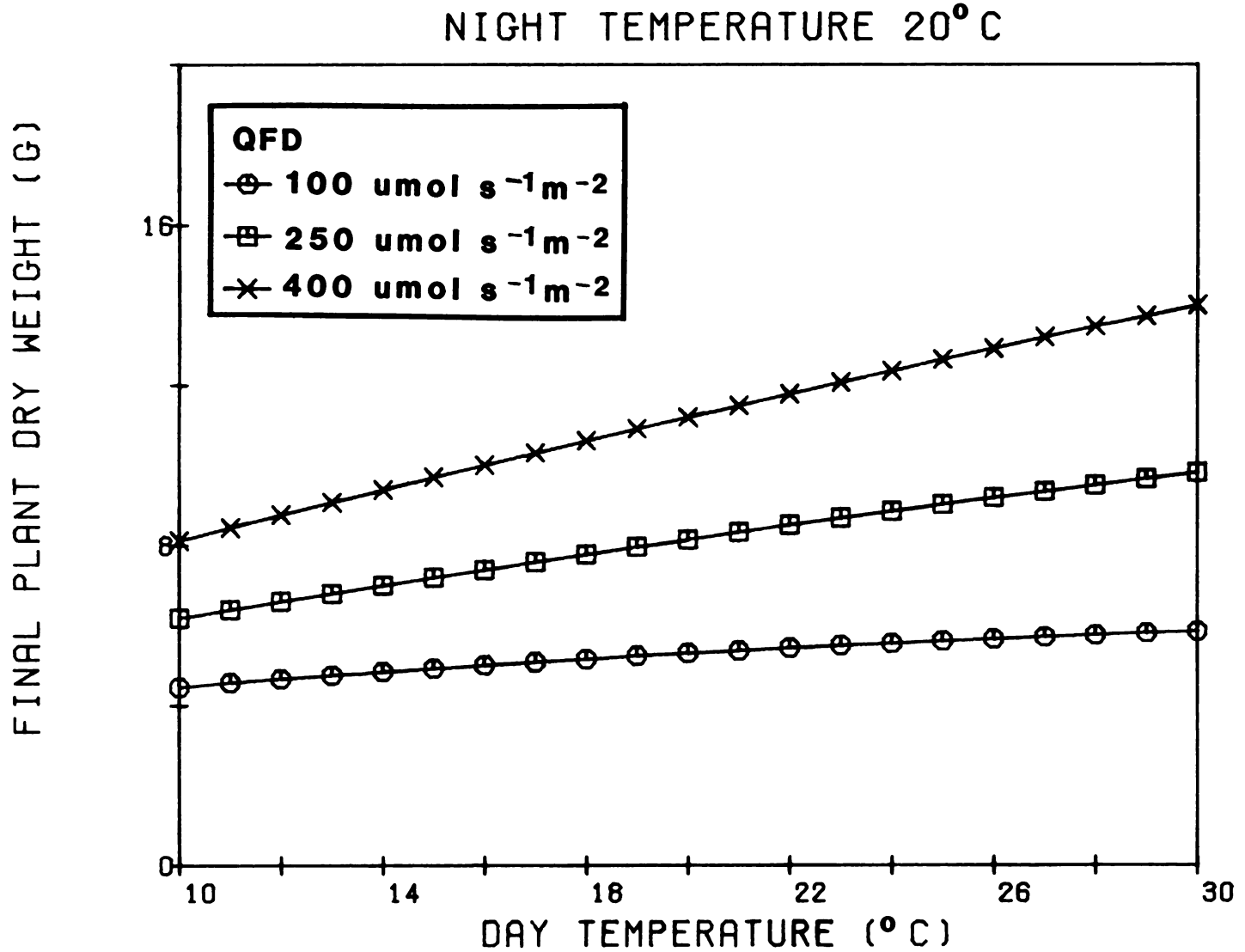

NIGHT TEMPERATURE 20° C
QFD
100 umol s⁻¹m⁻²
250 umol s⁻¹m⁻²
400 umol s⁻¹m⁻²
FINAL PLANT DRY WEIGHT (G)
0
8
16
10
14
18
22
26
30
DAY TEMPERATURE (° C)

Figure 2. Predicted proportion of dry weight partitioned to the roots as effected by day temperature and QFD for Chrysanthemum morifolium 'Bright Golden Anne' at 20° night temperature.

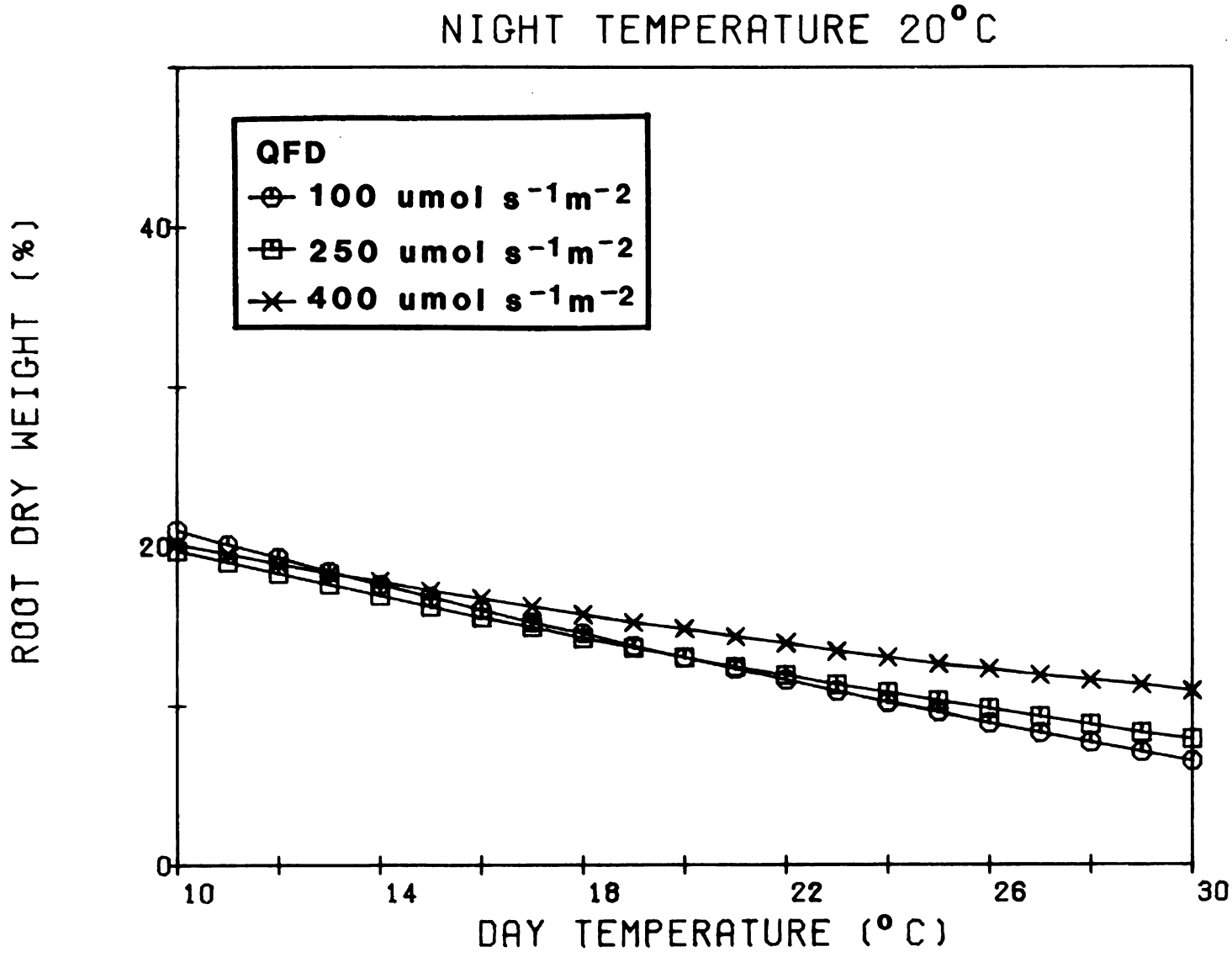

NIGHT TEMPERATURE 20°C
QFD
100 umol s⁻¹m⁻²
250 umol s⁻¹m⁻²
400 umol s⁻¹m⁻²
ROOT DRY WEIGHT (%)
40
20
0
10
14
18
22
26
30
DAY TEMPERATURE (°C)

Figure 3. Predicted proportion of dry weight partitioned to the stems as effected by day temperature and QFD for Chrysanthemum morifolium 'Bright Golden Anne' at 20° night temperature.

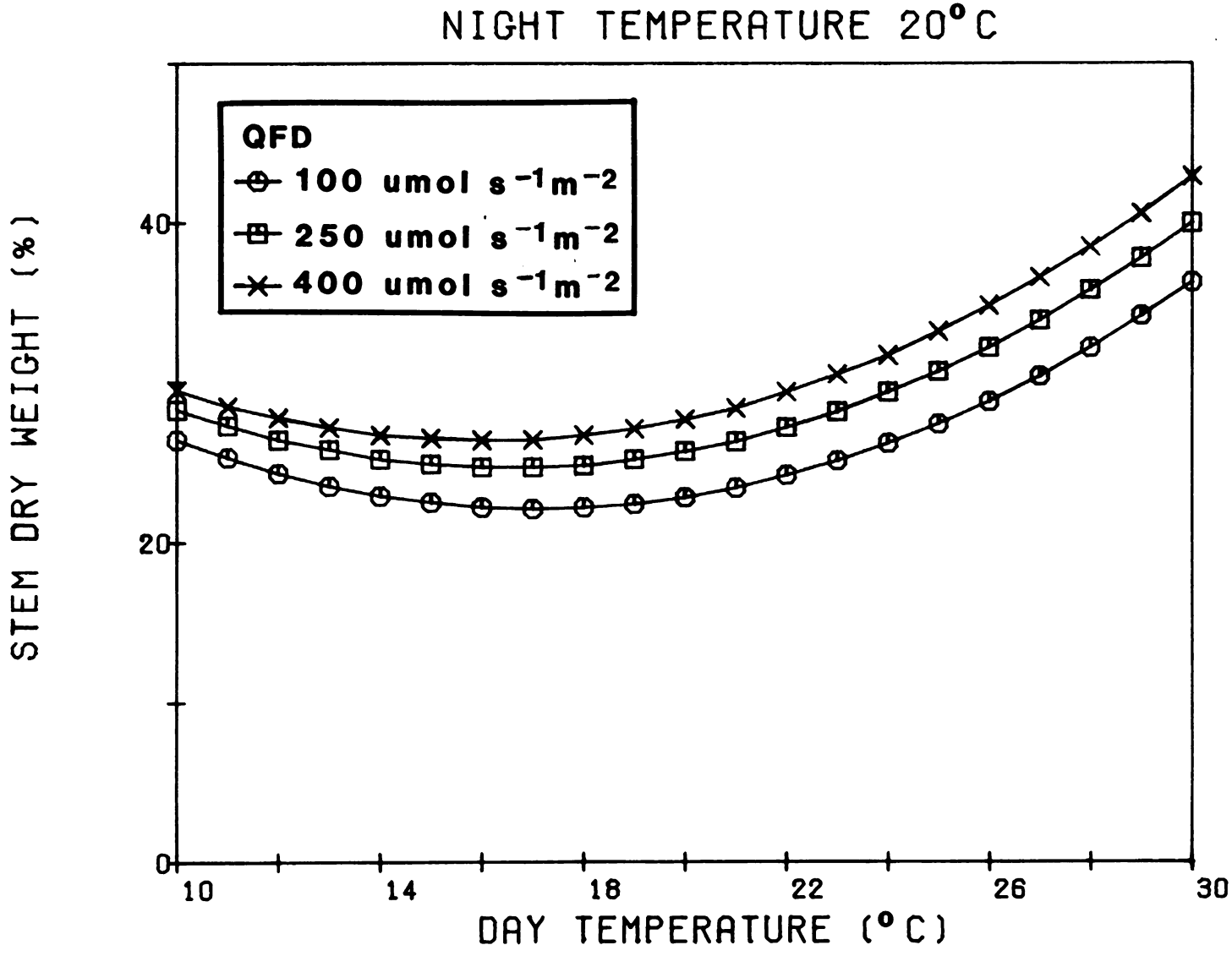

NIGHT TEMPERATURE 20°C
QFD
100 umol s⁻¹m⁻²
250 umol s⁻¹m⁻²
400 umol s⁻¹m⁻²
STEM DRY WEIGHT (%)
40
20
0
10
14
18
22
26
30
DAY TEMPERATURE (°C)

Figure 4. Predicted proportion of dry weight partitioned to the leaves as effected by day temperature and QFD for Chrysanthemum morifolium 'Bright Golden Anne' at 20° night temperature.

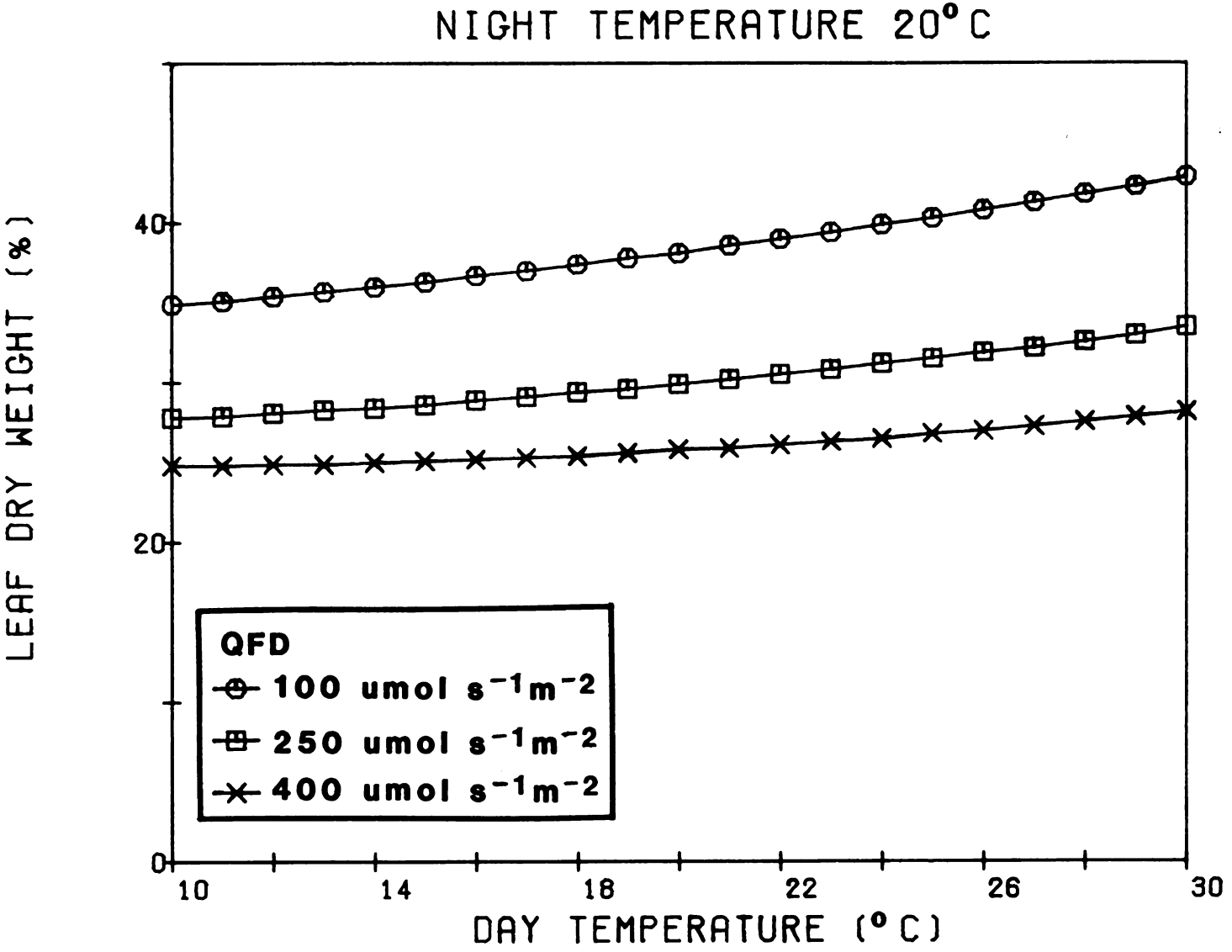
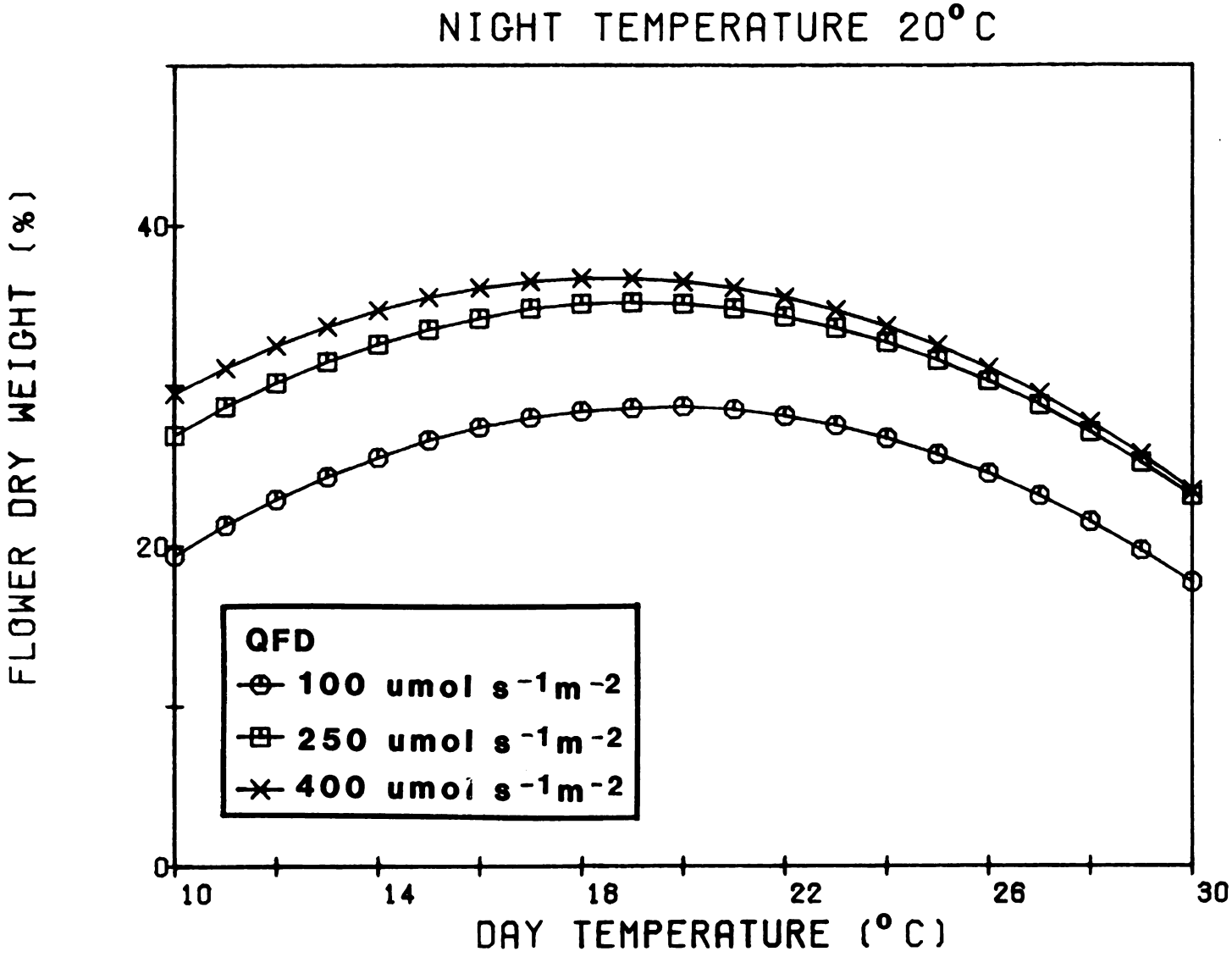

NIGHT TEMPERATURE 20° C
LEAF DRY WEIGHT (%)
40
20
0
10
14
18
22
26
30
DAY TEMPERATURE (° C)
QFD
100 umol s⁻¹m⁻²
250 umol s⁻¹m⁻²
400 umol s⁻¹m⁻²

Figure 5. Predicted proportion of dry weight partitioned to the flowers as effected by day temperature and QFD for Chrysanthemum morifolium 'Bright Golden Anne' at 20° night temperature.


NIGHT TEMPERATURE 20°C
FLOWER DRY WEIGHT (%)
40
20
0
10
14
18
22
26
30
DAY TEMPERATURE (°C)
QFD
100 umol s⁻¹m⁻²
250 umol s⁻¹m⁻²
400 umol s⁻¹m⁻²

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