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Selection of Day-neutral, Heat-delay-insensitive *Dendranthema ×grandiflora* Genotypes

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Abstract. Commercial garden and greenhouse chrysanthemums [*Dendranthema ×grandiflora* (Ramat.) Kitam. (syn. *Chrysanthemum xmorifolium* Ramat.)] are facultative short-day plants for flower bud initiation, obligate short-day plants for flower bud development, and are categorized into short-day response groups. Flower initiation can be delayed by high night temperatures. Recent research has identified true day-neutral genotypes. The purpose of this investigation was to test environments for selecting genotypes that are both day-neutral and heat-delay insensitive. One greenhouse and 18 garden genotypes were selected. A series of environments were used to select for day-neutral genotypes and then differentiate between these genotypes for heat delay insensitivity: short days, long days/red light, long days/far red light and high temperatures, and natural day lengths under field conditions. Day-neutral selections from these environments were then grown in a fifth environment of long days/continuous far red and red light with high temperature. Data were collected on the number of days to first and third flower, long day leaf number, stem length, number of strap-shaped leaves subtending the terminal flower, internode lengths, number of nodes with axillary branching, and flower bud development of the first to the sixth flowers. Genotypes required 3 to 8 weeks for complete flower bud initiation/development. Flowering responses in the first four environments were highly significant for both the first and third flowers. Genotypes ranged from obligate short-day to day-neutral for the first six flowers. Three day-neutral genotypes were selected that differed significantly for all traits in the fifth environment; flower bud development with the first six flowers occurred with only one genotype, 83-267-3. Broad sense heritability estimates ranged from $h^2 = 0.75$ for number of nodes with axillary branching, $h^2 = 0.79$ for long day leaf number and number of strap-shaped leaves, to $h^2 = 0.91$ for stem length. An ideotype for day-neutral and heat-delay-insensitive garden chrysanthemums was developed for use in breeding programs.

Cultivated greenhouse (cut flowers and potted flowering plants) and garden (cushion and upright types) chrysanthemums [*Dendranthema ×grandiflora* (syn. *Chrysanthemum xmorifolium*)] provide a diversity of flower forms, plant habits, and uses in the landscape and home. Flower initiation and development are controlled by shorter day lengths in late summer and fall (Post, 1949). Commercial production of chrysanthemums involves manipulation of photoperiod to produce flowering plants throughout the year. Chrysanthemums are short-day (SD) plants for flowering (Cathey and Borthwick, 1957, 1961, 1964). If a SD plant is grown under photoperiods exceeding the 13.5 h (average) critical SD photoperiod, it will not flower, i.e. it will not continue with flower bud development (FBD) after flower bud initiation (FBI). FBD of SD chrysanthemums is reversibly controlled by red (R, ≈660 nm) and far red (FR, ≈730 nm) light. Continuous or intermittent exposure to R light, using either incandescent (FR, R light) or fluorescent (R light) sources, in the middle of a long dark period (night), inhibits FBI and FBD in SD chrysanthemums (Borthwick and Cathey, 1962).

Cultivated chrysanthemums are categorized into SD response groups, defined as the number of weeks from the start of SD to anthesis. The critical photoperiod is ≤12 h for reproductive development and ≥13.5 h for vegetative growth (Cockshull, 1985). Early flowering cultivars (6 to 8 weeks response groups) are facultative SD for FBI and qualitative (obligate) SD plants for FBD (Cockshull and Kofranek, 1992). Later flowering response groups (>8 weeks of SD) are obligate SD for FBI and FBD; while they will initiate flower buds under long-day (LD) conditions, these will be crown buds that will not undergo FBD. Generally, the response group of garden types is 6 to 8 weeks, while greenhouse types are 6.5 to 11 weeks for flowering potted plants and 8 to 15 weeks for cut flowers (van Zanten, 1999; Yoder Brothers, 2000). All greenhouse and garden chrysanthemum cultivars eventually initiate terminal flower buds or crown buds, i.e., undergo autonomous FBI under LD conditions (Langton, 1977). Crown buds are characterized as floral meristems that have stopped developing at some point after initiation. Additionally, crown buds can be characterized by the presence of subtending strap-shaped leaves or bracts without axillary meristems.

The mean number of leaves (long-day leaf number, LDLN), initiated by the terminal meristem prior to undergoing FBI under a LD photoperiod, is a quantitative measure of vegetative growth (Cockshull, 1976; Cockshull and Kofranek, 1985). Selection for early initiation under LD yields plants with low LDLN (Langton, 1981). In previous studies, chrysanthemum cultivars that went on to develop their flowers to anthesis in LD were typically classified as day-neutral (DN) plants. However, true DN plants will undergo FBI and FBD to anthesis under SD or LD within the normal temperature range for the species (10 to 12 °C nights; Kawata and Toyoda, 1982).

Following autonomous FBI, development will continue for all flower buds (primaries, secondaries, tertiaries, etc.) under any photoperiod (Kawata and Toyoda, 1982). For example, FBD will continue under SD or any LD in which the duration of light is longer than the critical SD photoperiod, and with any combination of light quality Cathey and Borthwick, 1970; Langton, 1977; Schwabe, 1953).

Several DN chrysanthemum cultivars have been reported previously (Okada, 1957). Okada (1957) distinguished summer (June to July), August, and September flowering cultivars from autumn and winter types on the basis that FBI in the former groups

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was not affected by photoperiod, i.e., they were DN for FBI. He also reported that summer and August cultivars were also DN for FBD, unlike the September cultivars that required SD for FBD, and that 'Okayamaheiwa' chrysanthemum underwent FBI when grown under SD, but was DN for FBD. Other Japanese chrysanthemums were not sensitive to photoperiod, suggesting DN, but required vernalization to flower (Harada and Nitsch, 1959). Seeley (1966) reported two garden cultivars, Dr. Longley and Rosa, both flowered under 9, 13.5, 14.5, 17.5, and 24 h photoperiods and were DN. Satory (1986) discussed breeding DN garden chrysanthemum F_1 hybrids. Langton (1978) reported that the Japanese cultivar Mezame was DN for FBD. A genotype, 83-267-3, was patented that was DN for FBI and FBD under any photoperiod (Anderson, 1991; Anderson, et al., 1989). Kim and Lee (1998) used a DN genotype 'Jeongwoon' for grafting studies.

An advantage of DN cultivars for chrysanthemum growers would be elimination of a photoperiod requirement for flowering. Pulling black cloth over plants to simulate short days would be unnecessary. However, propagators would have to apply ethephon (Florel, Union Carbide Co., Research Triangle Park, N.C.) to inhibit flowering of DN stock plants (Strefeler, et al., 1996; Stuart, et al., 1988). DN garden chrysanthemums could offer home gardeners the potential for continuous flowering throughout the growing season, rather than during the fall season only, as is currently the case.

Temperature can also affect chrysanthemum development. High night temperatures (≥22 °C) can delay flowering and induce abnormal inflorescence development by delaying FBI and/or FBD (Cathey 1954; Cockshull, 1979; Crater, 1980; Whealy et al., 1987). Cockshull (1979) reported an increase in leaf production and a delay in capitulum initiation in response to high temperatures. This phenomenon is termed heat delay. Commercial cultivars that are susceptible to high temperature heat delay include 'Delano', 'Yellow Mandalay', and 'Sunny Mandalay' (Yoder Brothers, Inc., 2000). Commercial greenhouse cultivars that are heat delay insensitive (HDI) exist for summer forcing: 'Pink Akron', 'Purple Lima', 'Rapture', 'Star Stream', 'Sunray' (de Jong, 1978; Yoder Brothers, Inc., 2000). In many cultivars, a delay in flowering at high temperature is correlated with a similar delay at low temperature (10 °C) (de Jong, 1978). DN/HDI garden cultivars would have the added advantage of flowering throughout the growing season in both northern and southern regions. It has not been documented whether DN cultivars are HDI.

The objective of this research was to test critical environments for selecting phenotypically stable chrysanthemum genotypes that are DN and HDI, for use in chrysanthemum breeding programs. A series of environments were used to select DN genotypes and then subsequently differentiate between DN genotypes for HDI.

Materials and Methods

Genotypes. Eighteen genotypes of garden chrysanthemums were randomly selected for this study from the University of Minnesota breeding program (18/600 or 3% of the germplasm bank); one greenhouse genotype was also randomly selected. Named, commercial garden cultivars included 'Autumn Fire', 'Aurora', 'Minnautumn', 'Minnwhite', 'Rosy Glow', and 'Superior'. 'Ruby Mound', a commercial garden cultivar from Lehmann Gardens (Faribault, Minn.) and three early-flowering clonal selections from two commercial hybrids, 'Autumn Glory Seed Line-1' (AGSL-1; F_1 hybrid; seed lot no. N7387, Sakata Seed Co., Yokohama, Japan), 'Petit Point Seed Line-6' (PPSL-6; F_2 hybrid; Bodger Seed Co., Lompoc, Calif.), and 'Petit Point Seed Line-10' (PPSL-10) were also evaluated. A commercial greenhouse cultivar was also included, 'Foxy' (Yoder Brothers, Barberton, Ohio). Numbered, unnamed early-flowering inbred/hybrid selections from the University of Minnesota garden chrysanthemum breeding program included: 81-45-15, 82-81-3, 82-81-21, 82-119-5, 82-124-3, 83-14-13, 83-267-3 (U.S. Plant Patent 6,884), and 85-341-9. Two of the numbered selections were full-sibs (82-81-3 and 82-81-21) and two named hybrids were from the same seed lot (PPSL-6 and PPSL-10).

Cutting source. Stem cuttings of all plant material were obtained from indexed stock plants maintained in a vegetative state with a) LD photoperiods (12 to 16 h photoperiod plus night interruption lighting, 2200 to 0200 HR, using incandescent lamps), b) 20 °C days/17 °C (day/night) temperatures, and c) weekly sprays of 500 $mg \cdot L^{-1}$ ethephon (Florel) + 5 $mg \cdot L^{-1}$ gibberellic acid, (GA_3) (Strefeler, et al., 1996; Stuart, et al., 1988). Stem cuttings of 'Foxy' (Yoder Brothers, Inc.) were obtained from stock plants grown under similar conditions. Terminal stem cuttings were taken with one mature (fully expanded) leaf and a uniform stem length (4 cm). Upon harvest, cuttings were inserted in sand for rooting under an intermittent mist system, with the same conditions (photoperiod and temperature) as the stock plants. After rooting in 1 to 2 weeks, cuttings were potted and placed into greenhouses, the field, or growth chambers for photoperiod treatments. Plants in each treatment were grown (unpinched, no plant growth regulators) for 90 d from the commencement date.

Growing environments and experimental design. A completely randomized design was used within each environmental treatment. A series of environments were used to select for DN genotypes and differentiate between these genotypes for HDI. All 19 genotypes were included in four initial environments (with n = 4 plants per genotype per treatment): (1) short days (SD); (2) long days/R light night interruption (LD/R); (3) long days/FR light night interruption (LD/FR) with high temperature; (4) natural day lengths under field conditions (Natural). Subsequently, three DN selections were included in a fifth environment: (5) long days continuous 24 h/FR and R light environment with high temperature (Continuous FR+R) with eight plants per genotype.

The following temperatures were maintained in each environment: 1) SD = 20 ± 2/16.7 ± 1 °C (day/night); 2) LD/R = 20 ± 2/16.7 ± 2 °C; 3) LD/FR = 31 ± 2/26.7 ± 3 °C; 4) Natural = 27.5 ± 4/17.2 ± 5 °C; 5) Continuous FR+R = 28.3 ± 1 °C constant. For all environments, day temperatures commenced at 0800 HR while night temperatures began at 1600 HR. The natural environment was imposed by field conditions. SD, LD/R, and LD/FR were provided under greenhouse conditions, with black cloth pulled over or around the plants to eliminate light pollution. The continuous FR+R environment was provided in a growth chamber. The SD and LD/R environments were provided during January to April 1987, to minimize thermophotoperiodic interactions while screening for DN. LD/FR and natural environments were imposed during June to September, 1987, to maximize HDI screening. During the winter months (SD and LD/R environments), ambient daytime light conditions (20 $\mu mol \cdot m^{-2} \cdot s^{-1}$) were supplemented with high pressure sodium lamps when black cloths were open, from 0800 to 1600 HR at 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

The following photoperiod manipulations were applied in the

respective environments: 1) SD = black cloth pulled 0800/1600 HR, providing 16 h darkness; 2) LD/R = cool-white fluorescent lamps wrapped with red cellophane as the R light source (spectroradiometer reading of 4.72 $\mu W \cdot cm^{-2}$ at 630 nm and 1.59 $\mu W \cdot cm^{-2}$ at 750 nm; irradiance exceeded the minimal 2.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ required at the shoot apex) (Mastalerz, 1977), night interruption lighting 2200 to 0200 HR; 3) LD/FR = incandescent lamps as the FR light source (0.08 $\mu W \cdot cm^{-2}$ at 630 nm and 2.3 $\mu W \cdot cm^{-2}$ at 750 nm), night interruption lighting 2200 to 0200 HR; 4) Natural = a progression of LD to SD during June (1 June = 15.2 h) to September (1 Sept. = 13.25 h) at lat. 45 °N under field conditions (U.S. Nautical Almanac Office, 1977); and 5) continuous FR+R = 24 h continuous lighting using fluorescent (R light) and incandescent (FR+R) as light sources (4.8 $\mu W \cdot cm^{-2}$ at 630 nm and 2.3 $\mu W \cdot cm^{-2}$ at 750 nm).

The SD environment represented the commercial forcing treatment for flowering chrysanthemums and served as the control for comparison with the LD/R environment and to quantify the SD response group for each genotype (Cockshull, 1985; Dole and Wilkins, 1999). The LD/R environment represented the discriminatory test for distinguishing between DN and SD genotypes for FBI and FBD, with the SD environment serving as a control (Accati-Garibaldi et al., 1977; Cathey and Borthwick, 1961; H.F. Wilkins, 1989, personal communication). The LD/FR environment is the most common night interruption treatment used to maintain plant material in a vegetative state (Cockshull, 1985; Post, 1949). This environment was used to screen for DN and HDI genotypes—using incandescent lamps as a heat source in coordination with high night temperatures; the natural environment served as the control. The continuous FR+R environment was used to differentiate between DN and HDI under more stringent conditions of continuous lighting and higher temperatures (Cockshull and Kofranek, 1985).

DATA COLLECTION. From each plant in each environment, data were collected on the number of days to first (terminal) flower, number of days to third (second subtending lateral) flower, LDLN, stem length of main stem, number of strap-shaped leaves (bracts) subtending the terminal flower bud, internode length calculations (stem length per number of leaves +1), number of nodes with axillary branching, and flowering (+/–) of the first six flowers (terminal and the uppermost five subtending laterals).

STATISTICAL ANALYSES. Data analyses were performed using SPSS, Version 9.0 for Windows (Statistical Package for the Social Sciences, SPSS, Inc., Chicago, Ill.). Since not all genotypes flowered under all environments, data were divided into photoperiodic responses (for the first and third flowering data), and nonphotoperiodic responses (all other traits). Separate analysis of variance (ANOVA) and mean separations were performed for each environment for all traits except photoperiodic response.

For photoperiodic responses, F tests were not performed due to unequal group sizes (not all genotypes flowered in every environment) where the Type I error levels were not guaranteed. For traits other than flowering response, mean separations using Tukey's Studentized range test at $P = 0.05$ were performed. A binomial (z-test) analysis was performed for day-neutrality (observed proportion flowering plants: proportion nonflowering plants) for the first and third flowers of each genotype, pooled across four environments (SD, LD/R, LD/FR, and Natural). Genotypes with highly significant binomial z-tests ($P \leq 0.001$) for first and third flowerings in the SD, LD/R, LD/FR, and Natural environments were DN. Three DN genotypes were included in the final environment (Continuous FR+R) to select for HDI under a more rigorous environment.

Broad sense heritability (h^2) estimates, on an entry-mean basis, were calculated for LDLN, number of strap-shaped leaves, stem length, and the number of nodes with axillary branching in the SD, LD/R, LD/FR, and Natural environments (Fehr, 1987; Langton, 1981). A chi-square test for homogeneity of error across environments was performed, corrected for small sample sizes (Haynes, et al., 1996; Nyquist, 1991; Steel, et al., 1997). Since there was homogeneity of error for all environments (corrected $\chi^2 = 0.53$, df = 3, NS), the h^2 estimates were computed on the replications within each of four environments (SD, LD/R, LD/FR, and Natural). An exact confidence interval for the h^2 estimates was calculated (Knapp et al., 1985). These h^2 estimates are a ratio of the total genotypic variance (additive, dominance, and epistasis) to the phenotypic variance. Since a random group of garden genotypes was chosen from the University of Minnesota breeding program, the reference population is genotypes of the species, rather than a segregating population (Fehr, 1987).

Results

The first (terminal) and third (second subtending lateral) flower buds initiated, developed, and reached anthesis for all genotypes under the SD environment (Table 1). Mean number of days to flowering under SD for the first flower ranged from 22 (83-267-3) to 58 ('Rosy Glow') and from 27 (83-267-3) to 64 ('Rosy Glow') days for the third flower. SD response groups (no. weeks of SD to the first flower) of the 19 genotypes are as follows: 3 weeks (83-267-3), 4 weeks (PPSL-6, 85-341-9), 5 weeks ('Ruby Mound', 'Superior', 82-124-3, 82-119-5, and 83-14-13), 6 weeks ('Autumn Fire', PPSL-10, 'Minnwhite', 'Minnautumn', 82-81-21, and 81-45-15), 7 weeks ('Aurora', AGSL-1, and 'Foxy'), and 8 weeks ('Rosy Glow' and 82-81-3). The 3 to 5 week response group genotypes are earlier than those commercially available (van Zanten, North America 1999; Yoder Brothers, Inc. 2000). Related full-sib hybrids, e.g., 82-81-3 and 82-81-21, and PPSL-6 and PPSL-10 differed in SD response by nearly 2 weeks (Table 1).

'Autumn Fire', 'Aurora', AGSL-1, 'Foxy', PPSL-6, PPSL-10, and 'Ruby Mound' failed to undergo FBD and reach anthesis under LD/R, LD/FR, and natural environments (Table 1). These seven genotypes are obligate SD for FBD, rather than DN, for both the first and third flower buds. Three genotypes were obligate SD for FBD of the first flower bud, but partially DN for development of the third flower under ≥1 environment: LD/R ('Minnwhite' and 'Minnautumn'), LD/FR ('Minnautumn'), and natural ('Superior') environments. 'Rosy Glow' and 82-124-3 had variable responses for flowering of both the first and third flowers in LD/R, LD/FR, and natural environments (Table 1). The remaining genotypes were DN for FBD of the first and third flowers, reaching anthesis in all environments. Example flowering responses for a DN genotype (83-267-3, Fig. 1A) and an obligate SD genotype for FBD ('Aurora', Fig. 1B) are illustrated for SD and LD/R light environments, LD/FR light (Fig. 2), and natural conditions (Fig. 3).

Binomial (z) tests for day neutrality of the first and third flower buds pooled across the first four environments were not significant ($P > 0.05$) for SD genotypes, 'Autumn Fire', 'Aurora', AGSL-1, 'Foxy', PPSL-6, PPSL-10, 'Ruby Mound', and 'Superior' (Table 2). Partially DN genotypes ('Minnwhite', 'Rosy Glow', 82-119-5, 82-124-3, and 83-14-13) were also nonsignificant. 'Minnautumn' had significant *P* values for both the first and third flowers. DN genotypes (82-81-21, 81-45-15, 82-81-3, 83-

Table 1. Mean ±SD for number of days to first and third flowers for 19 chrysanthemum genotypes under four photoperiod treatments (SD = short days, LD/R = long days, red light, LD/FR = long days, far-red light, and Natural field conditions).

	Days to first (terminal) flower				Days to third (second subtending) flower			
Genotype	SD	LD/R	LD/FR	Natural	SD	LD/R	LD/FR	Natural
'Autumn Fire'	45 ± 6	---[z]	---	---	50 ± 6	---	---	---
'Aurora'	47 ± 2	---	---	---	49 ± 3	---	---	---
AGSL-1	48 ± 2	---	---	---	51 ± 2	---	---	---
'Foxy'	48 ± 1	---	---	---	57 ± 0	---	---	---
PPSL-6	31 ± 5	---	---	---	42 ± 20	---	---	---
PPSL-10	40 ± 1	---	---	---	44 ± 1	---	---	---
'Ruby Mound'	37 ± 2	---	---	---	41 ± 3	---	---	---
'Superior'	37 ± 2	---	---	---	41 ± 1	---	---	85 ± 0
'Minnwhite'	46 ± 5	---	---	---	36 ± 9	89 ± 1	---	---
'Minnautumn'	38 ± 2	---	---	---	44 ± 2	49 ± 0	75 ± 21	---
82-124-3	37 ± 2	79 ± 6	---	---	43 ± 2	84 ± 6	---	---
'Rosy Glow'	59 ± 11	77 ± 0	61 ± 0	---	64 ± 12	84 ± 4	87 ± 0	---
82-81-21	41 ± 5	70 ± 12	51 ± 5	64 ± 0	47 ± 5	75 ± 4	66 ± 7	73 ± 13
81-45-15	38 ± 10	48 ± 10	70 ± 15	55 ± 7	44 ± 11	57 ± 12	79 ± 8	64 ± 4
82-81-3	54 ± 6	82 ± 9	67 ± 14	66 ± 4	58 ± 6	83 ± 8	75 ± 12	71 ± 6
82-119-5	34 ± 1	52 ± 22	56 ± 21	66 ± 20	46 ± 8	80 ± 13	60 ± 20	81 ± 11
83-14-13	34 ± 3	36 ± 5	46 ± 5	64 ± 15	37 ± 5	42 ± 6	56 ± 14	73 ± 12
83-267-3	22 ± 5	48 ± 14	46 ± 2	88 ± 5	27 ± 6	56 ± 13	50 ± 2	89 ± 0
85-341-9	30 ± 2	38 ± 2	60 ± 17	64 ± 12	34 ± 1	41 ± 2	66 ± 14	72 ± 12

[z]Denotes when a plant did not flower in an environment.

14-13, 83-267-3, and 85-341-9) had highly significant z test *P* values (Table 2).

Flowering responses for the first six flower buds (terminal plus five consecutive, subtending laterals) provide an expanded conceptualization of the SD and DN photoperiodic responses (Table 3). In contrast with LD/R or LD/FR environments, all garden genotypes eventually flowered under natural (field) conditions on flower buds >sixth initial (data not presented), with the exception of 'Foxy', a greenhouse clone. Since flower buds are initiated sequentially in relation to the terminal, the critical photoperiod for FBD was reached at different times after FBI among the genotypes or there was a differential response to HDI (Table 3). For instance, under the natural environment, the sixth bud for 'Minnautumn' flowered while the third to sixth buds flowered for 82-81-21, 82-81-3, and 82-119-5. This is not correlated with SD response group classifications, e.g., 5 week genotypes had the second to sixth initials flowering ('Superior'), third to sixth initials flowering (82-119-5), or none of the first to sixth initials flowering ('Ruby Mound') (Table 3). Four DN genotypes, i.e., those with flowering for the 1st to 6th initials in all four environments, were found: 81-45-15, 83-14-13, 83-267-3, and 85-341-9 (Table 3). FBD differences between obligate SD 'Aurora' (Fig. 4A) and DN 83-267-3 (Fig. 4B) for the first four flower initials illustrate the trends noted under the LD/FR environment.

LDLN varied between environments for each genotype, with the lowest number occurring with either the SD or natural treatments (Table 4). There was no correlation between decreasing leaf number and SD response group of the genotypes. Mean values within genotypes varied as much as n = 20 leaves between photoperiodic treatments, particularly with SD genotypes such as 'Aurora' and 'Foxy' (Table 4). DN genotypes (85-341-9, 83-267-3, and 82-124-3) produced significantly less leaves than other

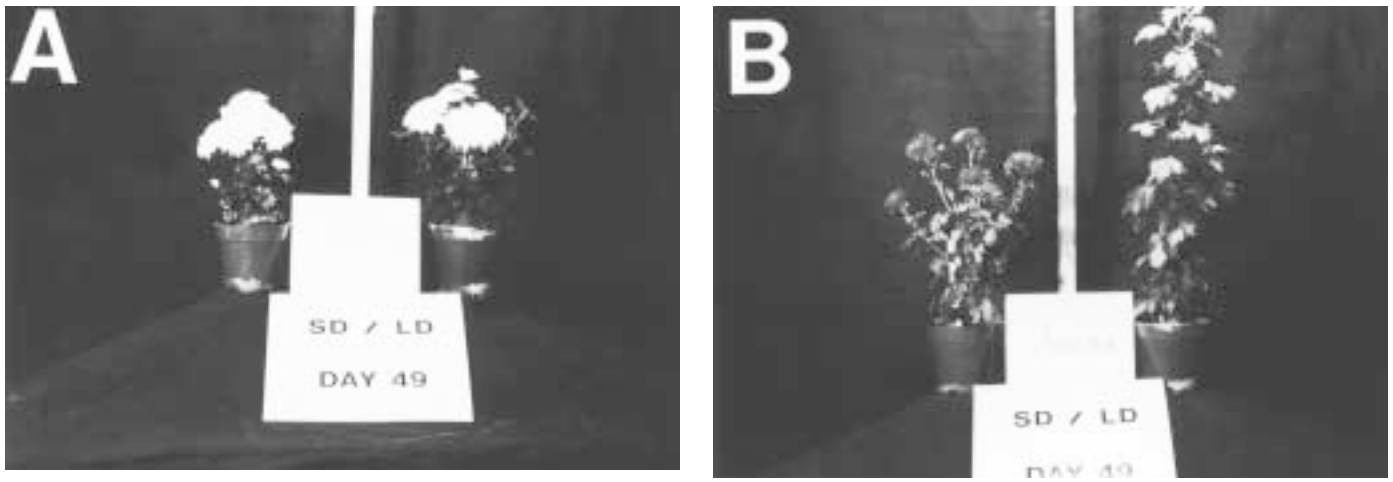

Fig. 1. Flowering of (**A**) day-neutral genotype 83-267-3 and (**B**) short-day genotype 'Aurora' chrysanthemum under SD and LD/R environments. Photographs with a meter stick denoting cm.; plants were growing in 12.5-cm-diameter pots.

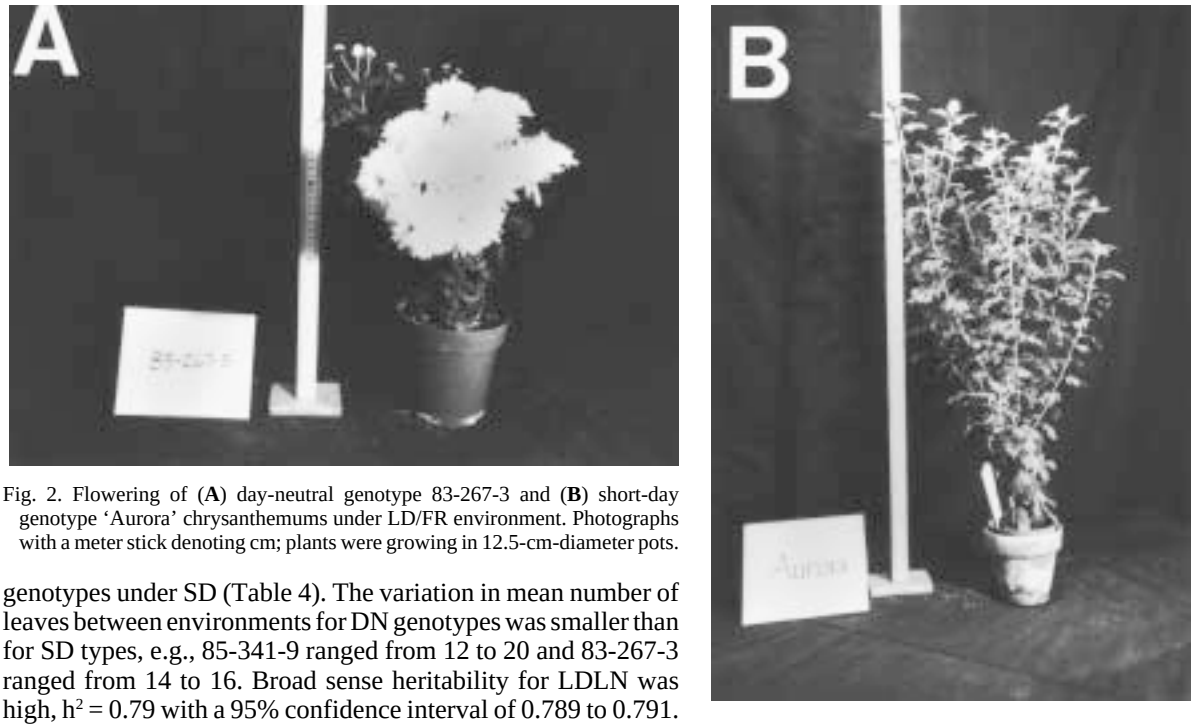

Fig. 2. Flowering of (**A**) day-neutral genotype 83-267-3 and (**B**) short-day genotype 'Aurora' chrysanthemums under LD/FR environment. Photographs with a meter stick denoting cm; plants were growing in 12.5-cm-diameter pots.

genotypes under SD (Table 4). The variation in mean number of leaves between environments for DN genotypes was smaller than for SD types, e.g., 85-341-9 ranged from 12 to 20 and 83-267-3 ranged from 14 to 16. Broad sense heritability for LDLN was high, $h^2 = 0.79$ with a 95% confidence interval of 0.789 to 0.791. Number of strap-shaped leaves subtending the terminal of DN or SD genotypes ranged from one to nine in different environments (Table 4). However, mean separations did not show significant differences between SD and DN types within environments. Broad sense heritability for the number of strap-shaped leaves was $h^2 = 0.79$ with a 95% confidence interval of 0.76 to 0.82.

Mean stem lengths of the terminal shoots were significantly longer for SD genotypes, particularly greenhouse 'Foxy' and garden 'Autumn Fire' types (Table 5). Stem lengths also varied across environments for each genotype; SD genotypes generally had a wider range in stem lengths (e.g., 'Foxy' ranged from 33 to 92) than DN types (e.g., 83-267-3 ranged from 18 to 24) (Table 5). Stem lengths had a broad sense heritability of $h^2 = 0.91$ with a 95% confidence interval of 0.90 to 0.92. Mean separations for the number of nodes with axillary branching overlapped considerably and appeared to be unrelated to SD vs. DN response. For instance, 'Foxy' and 82-81-3 did not differ significantly for apical dominance, while 82-124-3 was significantly different under SD (Table 5). The number of nodes with axillary branching had a broad sense heritability of $h^2 = 0.75$ with a 95% confidence interval of 0.74 to 0.76.

Mean internode lengths of genotypes overlapped within environments, with few significantly different mean separations (Table 6). In most cases, 'Foxy' had significantly longer internode lengths under all environments when compared with other genotypes, but no relationship could be found between SD and DN genotypes for internode lengths.

Three DN genotypes (81-45-15, 83-267-3, and 85-341-9), with the most highly significant binomial (z) tests ($P < 0.001$) for day neutrality in the SD, LD/R, LD/FR, and Natural environments (Table 2), were selected for subsequent study in the continuous FR+R environment. This environment was used to differentiate between DN and HDI under 24 h continuous light and high temperatures (days/nights of 28.3 °C). The first and third flowers reached anthesis only with 83-267-3 (Fig. 5), at 47 ± 3 d

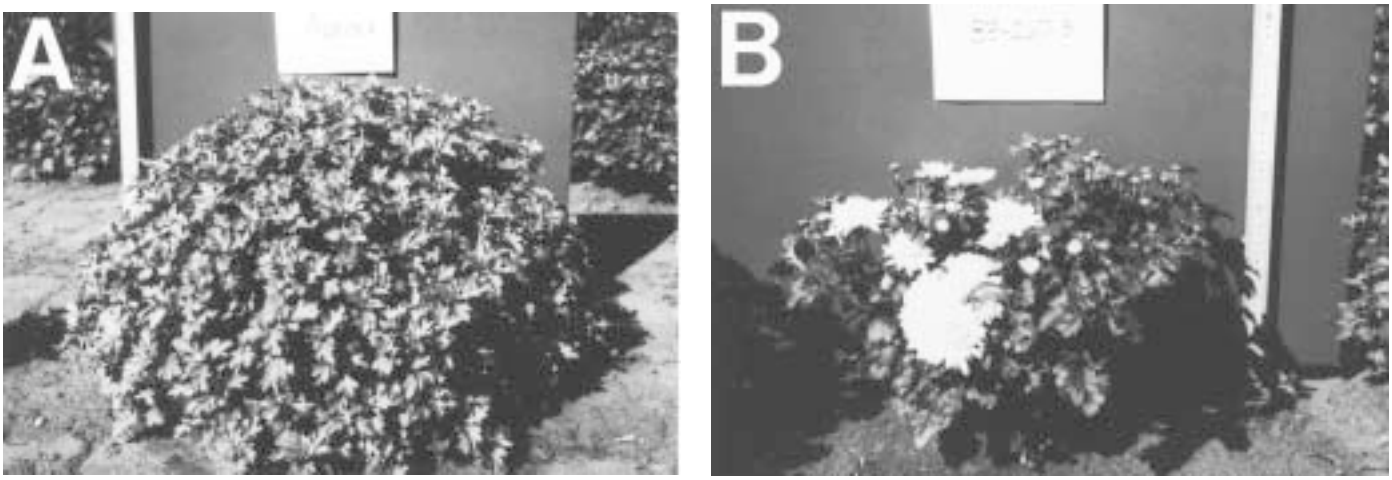

Fig. 3. Flowering of (**A**) short-day genotype 'Aurora' and (**B**) day-neutral genotype 83-267-3 chrysanthemums under the Natural environment. Photographs with a meter stick denoting cm.

Table 2. Binomial (z-test) analysis[z] of day neutrality (observed proportion flowering to nonflowering) for first and third flowers of 19 genotypes of greenhouse/garden chrysanthemums pooled across environments (SD, LD/R, LD/FR, and Natural).

	First flower		Third flower	
Genotype(s)	Observed proportion	*P*	Observed proportion	*P*
'Autumn Fire', 'Aurora', AGSL-1, 'Foxy', PPSL-6, PPSL-10, and 'Ruby Mound'	0.25:0.75	0.63^{NS}	0.25:0.75	0.63^{NS}
'Minnautumn'	0.50:0.50	0.027*	0.62:0.38	0.002**
'Minnwhite'	0.37:0.63	0.19^{NS}	0.37:0.63	0.19^{NS}
'Superior'	0.25:0.75	0.63^{NS}	0.31:0.69	0.37^{NS}
'Rosy Glow'	0.44:0.56	0.08^{NS}	0.56:0.44	0.007**
82-81-21	0.81:0.19	<0.001***	0.94:0.06	<0.001***
81-45-15	0.94:0.06	<0.001***	1.00:0.00	<0.001***
82-81-3	0.87:0.13	<0.001***	0.87:0.13	<0.001***
82-119-5	0.31:0.69	0.37	0.25:0.75	0.63
82-124-3	0.44:0.56	0.08	0.44:0.56	0.08
83-14-13	0.87:0.13	<0.001***	0.81:0.19	<0.001***
83-267-3, 85-341-9	1.00:0.00	<0.001***	0.81:0.19	<0.001***

[z]The null hpothesis (H_o) was the proportion (p) flowering ≤0.75.
^{NS,*,**,***}Nonsignificant or significant at *P* = 0.05, 0.01, or 0.001, respectively.

and 54 ± 5 d, respectively. None of the first to sixth flowers developed on 81-45-15, whereas the fourth to sixth flower buds developed with 85-341-9. Mean separations of leaf number, strap-shaped leaves subtending the terminal flower bud, number of nodes with axillary branching, and internode lengths were significantly different in almost all cases (Table 7). DN genotype 83-267-3 had the lowest average values for all traits recorded. All three DN genotypes had lower average leaf numbers in the continuous FR+R environment (Table 7) than in LD/FR (Table 4). Most other traits followed this trend.

Discussion

Under SD, the first to sixth flower buds for all greenhouse and garden genotypes completed FBI and FBD to anthesis (Tables 1 and 3), as would be expected (Cathey and Borthwick, 1957). Surprisingly, several named genotypes and unnamed selections were earlier than commercial genotypes (van Zanten, North America, 1999; Yoder Brothers, Inc., 2000). For instance, SD response groups varied from 3 (83-267-3) to 4 (PPSL-6 and 85-341-9) and 5 weeks ('Ruby Mound', 'Superior', 82-124-3, 82-119-5, and 83-14-13) (Table 1). Such early-flowering genotypes, most of which were DN, have not been quantified previously and constitute an important genetic base for chrysanthemum breeding programs. DN garden germplasm could be integrated with greenhouse genotypes, given the high heritability of stem length and LDLN, as well as cross-compatibility between the groups. If the selected DN genotypes were to be directly adapted to greenhouse potted plant production schedules, they would be produced significantly shorter than greenhouse genotypes (compare with stem lengths of 'Foxy', Table 5). Thus, a smaller pot size would be required. Use of a LD environment for increased vegetative growth would not provide added plant height, as most of these genotypes were also DN. These early flowering types could be produced under a production regime similar to 'Fleurettes' (7 to 8 week SD response group), an early, dwarf commercial series recommended for production in 2.5 to 3.5 inch (6 to 9 cm) diameter pots or cell packs (Yoder Brothers, Inc., 2000). It does not follow, however, that all DN genotypes will have low LDLN and short stature, since the garden genotypes were selected randomly from the germplasm. Thus, it may be possible to select for DN greenhouse cut chrysanthemums with high LDLN and longer stem lengths.

Table 3. Flowering responses [flowering (+) or nonflowering (–) for FBI and FBD] of the first six flower buds (1st = terminal bud; five consecutive, subtending laterals = 2nd, 3rd, 4th, 5th, and 6th) for 19 chrysanthemum genotypes grown under four environments (photoperiod, day/night temperature). Genotypes were classified based on the flowering response of most replications.

Flowering response (+/–) for flower buds						Genotype categorization within environment[z]			
						SD	LD/R	LD/FR	Natural
1st	2nd	3rd	4th	5th	6th	20/16.7 ºC	20/16.7 ºC	31/26.7 ºC	27.5/17.2 ºC
–	–	–	–	–	–		1-4,7-9,11	1-4,7-9,11,12	1-4,6-9,12,16
–	–	–	–	–	+				5
–	–	–	–	+	+				
–	–	–	+	+	+		6, 12, 15	6, 16	
–	–	+	+	+	+			5	10, 14, 15
–	+	+	+	+	+		11		
+	+	+	+	+	+	1-19	5,10,13,14,16-19	10,13-15,17-19	13,17-19

[z]Numerical code designators for genotypes: 1 = 'Autumn Fire', 2 = 'Aurora', 3 = AGSL-1, 4 = 'Foxy', 5 = 'Minnautumn', 6 = 'Minnwhite', 7 = PPSL-6, 8 = PSL-10, 9 = 'Ruby Mound', 10 = 82-81-21, 11 = 'Superior', 12 = 'Rosy Glow', 13 = 81-45-15, 14 = 82-81-3, 15 = 82-119-5, 16 = 82-124-3, 17 = 83-14-13, 18 = 83-267-3, and 19 = 85-341-9.

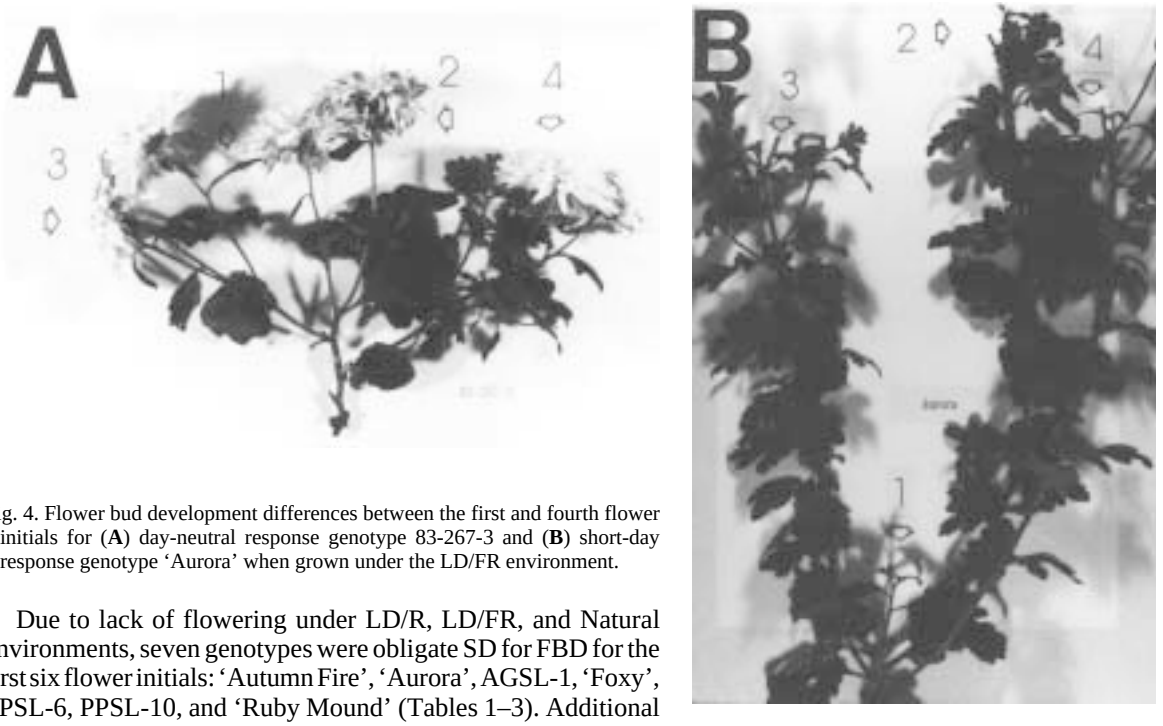

Fig. 4. Flower bud development differences between the first and fourth flower initials for (**A**) day-neutral response genotype 83-267-3 and (**B**) short-day response genotype 'Aurora' when grown under the LD/FR environment.

Due to lack of flowering under LD/R, LD/FR, and Natural environments, seven genotypes were obligate SD for FBD for the first six flower initials: 'Autumn Fire', 'Aurora', AGSL-1, 'Foxy', PPSL-6, PPSL-10, and 'Ruby Mound' (Tables 1–3). Additional genotypes also did not flower for the first to sixth flowers under LD/R ('Superior'), LD/FR ('Superior' and 'Rosy Glow') and Natural ('Rosy Glow' and 82-124-3) environments (Table 3). Others varied, depending on the floral position, whether SD are required for FBD. For instance, 'Minnwhite', 'Rosy Glow', and 82-119-5 are obligate SD for first to third flowers, but DN for the fourth to sixth in the LD/R treatment (Table 3). 'Minnwhite' and 82-124-3 had the same response under LD/FR. Regardless of DN and HDI, it took longer for DN genotypes to flower under all LD environments compared with SD, similar to previous reports for quantitative SD chrysanthemums (Langton and Cockshull, 1979).

Binomial (z) tests are useful to distinguish between DN and SD genotypes for each flower, with highly significant *P* values indicating DN. For instance, *P* values changed within genotypes if the first and third flowers differed for FBD requirements: 'Minnautumn' was obligate SD for the first flower (0.5:0.5, $P = 0.027$), but DN for the third (0.62:0.38, $P = 0.002$) flower (Table 2). Minor differences in replication response between first and third flowers, e.g., 'Superior', did not change significance (Table 2).

The necessity of recording FBD for the first six flower buds (terminal plus the five sequential subtending laterals), rather than just the first and third is clearly demonstrated by comparison of Tables 1 and 3. If just the first and third flower buds were observed, misclassification of 'Minnautumn' (Natural); 'Minnwhite', 'Rosy Glow', and 82-119-5 (LD/R); 'Minnwhite' and 82-124-3 (LD/FR); 'Superior' (Natural) would have occurred (Table 3). It is essential to document FBD in the first six flower initials to accurately determine the presence of absolute DN for all flower buds. This would be more important for potted and cut chrysanthemums than garden cultivars where the terminal is often the critical flower bud in commercial production (Yoder Brothers, Inc., 2000).

It was not possible to determine the effects of light quality (R vs. FR) during LD on flowering in these environments, since temperature differed between the LD/R and LD/FR environments. LD/R served as the discriminatory test environment for distinguishing between DN and SD genotypes for FBI and FBD, with SD serving as the control (Accati-Garibaldi et al., 1977; Cathey and Borthwick, 1961; H.F. Wilkins, 1989, personal communication). Since fluorescent lights (LD/R) are not the light source for commercial LD night interruption lighting, the LD/FR environment was used to duplicate the effects expected by growers (Cockshull, 1985; Post, 1949). The LD/FR environment was used to screen for DN and HDI genotypes. As expected, some genotypes that flowered under LD/R did not flower in the LD/FR environment (Tables 1 and 3). Whether this response was due to HDI and/or light quality differences between environments is unknown. The effects of light quality during HDI screening has not been studied, since heat delay occurs under SD conditions during FBI/FBD. Further research would be required to clarify this phenomenon.

Two phenomena, an actual delay in the number of days to flowering (Table 1) and a switch in photoperiod requirements for FBD in any or all of the first six flower initials (Table 3), were observed in genotypes with heat delay under LD/FR. Past research has focused on heat delay as the delay in flowering under SD conditions, since this is the commercial inductive photoperiod (Cockshull, 1979; van Zanten, North America, 1999; Yoder Brothers, Inc., 2000). When compared with LD/R, the LD/FR environment provided significant heat delay in FBD and anthesis for the first flower with 81-45-15 (21.9 d, Table 1) and 85-341-9 (23 d). In other cases, flowering dates were not significantly different, e.g., 82-119-5 (3.5 d) and 83-267-3 (1.5 d). These genotypes would be classified as thermozero temperature response (Cathey, 1955; de Jong, 1978; Langton and Cockshull, 1976). Surprisingly, several genotypes flowered earlier under LD/FR (heat delay conditions) than LD/R, including 'Rosy Glow' (16 d, Table 1), 82-81-21 (18.7 d), and 82-81-3 (15.2 d). Such genotypes are "thermopositive" (Cathey, 1955; de Jong, 1978; Langton and Cockshull, 1976). Thermozero genotypes have minimal interaction between genotype x environment and provide the widest adaptability across all production environments (Langton and Cockshull, 1976). Thermopositive genotypes are beneficial only in warmer production areas and do not

provide wide adaptation since flowering may be delayed under cooler, northern growing conditions (<15.5 °C) (Langton and Cockshull, 1976).

Evaluation of flowering dates under LD/FR heat delay conditions for the third flower show that genotypes responded similarly or differently than for the first flower (Table 1). For instance, 'Rosy Glow' flowered 3 d later under LD/FR than LD/R (thermonegative), 82-119-5 flowered 19.8 d earlier (thermopositive), whereas the remaining genotypes had the same response (thermozero). This demonstrates that flower position differs for temperature response. Future analyses of HDI and DN genotype screening would need to include the temperature response for the first to sixth flowers, allowing for selection of the same high temperature response with all flower buds.

Mean separation of leaf numbers under SD overlapped considerably between greenhouse and garden genotypes, with the most DN genotypes separated into a class with the smallest number of leaves (Table 4). Since considerable differences existed in the number of days to first flower (Table 1), denoting SD response groups ranging from 3 to 8 weeks, either leaf initiation rate and/or FBD differences account for the extreme differences in flowering response. Further studies would be necessary to partition the effects of these two factors. As expected, LDLN under LD/FR and LD/R environments increased; DN genotypes were again statistically significant from the others—the lowest LDLN group (Table 4). In addition, DN genotypes had the lowest variance in LDLN. Estimated marginal means for LDLN are not a useful selection tool, since both 'Foxy' (SD) and 83-267-3 (DN) had the lowest values

Table 4. Mean ±SD for long day leaf number (LDLN) and number of strap-shaped leaves (nodes without lateral buds, i.e., nonbranching) subtending the terminal flower bud of 19 chrysanthemum genotypes grown in four environments (photoperiod, day/night temperature). See text for day/night temperature regimes.

	LDLN				Number of strap-shaped leaves			
Genotype	SD	LD/R	LD/FR	Natural	SD	LD/R	LD/FR	Natural
'Autumn Fire'	20.5 ab[z]	36.8 f	41.2 d	29.0 c	2.5 abc	3.5 abc	8.8 abcd	5.2 bcd
	(2.4)	(4.6)	(2.2)	(2.2)	(1.7)	(1.3)	(2.1)	(0.9)
'Aurora'	21.0 ab	29.8 ef	28.8 bc	17.8 ab	4.0 bc	6.8 abc	5.2 ab	2.0 abc
	(4.7)	(6.3)	(9.1)	(3.4)	(0.0)	(3.9)	(2.1)	(1.4)
AGSL-1	18.5 ab	21.8 abcde	20.8 ab	18.0 ab	0.8 ab	6.5 abc	6.0 abc	3.5 abcd
	(2.4)	(4.6)	(4.8)	(6.1)	(0.5)	(3.1)	(1.2)	(2.6)
'Foxy'	24.0 ab	35.8 f	39.8 cd	21.5 bc	0.0 a	3.2 abc	3.8 ab	0.0 a
	(2.6)	(5.1)	(9.2)	(4.2)	(0.0)	(0.5)	(0.5)	(0.0)
PPSL-6	18.8 ab	18.2 abcd	22.2 ab	15.5 ab	2.2 abc	8.5 c	13.0 d	4.0 abcd
	(0.9)	(1.5)	(1.7)	(3.0)	(2.6)	(1.3)	(2.0)	(2.9)
PPSL-10	17.8 ab	25.8 bcdef	19.8 ab	13.2 ab	3.2 abc	6.0 abc	6.8 abcd	2.5 abc
	(1.7)	(2.8)	(4.6)	(3.6)	(0.9)	(2.2)	(1.5)	(1.3)
'Ruby Mound'	15.2 a	14.2 a	19.0 ab	17.2 ab	5.8 c	8.0 bc	9.2 bcd	7.2 d
	(5.2)	(2.1)	(2.6)	(3.7)	(1.7)	(0.0)	(1.3)	(1.5)
'Superior'	23.8 ab	31.5 ef	30.0 bcd	14.5 ab	3.8 abc	6.8 abc	12.8 cd	3.2 abcd
	(2.2)	(5.7)	(7.8)	(3.0)	(1.7)	(3.9)	(8.8)	(0.9)
'Minnwhite'	20.2 ab	23.5 abcde	18.8 ab	13.8 ab	3.5 abc	5.5 abc	9.0 abcd	5.5 bcd
	(2.5)	(4.0)	(0.9)	(4.2)	(1.9)	(1.3)	(1.4)	(2.4)
'Minnautumn'	12.8 a	18.0 abcd	15.5 a	15.2 ab	2.2 abc	2.8 abc	6.0 abc	4.0 abcd
	(2.5)	(4.7)	(3.1)	(2.9)	(1.2)	(2.9)	(2.0)	(1.8)
82-124-3	13.8 a	21.0 abcde	22.2 ab	14.5 ab	5.5 c	8.2 c	9.0 abcd	6.5 cd
	(1.5)	(2.0)	(1.9)	(1.7)	(1.7)	(3.8)	(3.2)	(3.1)
'Rosy Glow'	22.2 ab	26.5 cdef	23.0 ab	18.2 ab	0.5 ab	2.8 abc	4.2 ab	5.2 bcd
	(1.5)	(2.4)	(3.6)	(3.8)	(0.6)	(1.2)	(1.5)	(1.9)
82-81-21	26.5 ab	29.5 ef	14.8 a	12.0 a	3.2 abc	6.2 abc	4.8 ab	4.0 abcd
	(2.6)	(5.3)	(0.5)	(1.4)	(2.9)	(3.1)	(0.5)	(2.0)
81-45-15	20.8 ab	21.8 abcde	24.0 ab	10.0 a	1.5 ab	4.0 abc	4.5 ab	2.8 abcd
	(3.2)	(6.2)	(3.8)	(2.7)	(0.6)	(2.2)	(2.4)	(0.9)
82-81-3	24.8 ab	29.0 def	19.2 ab	14.0 ab	0.8 ab	2.0 ab	4.5 ab	2.5 abc
	(1.3)	(1.8)	(2.6)	(0.8)	(0.5)	(0.8)	(0.6)	(2.4)
82-119-5	29.8 b	15.0 ab	21.2 ab	11.5 a	1.2 ab	1.5 a	2.2 a	3.2 abcd
	(1.4)	(4.1)	(3.3)	(1.9)	(0.5)	(0.6)	(0.5)	(1.5)
83-14-13	16.0 ab	17.8 abc	14.8 a	10.5 a	3.8 abc	6.5 abc	5.8 ab	3.0 abcd
	(2.2)	(4.9)	(1.5)	(1.7)	(0.9)	(3.1)	(2.4)	(0.0)
83-267-3	15.0 a	15.8 abc	13.5 a	16.0 ab	1.2 ab	1.5 a	2.5 ab	1.5 ab
	(0.8)	(5.1)	(1.3)	(1.4)	(0.5)	(1.0)	(0.6)	(1.0)
85-341-9	12.2 a	13.2 a	19.8 ab	11.5 a	3.2 abc	3.8 abc	5.0 ab	4.0 abcd
	(1.7)	(0.9)	(2.8)	(4.4)	(1.5)	(1.3)	(2.6)	(1.4)
MSE[y]	30.37	17.93	19.61	10.31	2.04	5.32	7.03	3.24

[z]Mean separation within columns by Tukey's studentized range test $P < 0.05$.
[y]Estimate of mean square error (MSE) used to calculate HSD at $P < 0.05$ for mean separation.

(data not presented). The heat delay treatment (LD/FR) predominantly had lower LDLN than the LD/R environment, with the exception of two full-sibs, 82-81-3 (LDLN increase of 10) and 82-81-21 (LDLN increase of 15). Selection for DN and HDI genotypes is correlated with decreased mean and variance in LDLN for all environments. Langton and Dixon (1984) found that LDLN was a heritable, polygenic trait ($H_N = 0.55$). Thus, use of these selected DN and HDI genotypes as parents would produce a high frequency of progeny with low LDLN. However, as discussed earlier, it may be possible to select for DN/HDI cut flower genotypes.

The number of strap-shaped leaves, indicative of crown buds, were ≈10% to 20% of the LDLN in all environments (Table 4). The number of strap-shaped leaves was not correlated with either DN or HDI responses. All garden genotypes had a smaller number of strap-shaped leaves under SD than most other environments. Apparently, strap-shaped leaf number is not an important trait for selection of DN and HDI genotypes. Interestingly, only 'Foxy', a greenhouse genotype, did not possess any strap-shaped leaves in the SD treatment (Table 4).

Stem lengths of the terminal shoots were significantly higher within environments for SD genotypes, particularly 'Foxy' and 'Autumn Fire', than for DN genotypes (Table 5). This is not unexpected, since SD genotypes had higher LDLN. Additionally, SD genotypes had greater variation in stem lengths across environments whereas DN types did not. This would indicate that DN types have similar performance and stability in stem length across environments (minimal genotype x environment interaction), an important criterion for DN and HDI selection. Mean separations

Table 5. Mean ±SD for stem length and number of nodes (subtending the terminal flower bud) with axillary branching for 19 chrysanthemum genotypes grown under four environments (differing for photoperiod, day/night temperature). See text for description of day/night temperature regimes.

	Stem length				No. nodes with axillary branching			
Genotype	SD	LD/R	LD/FR	Natural	SD	LD/R	LD/FR	Natural
'Autumn Fire'	27.1 gh[z]	45.9 de	57.5 c	35.8 d	18.0 ab	32.8 f	33.0 de	22.5 d
	(2.3)	(7.4)	(5.2)	(8.1)	(3.7)	(5.6)	(3.7)	(2.4)
'Aurora'	23.6 defg	31.2 bcd	32.0 ab	19.6 ab	18.0 ab	21.5 bcdef	23.5 cde	15.8 cd
	(5.7)	(17.1)	(11.9)	(4.7)	(6.3)	(10.0)	(10.1)	(3.6)
AGSL-1	16.0 bcde	12.2 a	16.0 ab	11.5 ab	17.0 ab	15.0 abcd	14.8 abc	14.5 bcd
	(1.0)	(1.3)	(7.1)	(5.1)	(2.2)	(3.2)	(5.5)	(4.5)
'Foxy'	50.1 j	74.2 f	92.1 d	33.0 cd	23.8 b	29.5 ef	35.0 e	0.2 a
	(5.4)	(12.7)	(25.0)	(13.5)	(2.8)	(6.4)	(9.6)	(0.5)
PPSL-6	16.0 bcde	6.2 a	18.4 ab	8.2 ab	16.5 ab	9.8 ab	9.2 a	11.5 bc
	(0.6)	(0.6)	(3.1)	(1.9)	(2.6)	(0.5)	(1.5)	(3.3)
PPSL-10	16.8 bcdef	17.6 abc	18.9 ab	8.2 ab	13.8 ab	18.8 bcde	13.0 abc	9.8 bc
	(2.2)	(1.7)	(6.1)	(3.1)	(1.7)	(4.1)	(3.2)	(5.4)
'Ruby Mound'	11.2 ab	7.5 a	13.4 ab	13.5 ab	9.0 ab	6.2 a	10.2 ab	10.0 bc
	(3.2)	(3.0)	(1.4)	(9.0)	(4.5)	(2.1)	(1.5)	(5.0)
'Superior'	22.4 efg	24.8 abc	25.8 ab	8.5 ab	19.8 ab	24.5 cdef	22.2 bcd	11.2 bc
	(0.6)	(9.5)	(13.1)	(2.4)	(0.9)	(5.4)	(8.5)	(4.0)
'Minnwhite'	16.6 bcde	20.1 abc	11.6 a	7.5 ab	16.0 ab	18.0 abcde	9.8 a	7.8 abc
	(3.1)	(5.0)	(2.9)	(3.1)	(3.2)	(5.0)	(2.4)	(4.5)
'Minnautumn'	12.2 abc	20.1 abc	10.8 a	8.6 ab	11.0 ab	15.2 abcd	9.5 a	11.2 bc
	(2.9)	(5.2)	(2.8)	(2.5)	(2.2)	(7.0)	(2.6)	(2.9)
82-124-3	7.4 a	13.5 ab	18.2 ab	8.6 ab	8.8 a	12.8 abc	13.2 abc	8.0 abc
	(1.6)	(6.6)	(1.9)	(3.2)	(2.2)	(40)	(3.9)	(1.8)
'Rosy Glow'	22.4 efg	33.9 cde	28.5 ab	15.6 ab	21.5 ab	23.8 cdef	18.8 abc	13.0 bc
	(0.2)	(2.9)	(5.4)	(6.2)	(2.1)	(1.7)	(3.0)	(3.3)
82-81-21	40.2 i	50.8 e	34.2 b	15.1 ab	19.2 ab	20.2 bcde	10.0 ab	8.0 abc
	(3.3)	(3.1)	(6.2)	(3.4)	(5.1)	(4.3)	(0.8)	(1.8)
81-45-15	23.9 fg	22.4 abc	35.8 bc	5.5 a	18.8 ab	17.8 abcde	19.5 abc	7.0 ab
	(7.0)	(9.9)	(12.3)	(1.3)	(4.0)	(6.9)	(5.9)	(2.4)
82-81-3	33.6 hi	44.8 de	35.0 b	15.5 ab	23.8 b	26.2 def	14.8 abc	11.5 bc
	(2.1)	(3.5)	(5.7)	(4.4)	(1.3)	(1.5)	(2.8)	(3.0)
82-119-5	10.8 ab	10.9 a	21.8 ab	6.0 a	21.8 ab	13.8 abc	19.2 abc	8.2 abc
	(0.3)	(8.5)	(4.3)	(1.8)	(21.5)	(4.2)	(3.3)	(0.9)
83-14-13	15.0 bcd	10.4 a	15.8 ab	5.8 a	12.2 ab	11.2 ab	9.0 a	7.5 ab
	(1.2)	(3.0)	(2.2)	(0.9)	(2.2)	(2.1)	(2.2)	(1.7)
83-267-3	18.5 cdef	24.0 abc	23.8 ab	20.8 bc	14.5 ab	14.3 abcd	10.8 ab	14.2 bc
	(0.4)	(7.2)	(2.6)	(4.7)	(1.0)	(4.4)	(1.0)	(1.5)
85-341-9	14.6 bcd	16.4 abc	24.8 ab	11.4 ab	9.0 ab	9.2 ab	14.8 abc	9.0 bc
	(1.2)	(0.8)	(5.9)	(6.1)	(0.8)	(1.5)	(0.5)	(2.2)
MSE[y]	7.52	50.97	73.84	29.4	32.4	23.01	22.13	9.98

[z]Mean separation within columns by Tukey's studentized range test $P < 0.05$.
[y]Estimate of mean square error (MSE) used to calculate HSD at $P < 0.05$ for mean separation.

Table 6. Mean ±SD for internode length [terminal stem length/(no. nodes + 1)] for 19 chrysanthemum genotypes grown under four photoperiod treatments (SD, LD/R, LD/FR, and Natural).

	Internode length (cm)			
Genotype	SD	LD/R	LD/FR	Natural
'Autumn Fire'	1.3 ef[z] (0.0)	1.2 def (0.1)	1.4 cde (0.0)	1.2 cde (0.2)
'Aurora'	1.1 cde (0.1)	0.9 bcde (0.3)	1.1 abc (0.0)	1.0 abcde (0.2)
AGSL-1	0.8 abcd (0.0)	0.5 ab (0.0)	0.7 ab (0.2)	0.6 abcd (0.1)
'Foxy'	2.0 g (0.0)	2.0 g (0.2)	2.2 f (0.3)	1.4 e (0.5)
PPSL-6	0.8 abcd (0.0)	0.3 a (0.0)	0.8 ab (0.1)	0.5 a (0.2)
PPSL-10	0.9 bcd (0.1)	0.7 abcd (0.0)	0.9 abc (0.1)	0.6 abc (0.1)
'Ruby Mound'	0.7 ab (0.2)	0.5 ab (0.1)	0.7 ab (0.1)	0.7 abcd (0.3)
'Superior'	0.9 bcd (0.0)	0.8 abcd (0.2)	0.8 ab (0.2)	0.6 ab (0.1)
'Minnwhite'	0.8 abc (0.1)	0.8 abcd (0.2)	0.6 a (0.1)	0.5 a (0.1)
'Minnautumn'	0.9 bcd (0.2)	1.0 bcde (0.0)	0.6 a (0.1)	0.5 a (0.2)
82-124-3	0.5 a (0.0)	0.6 abc (0.3)	0.8 ab (0.0)	0.5 abc (0.2)
'Rosy Glow'	1.0 bcde (0.0)	1.2 def (0.2)	1.2 bcd (0.2)	0.8 abcde (0.3)
82-81-21	1.5 f (0.0)	1.7 fg (0.2)	2.2 f (0.4)	1.2 bcde (0.3)
81-45-15	1.1 cde (0.2)	1.0 bcde (0.2)	1.4 cde (0.4)	0.6 abc (0.2)
82-81-3	1.3 ef (0.0)	1.5 efg (0.1)	1.7 ef (0.3)	1.0 abcde (0.2)
82-119-5	0.5 a (0.3)	0.6 abc (0.3)	1.0 abc (0.0)	0.5 a (0.2)
83-14-13	0.9 bcd (0.0)	0.6 abc (0.4)	1.0 abc (0.0)	0.5 a (0.2)
83-267-3	1.2 def (0.0)	1.5 efg (0.4)	1.6 de (0.0)	1.2 de (0.2)
85-341-9	1.1 cde (0.1)	1.2 cdef (0.1)	1.2 bcd (0.2)	0.7 abcd (0.4)
MSE[y]	0.02	0.05	0.04	0.06

[z]Mean separation within columns by Tukey's studentized range test $P < 0.05$.
[y]Estimate of mean square error (MSE) used to calculate HSD at $P < 0.05$ for mean separation.

Fig. 5. Flowering of day-neutral and heat-delay insensitive genotype 83-267-3 under Continuous FR+R and high temperature treatment. Plant is growing in a 12.5-cm-diameter pot.

for the number of nodes with axillary branching were similar and overlapped considerably (Table 5). The number of branched nodes is independent of photoperiod response and heat delay. Similar trends were found with internode lengths (Table 6).

The discriminatory power of the last experiment (continuous FR+R, high temperature) is evident in the significant differences between three DN genotypes (Table 7). In all cases except stem length, 83-267-3 was significantly different from the others. Since growth chambers were used to institute this environment, early selection of potentially DN and HDI genotypes would be difficult, and potentially more costly, than greenhouse screening. As the LD/R environment is the most rigorous in differentiating between SD and DN genotypes for FBI and FBD of all six floral initials, but lacked HDI screening, the following scenario is proposed for future selection. Initial screening would begin during the summer months in the greenhouse using the SD (control) and LD/R environments, both with high night temperatures (≥27C), to provide the initial selection of DN and HDI genotypes. Both the LD/FR and Natural environments would be

Table 7. Mean ±SD for long day leaf number (LDLN), no. of strap-shaped leaves subtending the terminal flower bud, stem length, no. of nodes (subtending the terminal flower bud) with axillary branching, and internode length (terminal stem length/[no. nodes +1]) for three day neutral chrysanthemums grown in continuous FR+R light.

Genotype	LDLN	No. strap-shaped leaves	Stem length (cm)	No. nodes with branching	Internode length (cm)
81-45-15	22.8 c[z] (1.3)	3.6 ab (0.5)	14.6 b (3.7)	19.0 c (2.5)	19.0 c (0.2)
83-267-3	10.2 a (2.7)	3.0 a (0.4)	9.4 a (1.8)	7.2 a (3.1)	7.2 a (0.9)
85-341-9	18.1 b (2.5)	4.4 b (0.6)	10.6 a (2.2)	13.8 b (2.1)	13.8 b (0.5)
MSE[y]	9.9	0.8	9.2	8.8	0.7

[z]Mean separation within columns by Tukey's studentized range test $P < 0.05$.
[y]Estimate of mean square error (MSE) used to calculate HSD at $P < 0.05$ for mean separation.

eliminated. Selection of DN and HDI genotypes would be based on flowering of all first to sixth flower buds in both environments, using the binomial (z) test of day neutrality (*P* values for all flowers must be <0.001, with the observed proportion of flowering at ≥0.9) (Table 2), as well as the remaining phenotypic traits (Tables 3 to 6). The selected DN and HDI genotypes would then be screened in continuous FR+R at 28 °C constant, using the statistical tests for flowering response and phenotypic traits outlined below.

We propose the following ideotype for DN and HDI garden chrysanthemums, with possible applicability to greenhouse potted chrysanthemums. Plant ideotypes are models for predictable plant growth in a defined environment (Donald, 1968). In plant breeding programs, ideotypes are used to select plants with the suite of traits modeled in the prescribed environments. Langton and Cockshull (1976) developed an ideotype for cut spray chrysanthemums. Ascher (1986) also presented an ideotype for F_1 hybrid (seed-propagated) chrysanthemums.

The garden chrysanthemum DN and HDI ideotype consists of the following traits across all three test environments of SD = ≥16.7 °C (night), LD/FR ≥ 26.7 °C (night), and Continuous (24 h) FR+R = ≥28.3 °C (days/nights). Selection for DN and HDI genotypes would encompass all of these traits, using cuttings as the source material, rather than seedlings (de Jong, 1981).

The ideotype

FBI AND FBD IN SD AND LD. The DN and HDI ideotype would quickly initiate and develop a terminal flower bud in any photoperiod. All subtending lateral flower buds would undergo rapid FBI and FBD. Selection would not favor genotypes with large LDLN and delayed flowering (Langton and Cockshull, 1976; Vince, 1958). Flowering and nonflowering of the first to sixth flower buds (Table 3) and statistical tests (binomial analysis, $P <$ 0.001, Table 2) for flowering responses would be used to distinguish between genotypes. Sufficient vegetative growth (LDLN) must occur to produce a commercially acceptable plant stature.

FLOWERING RESPONSE GROUP. Selection for early flowering of the terminal bud would concordantly provide the ideotype with decreased flowering response groups (under SD or LD). Ideally, a 3 to 6 week response group cutoff would provide early genotypes with sufficient vegetative growth to achieve proper stem height (Table 5).

THERMOZERO TEMPERATURE RESPONSE. The ideotype possesses a flat response to temperature above or below 15.5 °C and is thermozero in all photoperiods for flowering (Cathey, 1955; Langton and Cockshull, 1976). Stock plants would also be maintained in a vegetative state at high temperatures with the application of ethephon (Searle and Machin, 1968; Strefeler, et al., 1996; Stuart, et al., 1988).

LOW LDLN AND HIGH LEAF INITIATION RATE. LDLN should remain in the range of 13 to 20 across all environments to ensure early FBI and FBD, as found for DN and HDI genotypes (Tables 4 and 7). Subtending, branching laterals provide added height to the SD genotypes (Fig. 4B), but not DN (Fig. 4A). Thus, the DN phenotype is a well-branched, dense canopy with multiple flower buds (Figs. 4A, 5). Since LDLN is heritable, with a broad sense heritability of $h^2 = 0.79$ in this germplasm, selection should be effective. The ideotype also has a high leaf initiation rate. Leaf initiation rates should be determined with selection of genotypes with at least 0.58 to 0.82 leaves/d (Cockshull, 1976). Leaf initiation rates have a broad sense heritability of $h^2 = 0.767$ in greenhouse germplasm (Langton and Cockshull, 1976).

STEM LENGTH OF TERMINAL SHOOT. The ideotype has low mean and variance for stem lengths (Tables 5 and 7), due to the corresponding lower LDLN. Since this trait is highly heritable, $h^2 = 0.91$, and at least one DN/HDI genotype exists with consistently short stem lengths across environments (Table 7), a breeding program could select for additional dwarf genotypes (Langton, 1987). Stem lengths of the terminal shoots were significantly higher for SD than for DN genotypes (Table 5). Additionally, SD genotypes had greater variation in stem lengths across environments whereas DN types did not. This would indicate that DN types have similar performance and stability in stem length across environments (minimal genotype × environment interaction), an important criterion for DN and HDI selection.

The ideotype for DN and HDI chrysanthemums includes five traits for which significant differences were found between garden and greenhouse chrysanthemum genotypes under five photoperiods. Many of the traits are biologically related and may not be independently manipulated (Langton and Cockshull, 1976). Thus, all traits in the ideotype are simultaneously selected in a sequential series of environments with application of appropriate statistical tests. Initially, genotypes selected in subsequent screenings of the ideotype will resemble 83-267-3 for the identified traits, but differ for nonideotype traits such as flower color and flower type. Future breeding research will focus on inheritance studies of these traits, with the ultimate objective being transference of garden DN, HDI germplasm into greenhouse, potted, or cut chrysanthemum production.

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