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Path Analysis of Chrysanthemum Growth and Development

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Abstract. **Plants of chrysanthemum (*Dendranthema grandiflora* Tzvelev.) were grown under one of 25 irradiance and temperature combinations from start of short days to flower. Four phases of development were defined as 1) the start of short days to the appearance of 4-mm terminal flower buds (phase I), 2) appearance of 4-mm terminal flower buds to removal of lateral flower buds when the terminal flower bud was 7 to 8 mm (phase II), 3) removal of lateral flower buds to flower buds showing first color (phase III), and 4) flower buds showing color to flowering (phase IV). Path analysis was used to study the influence of development time and relative dry weight gain during each of these four phases on development time and relative dry weight gain of subsequent phases. Relative dry matter accumulation during phases I, II, III, and IV significantly influenced cumulative relative dry weight gain, with phase I having the greatest influence. Increasing relative dry weight gain during phase I had a significant negative effect on relative dry weight gain in phase II. Time within each phase significantly affected total time to flower. Under the constant environmental conditions of this experiment, time in one phase did not influence the length of time in later phases.**

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

Wright (29, 30) developed a statistical method termed "path analysis" to quantify interactions among yield components and measure their contribution to total yield. In path analysis, the direct effects of independent variables are studied with the indirect effects removed. The advantage of such an analysis is that the effect of one component on another can be isolated from influences of other components. A high path coefficient between two components indicates that a change in one will result in a substantial relative change in the other when additional influences are removed. Path coefficients not significantly different from zero indicate that a change in one component will have little direct effect on a corresponding component. Path coefficients can be calculated only if their dependence structure is known. Yield components, for example, often develop sequentially, and those that develop late cannot affect early components. The directionality of dependencies can be determined in these situations.

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

Although several workers have described the growth of chrysanthemums by mathematical models (1, 7, 12, 14, 15, 18), none

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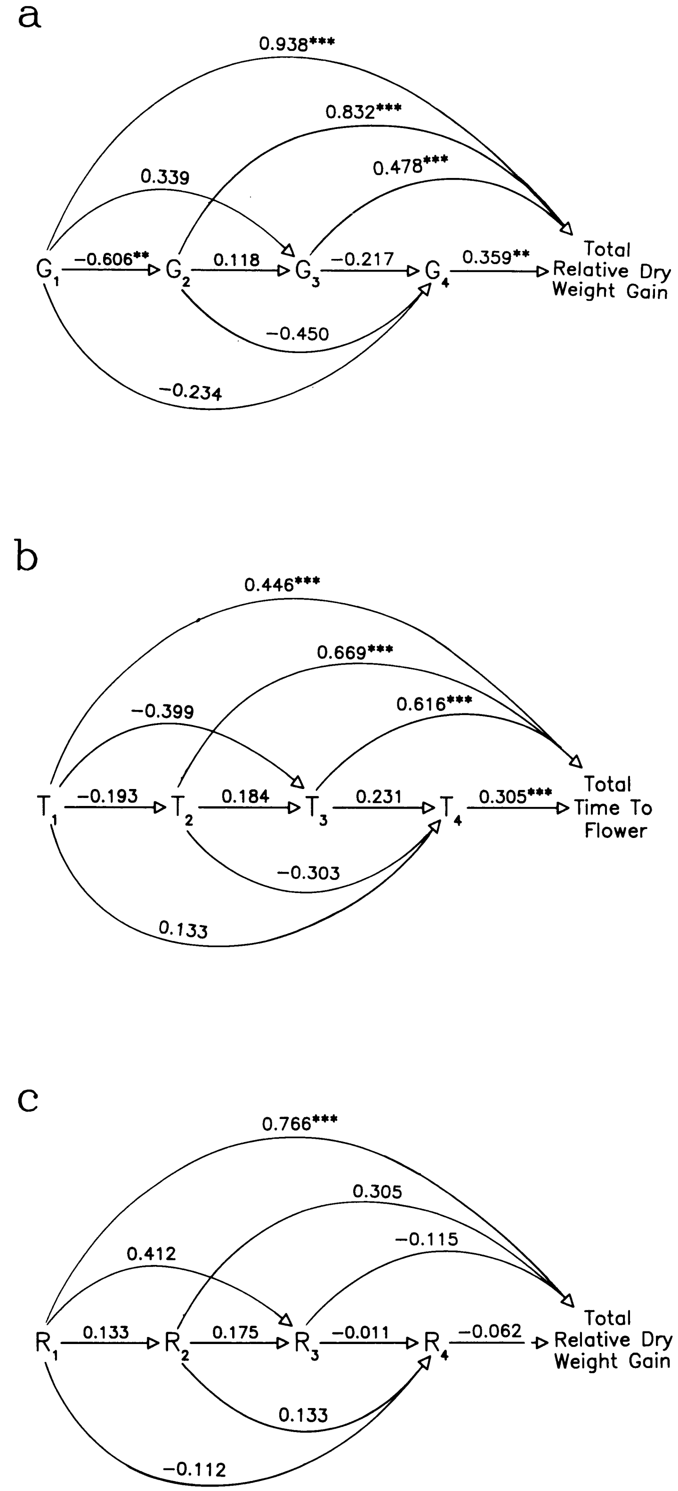

Fig. 1. Path diagram indicating the interrelationships in chrysanthemum. (**a**) Among increments of relative dry-weight accumulation (G) during four developmental phases and total relative dry-weight increase. (**b**) Among days of four developmental phases (T) and total number of days to flower. (**c**)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

have determined how variation in growth during a particular developmental phase influences subsequent development and time to flower. The objectives of this study were to determine how relative growth rate and developmental time in one phase influenced relative growth rate and time in later phases and to identify the most critical developmental phases for total dry-matter accumulation and time to flower in chrysanthemum.

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

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

Plants were grown in a commercial peatlite medium (Michigan Peat Co.) and irrigated up to three times daily. The fertilizer program consisted of 14.3 $mol \cdot m^{-3}$ (14.3 mM) N and 5.1 $mol \cdot m^{-3}$ (5.1 mM) K added through the watering system. The pH of the medium was maintained at 6.0 ± 0.2 by adjusting water pH with nitric acid.

A central composite design was used to select treatment combinations (3, 10). Temperatures ranged from 10° to 30°C and PPF from 1.8 to 21.6 $mol \cdot day^{-1} \cdot m^{-2}$ (50 to 600 $\mu mol \cdot s^{-1} \cdot m^{-2}$, 10 hr/day). The 15 treatment combinations required in the statistical design were supplemented with 10 additional treatments at the endpoints of the PPF and temperature ranges (Table 1).

Five stages of development were distinguished: start of SD, visible bud (VB, appearance of 4-mm terminal flower buds), disbud (DB, removal of lateral flower buds when the terminal bud was 7 to 8 mm in diameter), flower buds showing first color, and flowering (outermost petals reflexed to a horizontal position). Four sequential developmental phases (I–IV) were defined as the intervals between the five stages. Dry weights of roots, stems, leaves, and flowers were determined on five random plants at the five developmental stages. Dry matter accumulation during each phase and the length of each phase were calculated based on the observations at the five sampling occasions.

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

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

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

The G_i variables were used to define growth as the relative dry-weight increase for each developmental phase, but this analysis ignores the time required to complete the de-

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

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

[z]When the flowers had reflexed their outermost petals to a horizontal position.
[y]± SE.
[x]Treatments added to the 15 basic treatments in the central composite design.
[v]Not used in analysis due to lack of flower initiation.

velopment from one stage to another (T_1 through T_4). An additional analysis therefore was performed using the mean relative growth rates (R_i variables) of each phase.

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

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

Path analysis was performed on the defined variables using SPSS subprogram "regression" (22). A series of least-square regressions was computed with one variable at a time as the dependent variable and the preceding variables in the path as the independent variables. The standardized β values were used as the path coefficients.

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

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

The length of time in phase I was generally longer than the length of time in phase II, and more dry weight could accumulate during phase I compared to phase II. The negative effect of G_1 on G_2 therefore might be related to the different length of phase I and II. Variations in T_1, T_2, T_3, and T_4 contributed significantly to variations in total time to flower, but the influence of the T variables on each other was not significant (Fig. 1b). These results suggest that, when the environmental conditions were kept constant throughout chrysanthemum development, the plants reponded directly to the environment without conditioning effects from earlier phases. The plant response to an earlier phase, however, is affected if the environment is changed from one phase to another (17).

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

Phasic analysis of plant growth can provide insight into growth and development of a plant. The G variables for all four phases significantly affected G_T. G_1 and R_1 were most highly associated with G_T when the influences of intermediate phases were removed, suggesting that it is most critical to optimize environmental conditions during early development. An early large relative dry-weight gain was expected to result in a large leaf area and, therefore, sequentially larger relative dry-weight gains. However, neither the analysis of G variables or R variables supported this hypothesis (Fig. 1a and c).

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

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

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

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Screening Rootstocks of *Prunus* for Relative Salt Tolerance

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Abstract. **A nondestructive method for evaluating the salt tolerance of *Prunus* seedlings was devised for greenhouse sand-culture with 60 days of saline drip irrigation. The treatments contained half-strength Hoagland's solution using distilled water and supplementary chloride and sulfate salts of Na, Ca, and Mg to reach 1.5 $dS\cdot m^{-1}$ for control, 4.5 $dS\cdot m^{-1}$ for the first trial, and 6.0 $dS\cdot m^{-1}$ for the second and third trial screenings. After 60 days of irrigation with 6.0 $dS\cdot m^{-1}$ Nemaguard, the standard peach [*P. persica* (L.) Batsch] rootstock averaged 46% of the fresh weight, 53% of the volume, 66% of the height, and 74% of the foliar health ratings of the control seedlings. Percent of control values were compared for a tentative ranking of salt tolerance: 'Titan' almond x Nemaguard and *P. mexicana* Wats. > Nemaguard and Nemared > Myrobalan plum (*P. cerasifera* J.F.Ehrh.) and bitter almond (*P. amygdalus* var. *amara* Focke.). Correlation coefficients were used in selecting useful sets of evaluation parameters. Height was rejected as a screening parameter. Final fresh weight and a final foliar health rating are recommended for cursory screenings of *Prunus* germplasm. The last three weekly foliar health scores are useful for comparing rates of decline. Volume displacements are useful for comparing root vs. shoot growth.**

Growers of almonds and fresh-market peaches, plums, and apricots are attracted to the lower latitude, semi-arid regions where earlier market windows and fewer chemical inputs combine for a better return on investment than obtained elsewhere. These same regions are facing a steady deterioration in the quantity and quality of available irrigation water. One-third of the world's irrigated acreage already is affected adversely by salinity (15).

There is little information available on the relative salt tolerance of *Prunus* spp. to help growers select rootstocks for new plantings. Current generalizations (2, 14) are based on a few long-term studies at the United States Salinity Laboratory (1, 3, 9) and observations in the field (4). A soil is not classified as saline until 4 $dS\cdot m^{-1}$ ECe (20), yet Maas (14) has calculated a threshold of 1.5–1.7 $dS\cdot m^{-1}$, beyond which *Prunus* spp. begin to show symptoms of yield depression, stunting, foliar burn, and premature senescence (9–11). Maas (14) calculated slopes of decline that rank salt tolerance of the commercial *Prunus* spp. as plum > almond > peach > apricot. Bernstein (2) ranked rootstocks in terms of tolerance to soil chloride: Marianna plum >> Lovell peach ≥ Shalil peach > Yunnan peach. Field observations reviewed by Day (4) ranked rootstocks in terms of tolerance to excess alkali salts as almond > apricot > Myrobalan plum ≥ peach. Studies outside of these reviews have found Marianna 2624 to be more salt-tolerant than Myrobalan 3-J (19); Lovell peach to be more

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