Chrysanthemum dry matter partitioning patterns along irradiance and temperature gradients

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Karlsson, M. G. and Heins, R. D. 1992. **Chrysanthemum dry matter partitioning patterns along irradiance and temperature gradients.** Can. J. Plant Sci. 72: 307-316. The influence of photosynthetic photon flux (PPF, 1.8-21.6 mol d^{-1} m^{-2}) and day (DT) and night (NT) temperature (10-30°C) on dry matter accumulation and partitioning was studied in *Chrysanthemum morifolium* Ramat. 'Bright Golden Anne'. Total plant dry matter varied from 3.6 to 17.2 g at flowering. Plants with the greatest dry matter were from treatments with high PPF levels and temperatures. Accumulation of dry matter in roots, stems, leaves and flowers examined on a normalized time and normalized dry matter basis showed similar trends independent of DT, NT and PPF during development. Accumulated dry matter in roots, stems and leaves increased to a maximum and then decreased as the flowers were developing. Maximum leaf, root and stem dry matter was reached at 81, 85 and 91%, respectively, of required time from start of short days (SD) to flower. Proportion root dry matter increased and proportion leaf dry matter decreased in the plants as PPF increased. Partitioning to roots decreased as the DT increased. The root/shoot dry matter ratio decreased as plants developed from start of SD to flowering at all studied combinations of PPF, DT and NT. A positive difference between DT and NT (DIF) resulted in a higher percentage stem dry matter compared to plants grown at a negative DIF. Partitioning to flowers was not strongly correlated with the levels of PPF, DT and NT.

Key words: *Chrysanthemum morifolium*, *Dendranthema grandiflora*, dry matter accumulation and partitioning, temperature, irradiance

Karlsson, M. G. et Heins, R. D. 1992. **Répartition de la matière sèche dans les plantes de chrysanthème selon la température et le rayonnement global incident.** Can. J. Plant Sci. 72: 307-316. L'influence du rayonnement global incident, exprimé par le flux de photons photosynthétisants (FPP, 1,6 à 21,6 mol jour m^{-2}), ainsi que des températures diurnes (TD) et nocturnes (TN): 10 à 30°C, sur l'accumulation et sur la répartition de la matière sèche (m.s.) a été sur *Chrysanthemum morifolium* Ramat, 'Bright Golden Anne'. L'accumulation totale de MS par la plante fluctuait de 3,6 à 17,2 g à la floraison, les plantes les plus riches en MS étant obtenues dans les régimes à FPP et à températures élevés. L'accumulation de MS dans les racines, les tiges, les feuilles et les fleurs, calculée selon les valeurs normalisées de température et de MS, manifestait des tendances semblables, indépendamment des TD, des TN et des FPP observés durant le développement de la plante. La quantité de MS accumulée dans les racines, les tiges et les feuilles atteignait un maximum, pour ensuite diminuer à mesure que les fleurs se développaient. L'accumulation maximale dans les feuilles, les racines et les tiges survenait, respectivement, à 81, 85 et 91% de l'intervalle de temps requis entre le début des jours courts (JC) et la floraison. La proportion de MS dirigée vers les racines augmentait, et celle dirigée vers les feuilles diminuait, à mesure que FPP augmentait. La part de MS allant aux racines régressait avec l'élévation des TD. Le rapport MS racine/MS parties aériennes diminuait du début de la phase de JC à la floraison et cela à toutes les combinaisons étudiées de FPP, de TD et de TN. Une différence positive entre TD et TN durant la croissance a donné lieu à un plus fort pourcentage de MS dirigé vers la tige qu'une différence négative. La part de m.s. dirigée vers les fleurs n'était pas fortement corrélée avec les niveaux de FPP, de TD et de TN.

Mots clés: *Chrysanthemum morifolium*, *Dendranthema grandifolia*, accumulation et répartition de la matière sèche, température, rayonnement global incident

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The quality of bedding plants and flowering potted plants is determined by plant characteristics such as height, flower size, and leaf and flower numbers. Plants respond to environmental conditions by modifications in morphology to utilize most efficiently available resources for growth. As plant morphology changes, dry matter accumulation and partitioning are also expected to be influenced by the environment during growth. By maintaining suitable growing conditions, plants with desired dry matter partitioning, characteristics and qualities can be produced.

Efforts have been made to study the influence of environmental factors on morphology, dry matter accumulation and partitioning for plant populations growing in their natural field habitats. Comparisons of growth among plant populations or among years are confounded by the variable growing conditions at the different locations. Effects of environmental factors on growth are difficult or impossible to separate from the effects of other gradients at the field locations (Jurik 1983; Ashmun et al. 1985) and controlled experimental conditions may be necessary to determine the response to factors influencing dry matter accumulation and partitioning. The objective of this study was to determine the dry matter accumulation and partitioning responses in *Chrysanthemum morifolium* Ramat. to variations in irradiance, day temperature (DT) and night temperature (NT). Functional relationships were developed to quantify and describe the influence of irradiance, DT and NT on dry matter accumulation and partitioning patterns during plant development from start of short photoperiods for flower initiation to flowering.

MATERIALS AND METHODS

Rooted cuttings of *C. morifolium* 'Bright Golden Anne' were planted individually in 10-cm pots and placed in growth chambers under a photosynthetic photon flux (PPF) of 18.7 mol d^{-1} m^{-2} (325 μmol s^{-1} m^{-2} for 16 h d^{-1}) at a constant temperature of 20°C for 7 d. On the seventh day, a short day (SD) photoperiod was initiated (10 h light, 14 h dark), plants were pinched to 6 nodes and 84 plants were placed under each of the 25 treatment combinations (Table 1) with the thermoperiod paralleling the photoperiod. PPF was provided by cool-white fluorescent lamps and incandescent lamps with an input wattage of 80:20, respectively. A Li-Cor LI-185B Meter and LI-190SB quantum sensor were used to monitor PPF and the shelves supporting the plants were lowered weekly if necessary to maintain the desired PPF at the canopy top. Average daily temperature fluctuated ±1°C from the set-point and PPF varied ±10% over the canopy. Plants were grown in a commercial peat-lite medium (Michigan Peat Co.) and were automatically irrigated one to three times daily depending on plant size. Nutritional program consisted of 14.3 mol m^{-3} (14.3 mM) N and 5.1 mol m^{-3} (5.1 mM) K added through the watering system. Media pH was maintained at 6.0±0.2 by adjusting water pH with nitric acid.

A central composite statistical design was used to select treatment combinations (Gardiner et al. 1967; Armitage et al. 1981). The PPF levels ranged from 1.8 to 21.6 mol d^{-1} m^{-2} (50-600 μmol s^{-1} m^{-2} for 10 h d^{-1}) and both DT and NT ranged from 10 to 30°C, respectively. The ranges of PPF, DT and NT were selected to correspond with possible conditions of a commercial greenhouse. To strengthen the data base, the 15 treatment combinations required in the statistical design were supplemented with 10 additional treatments at the endpoints of the PPF and temperature ranges. The 25 treatment combinations of PPF, DT and NT are given in Table 1.

Data were collected on five randomly selected plants in each treatment at start of SD and every 10 d thereafter. The treatments were terminated when approximately half of all flowers had reflexed their outermost petals to a horizontal position. On each sample date, the growing medium was washed off the roots and the plant was separated into roots, stems, leaves and flowers. The various plant components were weighed after several days of drying at 60°C to determine dry matter.

Regression equations to determine maximum dry matter in roots, stems, leaves and flowers during the growth from start of SD to flowering were developed by stepwise regression analyses (Wilkenson 1986). Linear, quadratic, cubic and interaction terms of DT, NT, PPF, average daily temperature and DIF (difference between DT and NT) were the independent variables available for inclusion. Time and accumulated dry matter in roots, stems, leaves and flowers were normalized for plants in each treatment to facilitate data analyses. The data values were transformed to values between 0 and 1 by division with the observed maximum value for each time and dry matter variable. Stepwise regression analyses was performed on the

Table 1. Influence of photosynthetic photon flux (PPF), day and night temperature regimes on total dry matter and partitioning at flowering in *Chrysanthemum morifolium* 'Bright Golden Anne.' The individual experiments were terminated when approximately 50% of the flowers had reflexed their outermost petals to a horizontal position

Environment			Days to experimental termination	Total plant dry matter (g)[z]	Dry matter partitioning at flowering (%)			
PPF	Temp. (°C)							
($\text{mol day}^{-1}\text{ m}^{-2}$)	Day	Night		At flowering	Roots	Stems	Leaves	Flowers
1.8	10	10[y]	120	3.8±0.02	19	33	35	13
1.8	30	10[yx]	-	—	-	-	-	-
1.8	20	20	90	3.6±0.14	8	20	40	32
1.8	10	30[yx]	-	—	-	-	-	-
1.8	30	30[yx]	-	—	-	-	-	-
5.8	14	14	70	5.3±0.10	12	27	28	33
5.8	26	14	80	5.9±0.09	4	36	28	32
5.8	20	20[y]	70	6.2±0.07	17	21	27	35
5.8	14	26	80	6.6±0.10	13	31	29	27
5.8	26	26	90	8.6±0.38	6	33	36	25
11.7	20	10	70	10.7±0.09	9	39	22	30
11.7	10	20	70	5.9±0.07	24	25	21	30
11.7	20	20	70	10.0±0.22	7	26	22	45
11.7	30	20	90	10.6±0.05	4	41	30	25
11.7	20	30	80	9.3±0.16	9	31	30	30
17.6	14	14	70	10.9±0.40	13	30	23	34
17.6	26	14	75	14.3±0.42	9	38	20	33
17.6	20	20[y]	70	10.7±0.19	20	22	20	38
17.6	14	26	70	11.0±0.14	12	29	25	34
17.6	26	26	80	17.2±0.56	8	37	30	25
21.6	10	10[y]	80	10.5±0.18	26	27	24	23
21.6	30	10[y]	80	11.6±0.38	5	51	30	14
21.6	20	20	60	15.3±0.12	24	24	22	30
21.6	10	30[y]	90	14.6±0.41	23	32	21	24
21.6	30	30[y]	120	14.5±0.23	14	36	43	7

[z] ±SE. Dry matter was determined after drying plant tissue at 60°C for several days.

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

[x] Not used in analysis due to lack of flower initiation after 100 short days.

normalized values with linear, higher order and interactions terms of the environmental variables. Regression analysis was also performed using only linear and higher order terms of normalized time as independent variables. The regression equations were selected based on the number of included variables, significance of included variables, F and R^2 values of the equations and prediction adequacy determined by examining residuals and graphs with observed and calculated values for each treatment. All independent variables included in the final equation were significant at the 5% level as indicated by a two-tailed t-test.

RESULTS AND DISCUSSION

Total plant dry matter varied at flowering from 3.6 to 17.2 g among plants developing at the studied combinations of PPF, DT and NT (Table 1). Predicted total plant dry matter in plants grown at 20°C NT and combinations of DT from 10 to 30°C and PPF from 2 to 20 mol d^{-1} m^{-2} is shown in Fig. 1. Total plant dry matter was more responsive to PPF than either DT or NT. The higher PPF and temperature levels maintained during plant development resulted in larger total plant dry matter. Plants grown under the five temperature combinations at 5.8 mol d^{-1} m^{-2} had significantly less dry matter than plants in the same five combinations at 17.6 mol d^{-1} m^{-2} (Table 1). As both DT and NT increased from 14 to 26°C, total plant dry matter increased by 62% at 5.8 mol day^{-1} m^{-2} and 58% at 17.6 mol day^{-1} m^{-2}. Heins et al. (1986) measured increased photosynthesis in

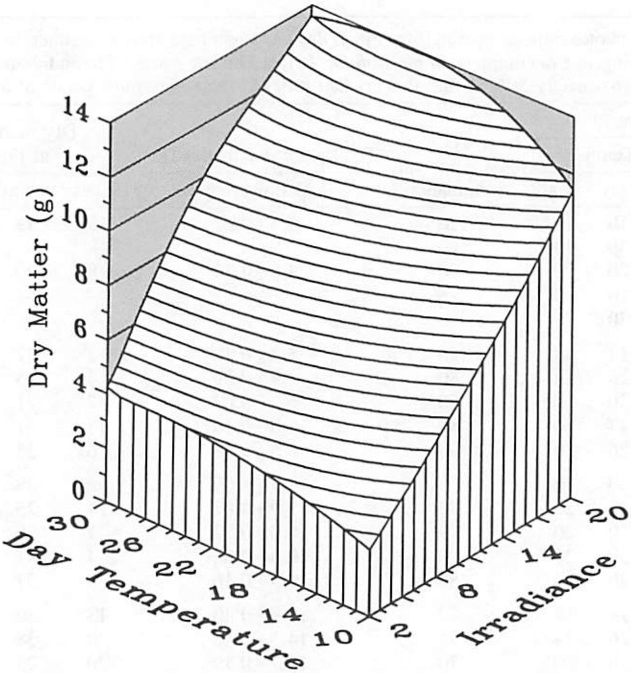

Fig. 1. Predicted total plant dry matter at flowering of *Chrysanthemum morifolium* 'Bright Golden Anne'. Dry matter was estimated by developed functional relationships at 20°C night temperature. Irradiance measured in mol d^{-1} m^{-2} and day temperature in °C.

chrysanthemum from 20.1 to 33.8 mg CO_2 dm^{-2} h^{-1} as the PPF level increased from 450 to 2000 μmol s^{-1} m^{-2} at 830 μL L^{-1} CO_2 and 21°C. The photosynthetic rate also increased (from 12.1 to 20.1 mg CO_2 dm^{-2} h^{-1}) for a temperature increase from 13 to 21°C at 450 μmol s^{-1} m^{-2} PPF and 830 μL L^{-1} CO_2 in the study by Heins et al. (1986). Increased photosynthesis at growing conditions with high PPF and temperature levels can be expected to result in a larger dry matter content for many plants (Björkman 1981; Charles-Edwards et al. 1986).

Figure 2 shows the predicted amount of dry matter in the different parts of the plant at flowering for plants grown at 20°C NT and combinations of DT from 10 to 30°C and PPF from 2 to 20 mol d^{-1} m^{-2}. At a constant 20°C NT, root dry matter at flowering was predicted to vary from 0.3 to 3.3 g as the DT decreased from 30 to 10°C and PPF increased from 2 to 20 mol d^{-1} m^{-2} (Fig. 2a). Stem and leaf dry matter amount in plants increased as PPF increased from 2 to 20 mol d^{-1} m^{-2} and DT increased from 10 to 30°C (Figs. 2b-c). The stem dry matter was predicted to increase from 0.9 to 5.2 g and leaf dry matter from 0.5 to 3.7 g as PPF and DT increased. Flower dry matter increased with increasing PPF, while the optimum DT for largest flower dry matter varied from 18 to 22°C depending on the PPF level (Fig. 2d). The predicted largest flower dry matter at 20 mol d^{-1} m^{-2} and 20°C NT was 4.5 g at 18.5°C DT.

Accumulation of dry matter in roots, stems, leaves and flowers as the plant developed showed similar trends for plants grown at the studied combinations of DT, NT and PPF when examined on a relative time and relative dry matter basis (Fig. 3). Use of relative scales enabled the comparison of plants at the same morphogenetic age without interference of variable rates of development and plant part dry matter (Hunt 1982). The functional

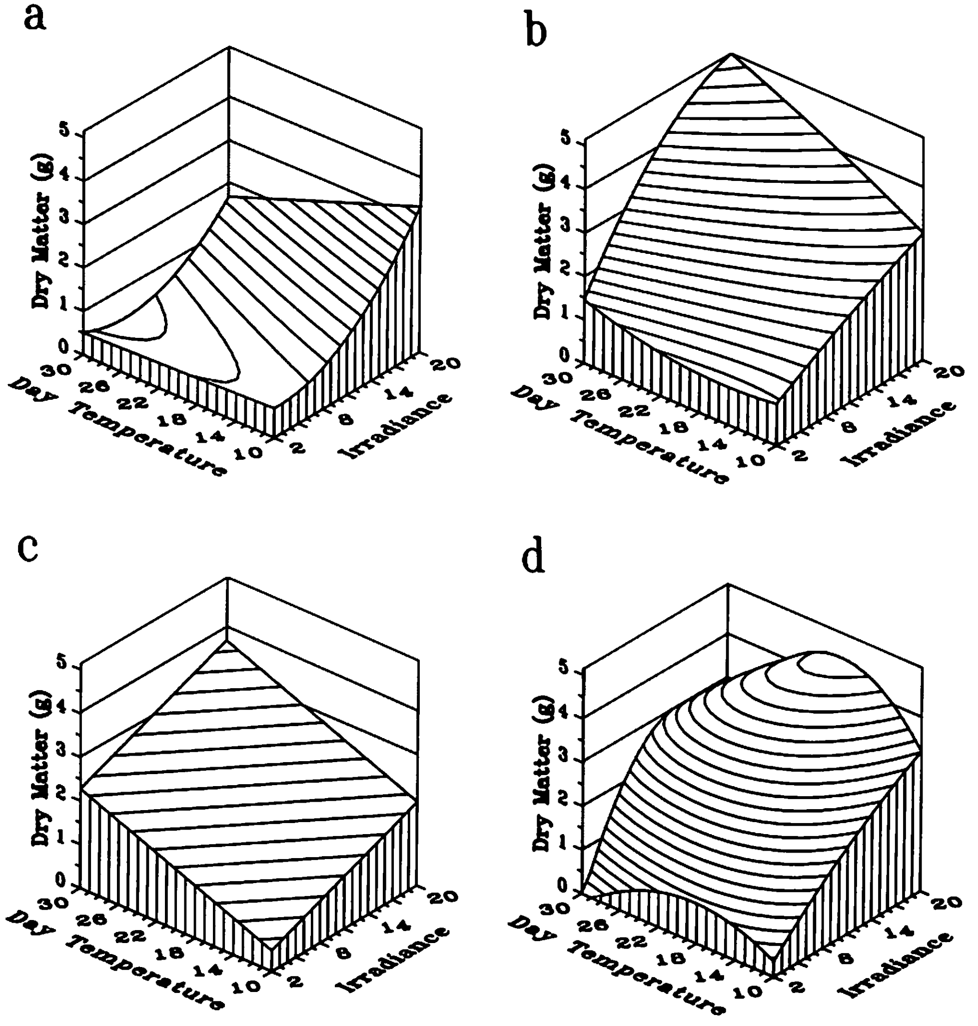

Fig. 2. Predicted dry matter in roots, stems, leaves and flowers at flowering of *Chrysanthemum morifolium* 'Bright Golden Anne'. Dry matter in different plant parts was estimated by developed functional relationships at 20°C night temperature. Irradiance measured in mol d^{-1} m^{-2} and day temperature in °C. (a) Root dry matter. (b) Stem dry matter. (c) Leaf dry matter. (d) Flower dry matter.

relationships using linear and higher order terms of normalized time (Table 2) were superior to functions that also included environmental factors for describing the relative accumulation of dry matter in the different plant parts. The absence of differences in relative dry matter accumulation despite the large variability in plant dry matter and required time for flowering (Table 1) indicated the growth of plant parts to be determinate in plants developing at a wide range of irradiance and temperature conditions. Maximum dry matter was first reached by leaves at 81%, followed by roots at 85% and stems at 91% of the time required from start of SD to flowering (Fig. 3). The flowers acquired dry matter at a continuously increasing rate from the first observed accumulation at 50% of time required for flowering until termination of the experiment.

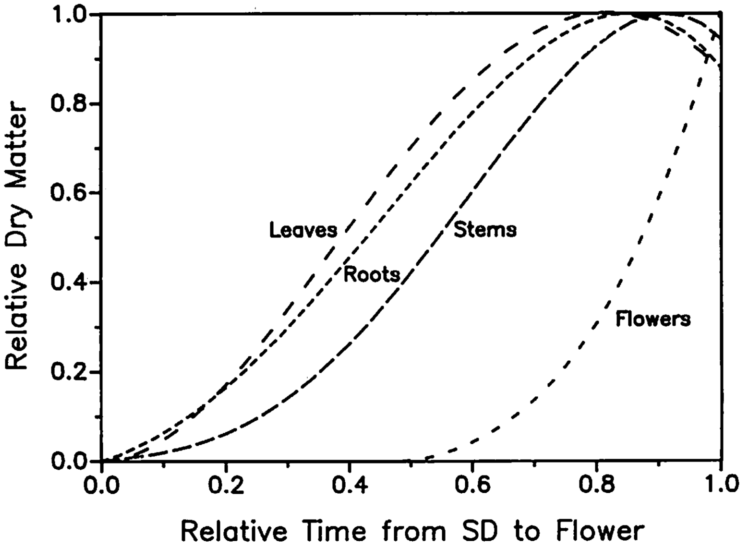

Fig. 3. Normalized dry matter accumulation in roots, leaves, stems and flowers plotted against normalized time from start of short days (SD) to flowering in *Chrysanthemum morifolium* 'Bright Golden Anne'.

Table 2. Regression coefficients for functions relating normalized quantity of dry matter in roots, stems, leaves and flowers over normalized time (NDAY) from start of short days to flowering in *Chrysanthemum morifolium* 'Bright Golden Anne.' Dry matter and time required for flowering were scaled to attain values between 0 and 1. (Regression variables significant at $P<0.05$)

Regression variable	Normalized amount of dry matter in			
	Roots	Stems	Leaves	Flowers
NDAY	0.4403	0.1541	—	—
$NDAY^2$	1.9834	—	5.3947	—
$NDAY^3$	—	4.6998	−5.8463	−1.0076
$NDAY^4$	−1.5445	−3.9105	1.3252	2.0110
R^2	0.95	0.99	0.98	0.97

At the fastest rate of flower dry matter accumulation, the dry matter in roots, stems and leaves decreased on a percentage basis (Fig. 4) as well as on an absolute basis (Fig. 3). Total plant dry matter increased continuously from start of SD to flowering.

The partitioning pattern of dry matter within a plant varied with the PPF, DT and NT conditions during development. Dry matter allocation to roots increased as the PPF in the growing conditions increased from 1.8 to 21.6 mol d^{-1} m^{-2} (Figs. 4a-b). Similarly, Lambers and Posthumus (1980) showed dry matter accumulation decreased more in roots than shoots and the root/shoot ratio decreased under growing conditions with decreased irradiance for *P. lanceolata* and *Z. mays*. Percentage root dry matter at flowering decreased for plants grown at high DT (Table 1). At a PPF of 5.8 mol d^{-1} m^{-2} and 14°C NT, root dry matter decreased from 12 to 4% for a DT increase from 14 to 26°C. A similar trend was observed at 17.6 mol d^{-1} m^{-2} and 14°C NT where the percentage root dry matter at flowering decreased from 13% at 14°C to 8% at 26°C. The root/shoot ratio in *Z. mays* was also found to decrease as the temperature increased from 10 to 30°C in studies by Rajan et al. (1971). In contrast to the DT response (Figs. 4c-d), plants did

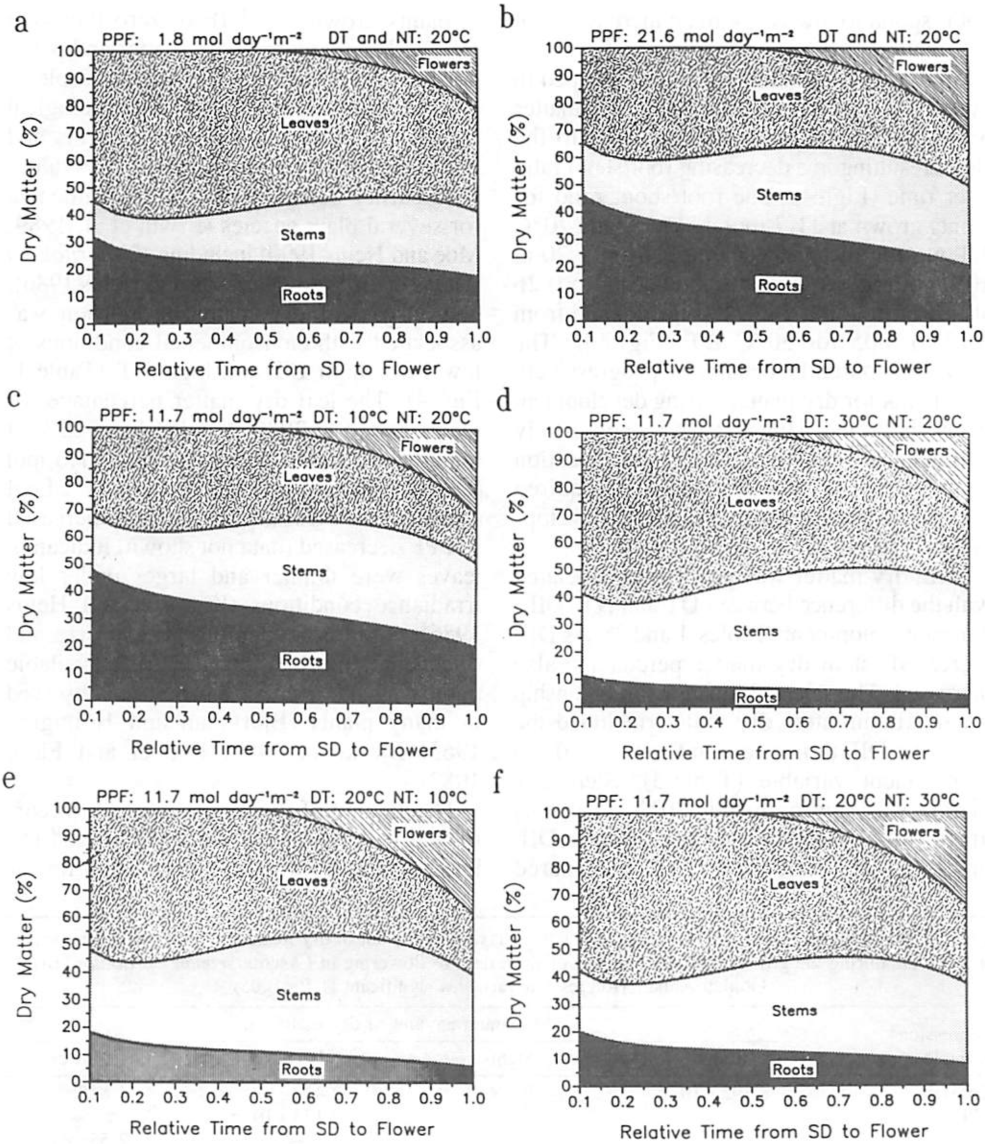

Fig. 4. Predicted dry matter allocation to roots, stems, leaves and flowers over time expressed in normalized units from start of short days (SD) to flowering in *Chrysanthemum morifolium* 'Bright Golden Anne' using developed functional relationships. (a) Photosynthetic photon flux (PPF) of 1.8 mol d^{-1} m^{-2} with day temperature (DT) and night temperature (NT) at 20°C. Observed time to flower was 90 d and total plant dry matter at flowering 3.6 g. (b) PPF of 21.6 mol d^{-1} m^{-2} with DT and NT at 20°C. Observed time to flower was 60 d and total plant dry matter at flowering 15.3 g. (c) PPF of 11.7 mol d^{-1} m^{-2} with DT at 10°C and NT at 20°C. Observed time to flower was 70 d and total plant dry matter at flowering 5.9 g. (d) PPF of 11.7 mol d^{-1} m^{-2} with DT at 30°C and NT at 20°C. Observed time to flower was 90 d and observed total plant dry matter at flowering was 10.6 g. (e) PPF of 11.7 mol d^{-1} m^{-2} with DT at 20°C and NT at 10°C. Observed time to flower was 70 d and total dry matter at flowering 5.9 g. (f) PPF of 11.7 mol d^{-1} m^{-2} with DT at 20°C and NT at 30°C. Observed time to flower was 80 d and total plant dry matter at flowering 9.3 g.

not respond to low NT with an increased root dry matter in our study (Figs. 4e-f).

As the chrysanthemum plants developed in this study, a smaller proportion of dry matter was allocated to the roots compared to the shoot resulting in a decreasing root/shoot ratio over time (Fig. 4). The root/shoot ratio for plants grown at 11.7 mol d^{-1} m^{-2} and 20°C NT was predicted to decrease from 1.20 at 10% of time required for flowering to 0.26 at flowering for 10°C DT (Fig. 4c) and from 0.17 to 0.05 for 30°C DT (Fig. 4d). The flowers apparently became a progressively larger sink for dry matter during development (Cockshull and Hughes 1968) and newly produced dry matter as well as reallocation from other plant parts (Fig. 3) were required to support the rapid expansion and development of floral parts.

Stem dry matter was positively associated with the difference between DT and NT (DIF) during development (Tables 1 and 3). As DIF increased, stem dry matter percentage also increased. The selected functional relationship for maximum stem dry matter included the quadratic DIF term as a significant ($P<0.05$) independent variable (Table 3). Stem dry matter was approximately 10% (Table 1) greater in plants grown with a positive DIF of 12 (DT at 26°C, NT at 14°C) compared to plants grown at a DIF of zero (constant 14°C). The increase in dry matter and partitioning to stems at large DIF values (Table 1; Fig. 4) was associated with morphological changes to taller plants. Longer stems and internodes at increasing positive DIF values have earlier been reported and documented for several plant species (Erwin et al. 1989; Moe and Heins 1990) including *C. morifolium* (Heins et al. 1986; Karlsson and Heins 1986).

A large leaf dry matter proportion was associated with environmental conditions of low PPF, high DT and high NT (Table 1; Fig. 4). The leaf dry matter percentage for plants grown at 20°C doubled from 22% of total dry matter at an irradiance of 21.6 mol d^{-1} m^{-2} to 40% at 1.8 mol d^{-1} m^{-2}. Leaf area per gram leaf dry matter also increased as PPF decreased (data not shown) indicating leaves were thinner and larger under low irradiance conditions (Karlsson and Heins 1986). Similar adaptations in leaf size and thickness to more efficiently utilize available photosynthetic irradiance have been observed in many plants (Björkman and Holmgren 1963; Björkman 1981; Kappel and Flore 1983).

The amount of flower dry matter was correlated with the interactions of PPF and DT levels (Table 3) while the proportion flower

Table 3. Regression coefficients for functions relating maximum amount of dry matter (g) in roots, stems, leaves and flowers during the growth period from start of short days to flowering in *Chrysanthemum morifolium* 'Bright Golden Anne.' (Regression variables significant at $P<0.05$)

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

[z] PPF = photosynthetic photon flux (mol d^{-1} m^{-2}), DT = day temperature (°C), NT = night temperature (°C), DIF = difference between DT and NT.

dry matter within a plant was less variable. About 1/3 of the dry matter in the plant was allocated to the flowers at the termination of the experiment. The proportion dry matter allocated to chrysanthemum flowers remained similar over a wide range of environmental conditions independent of the flower number per plant in studies by Cockshull (1982). The production of flowers and reproductive characteristics tend to be highly determined in many plants (Bazzaz et al. 1987). The proportion dry matter partitioned to reproduction will only change when plants are exposed to unfavorable environmental conditions requiring a higher dry matter proportion for maintenance (Soule and Werner 1981). Extreme conditions such as high DT and/or NT (30°C) in combination with a low PPF level (1.8 mol d^{-1} m^{-2}) resulted in an altered partitioning pattern that prevented chrysanthemum flower initiation (Table 1). Increasing the PPF level to 21.6 mol d^{-1} m^{-2} at 30°C resulted in the development of flowers, although only 7% of total dry matter had been partitioned to flowers at the termination of the study.

Although plant dry matter at flowering varied from 3.6 to 17.2 g and the number of SD to flower from 60 to 120 (Table 1), dry matter accumulation in roots, stems and leaves on a relative scale was similar, reaching a maximum and then decreasing in dry matter as the flowers developed (Fig. 3). The percentage dry matter partitioned to the different parts, however, was dependent on environmental conditions during plant development (Fig. 4). Flower initiation was morphologically delayed at high DT and NT with an increased number of leaves forming below the flower (Karlsson et al. 1989) and the dry matter proportion to leaves increased at the expense of partitioned root dry matter. At low PPF levels, a larger proportion dry matter was also partitioned to leaves at the expense of root dry matter. High DT in combination with low NT resulted in an increased stem dry matter proportion and longer stems and internodes (Karlsson et al. 1989).

A genotype with good performance under favorable environmental conditions and poor performance under unfavorable conditions exhibits a large degree of plasticity (Taylor and Aarssen 1988). *Chrysanthemum morifolium* 'Bright Golden Anne' showed a large degree of plasticity in growth response and dry matter partitioning to irradiance, day temperature and night temperature. 'Bright Golden Anne' and other cultivars of chrysanthemum may have been selected for their ability to respond with changes in morphology and dry matter partitioning to produce flowering plants at common greenhouse irradiance and temperature conditions.

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