Early Generation Evaluation in *Antirrhinum majus* for Prediction of Cutflower Postharvest Longevity

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ABSTRACT. On-plant floret longevity and cutflower postharvest longevity (PHL) of *Antirrhinum majus* L., snapdragon, were evaluated using inbreds P1 (16 day PHL) and P2 (6 day PHL), F₁ (P1 × P2), F₂ (F₁ self-pollinated), F₂ × F₂ (among and within PHL categories: long, 17 to 25 days; middle, 9 days; and short, 2 to 3 days), and F₃ families (F₂ self-pollinated). F₂ on-plant floret longevity and PHL correlated to later generation PHL. Prediction of progeny PHL from F₂ × F₂ matings appears feasible if genotypic value for PHL of F₂ is known. Selection for PHL is best based on evaluation of multiple cutflowers per genotype. Significant additive and dominant genetic variance components contribute to PHL.

Cutflowers are highly perishable and cutflower postharvest longevity (PHL) is critical to market value. Historical and current research uses chemical treatments to extend PHL by only a few days. Several of these compounds are carcinogens, long lasting in the environment, and toxic at low concentrations (Nell, 1992; Ohkawa et al., 1999). With chemicals available to industry being limited in efficacy and in number, a need exists to explore alternative methods of extending PHL.

Despite the importance of PHL in determining quality and consumer preference, information on inheritance and response to selection for PHL remains scarce. Variability for PHL has been observed in *Antirrhinum majus* L. (Stieve and Stimart, 1994), *Begonia xcheimantha* Everett (Hvoslef-Eide et al., 1995), *Calistephus chinensis* L. (Patil and Rane, 1999), *Eustoma* sp. Raf. (Ohkawa and Sasaki, 1999), *Leptospermum* sp. (Bicknell, 1995), *Limonium* sp. (Burge et al., 1998), *Lupinus havardii* Wats (Mackay and Davis, 1998), *Paeonia* sp. (Heuser and Evensen, 1986), and members of the Proteaceae (Joyce and Beal, 1999). Genetic variance components, of greater immediate utility for improving PHL, have been reported in: *A. majus* (Schroeder and Stimart, 2001), *Dendrobium* cultivars (Bobisud and Kamemoto, 1982), *Gerbera* sp. (Muceniec et al., 1978; Wernett et al., 1996a), *Lilium* sp. (van der Meulen-Muisers et al., 1998, 1999), *Rosa* cultivars (De et al., 1999), and *Tulipa* sp. (van Eijk and Eikelboom, 1980). Direct and indirect selection for PHL, performed upon the trait of interest or correlated traits, respectively, has been proposed for *Gerbera* sp. (Wernett et al., 1996a, 1996b), *Lilium* sp. (van der Meulen-Muisers and van Oeveren, 1996; van der Meulen-Muisers et al., 1997), *Petunia* sp. (Krahl and Randle, 1999), *Rosa* sp. (Halevy and Mayak, 1975), and *Tulipa* sp. (van Eijk and Eikelboom, 1980). Selection response against stem bending, folding and wilting (Wernett et al., 1996a), and for productivity as yield in flowering stems (Harding et al., 1981) have been reported in *Gerbera* populations. Successful selection in *Dianthus caryophyllus* L. for postharvest flower life was recently described by Burchi et al. (1999) and Onozaki et al. (2001).

Development of commercial ornamental breeding lines is a lengthy and resource-consuming process even considering relatively short lifecycles. Analysis of *A. majus* PHL is based on lifecycle attributes of the species, genetic variability for PHL, and with the goal to extend PHL through breeding. Preliminary work in *A. majus* genetics revealed PHL as a readily manipulated, quantitative trait with significant additive and dominant genetic components (Schroeder, 1995, 2000; Schroeder and Stimart, 2001). Further, selection for PHL in *A. majus* is possible and F₁ hybrids may be of utility to maximize PHL (Schroeder, 2000). This study investigated early generation crossing and evaluation to examine timing for selection, necessity of progeny testing, possibility for indirect selection, and resolution of underlying gene action for PHL in *A. majus*.

Materials and Methods

GERMPLASM. Forty-seven commercial inbred lines of *Antirrhinum majus* L. were evaluated for PHL in 1991 and 1992 at the University of Wisconsin-Madison (Stieve and Stimart, 1994). Two lines selected represented extremes in PHL, P1 with 16 d and P2 with 6 d (Stieve and Stimart, 1994). Commercial *A. majus* inbreds are maintained through bulked pollen methods; therefore, P1 and P2 were self-pollinated and advanced by single seed descent to F₆ to establish genetic purity. Inbreds were crossed in fall 1997 to produce F₁ (P1 × P2), 12 d PHL, and F₂ (F₁ self-pollinated). Four hundred sixty F₂ individuals were grown to anthesis in a polyhouse at the University of Wisconsin-Madison according to standard forcing procedures (Rogers, 1992). Briefly, seeds were germinated in a cell of a cell pack and seedlings individually transplanted to 96-cell (65-cm³) flats. Seedlings were transplanted to square plastic pots (1250 cm³) when the third to fourth set of true leaves appeared and grown through anthesis. Growing medium consisted of equal volumes soil, peat and perlite. Plant bench spacing was on 22-cm centers. Plants were fertilized every other week with 200 mg·L⁻¹ N using Peter's 20N–8.7P–16.6K (Scott's Sierra Horticultural Products Co., Marysville, Ohio) and provided supplemental light of 27 μmol·m⁻²·s⁻¹ at bench level using 1000-W high-pressure sodium lamps from 0600 through 2400 HR. F₂ plants were pinched above the third node and resulting axillary stems thinned to two stems per plant; other generations were not pinched.

Upon F₂ anthesis, one stem was retained on the plant while the other stem was harvested for PHL evaluation. The stem for

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Fig. 1. Segregation in the F_2 of *Antirrhinum majus* L. for cutflower postharvest longevity.

PHL evaluation was harvested when the first five florets opened thereby equalizing developmental stage. Harvested stems were immediately placed in distilled water (dH_2O) and transported to the laboratory. Stems were adjusted to 40 cm below the lowest floret with the bottom 15 cm of leaves removed; the 40-cm stem and inflorescence are herein termed cutflower. Cutflowers were placed in a 3×5 grid (7.5×7.5 cm) supported upright with a wire mesh in plastic storage containers $34 \times 22 \times 15$ cm (L $\times$ W $\times$ H) containing 3 L of dH_2O , a 4-cm depth. Holding solutions were maintained daily by addition of dH_2O but not exchanged. Cutflowers were evaluated at 23°C under continuous cool white fluorescent illumination of $11 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at bench level. Cutflower senescence was defined as 50% of the florets browning/drying or wilting (Marousky and Raulston, 1970). Dates of harvest and senescence were recorded for each cutflower and PHL determined from their difference.

The first five florets of each F_2 were individually monitored for dates of anthesis and senescence using the on-plant stem. Floret senescence was defined as the floret wilting or 50% of the floret browning/drying. Difference between dates of floret anthesis and senescence is herein termed on-plant floret longevity. Upon completion of the on-plant study, F_2 individuals were self-pollinated to create F_3 families. F_2 individual plants were randomly selected from extremes in PHL (long = 17 to 25 d and short = 2 to 3 d) and the mean of the population (middle = 9 d) (Fig. 1). Seventeen F_2 individuals were selected from each category; however, due to infertility several individuals were lost resulting in 15 individuals maintained per category. A half-diallel mating scheme within PHL categories and a full-diallel mating scheme among PHL categories, using the selected F_2 individuals, were completed in Fall and Winter 1997–98 to create $F_2 \times F_2$ progeny. Unrelated $F_2 \times F_2$ progeny were selected for PHL evaluation to maximize the number of F_2 individuals being progeny tested.

Thirty individuals from each of P_1 , P_2 , F_1 ($P_1 \times P_2$), 41 F_3 (F_2 self-pollinated) families, and 68 $F_2 \times F_2$ progeny were grown for PHL evaluations as described above. Due to logistic limitations, $F_2 \times F_2$ progeny and corresponding F_3 families were randomly assigned to three planting times. The plants were grown in a randomized complete block design (six blocks, five plants/genotype/block) in

Fall, Winter, and Spring 1998–99. Harvested stems were adjusted and evaluated for PHL as defined above.

STATISTICS. Data from Fall, Winter, and Spring 1998–99 plantings were checked for homogeneity of variances and seasonal effects on PHL. Samples of F_3 families, repeated over plantings, were used as controls; 18 between fall and spring, 10 between winter and spring, and two between fall and winter. Pair-wise comparisons of control means across plantings were completed (Littell et al., 1996; Steel and Torrie, 1980) and significant seasonal effects were not found. Equality of residual error variances across plantings was checked using Levene's test (Littell et al., 1996) to verify legitimacy of assumptions associated with linear regression analyses (Steel and Torrie, 1980). Residual errors were calculated and compared using mixed models analysis with

Satterthwaite (1946) corrections for degrees of freedom (Littell et al., 1996). Specifically, plantings and genotypes were considered as fixed and other components of the experimental design as random (Littell et al., 1996; Steel and Torrie, 1980). Analysis confirmed uniformity of residual errors. Least-squares genotypic PHL means were calculated from the three plantings (Littell et al., 1996; Steel and Torrie, 1980). Linear regressions, to determine trait relationships, were completed using mixed model analysis with Satterthwaite (1946) corrections for degrees of freedom (Littell et al., 1996). R^2 values from regression were compared with established tables for significance (Steel and Torrie, 1980). Narrow sense heritability estimates were calculated as parent-offspring regressions (Falconer and Mackay, 1996).

Due to post-analysis inaccuracies in describing F_3 family PHL based on F_2 PHL, described below, classification of the $F_2 \times F_2$ progeny into PHL categories was reassessed based on F_3 (F_2 self-pollinated) family PHL values. Midparent values were calculated as if $F_2 \times F_2$ progeny were generated from $F_3 \times F_3$ crosses. Classification of nine evaluated $F_2 \times F_2$ progeny, distributed across the PHL range, was not possible due to poor germination in related F_3 families and thus were omitted from further analyses. Based on F_3 family PHL means, midparent and high parent values were calculated for each of 59 $F_2 \times F_2$ progeny evaluated (Hallauer and Miranda, 1988). Heterotic deviations of $F_2 \times F_2$ progeny were quantified as day and percentage of deviation from the respective midparent and high parent PHL on a progeny basis and then averaged within cross categories. Positive average deviations represent progeny PHL values greater than midparent and high parent PHL, respectively. Least significant differences among average deviations were calculated (Littell et al., 1996).

Results and Discussion

F_3 family cutflower PHL was significantly and positively correlated to F_2 on-plant floret longevity, $R^2 = 0.22$ (Fig. 2B). Three non-outlier points influenced the significant, positive correlation of F_2 individual PHL with F_2 on-plant floret longevity, $R^2 = 0.09$ (Fig. 2A). Increased significance, with regard to F_3 family versus F_2 individual PHL, is likely due to greater precision of the F_3 family mean due to increased sampling. On-plant longevity was generally two to three times longer than PHL (Fig. 2A and B). Correlations of on-plant floret longevity to PHL may suggest

Fig. 3. Regression of F_3 family cutflower postharvest longevity on F_2 individual cutflower postharvest longevity in *Antirrhinum majus* L. *Significant at $P \leq 0.05$.

similar underlying floral senescence biology regardless of on-plant or cutflower evaluation since observed senescence symptoms were similar. F_2 on-plant floret longevity provides information toward F_2 individual and F_3 family PHL. Therefore, selection for extended

Fig. 2. Regression of F_2 individual cutflower postharvest longevity (A) and F_3 average family cutflower postharvest longevity (B) on F_2 on-plant floret longevity in *Antirrhinum majus* L. ***Significant at $P \leq 0.05$ or 0.01, respectively.

PHL can be initiated in the F_2 based on on-plant longevity. Data from *Lilium* sp. (van der Meulen-Muisers et al., 1999), *Petunia* sp. (Krahl and Randle, 1999) and *Tulipa* sp. (van Eijk and Eikelboom, 1980) suggest similar correlations may hold across species.

F_3 family PHL was significantly and positively correlated to F_2 individual PHL, $R^2 = 0.11$ (Fig. 3). Observed ranges for F_2 and F_3 individual PHL were similar (data not shown); however due to averaging to obtain F_3 means, the range for F_3 family PHL was roughly one-half that of F_2 individual PHL. Broad distributions of F_3 PHL were observed within F_2 PHL categories (Fig. 3). The nature of these distributions and correlation magnitude suggest evaluation of F_2 individual cutflower stems can be used, though very cautiously, to predict F_3 family PHL. Due to the quantitative nature of *A. majus* PHL (Schroeder, 2000), sampling single F_2 cutflowers is thought to be the main source of error in predicting F_3 PHL. In contrast, sampling tails of a parental distribution is known to give accurate regression estimates (Nyquist, 1991). To improve correlation between F_2 and F_3 PHL, multiple cutflowers from F_2 plants may be evaluated and may be obtained by pinching or clonal propagation as in *D. caryophyllus* (Burchi et al., 1999; Onozaki et al., 2001). Evaluation for PHL can be accurately based on multiple F_3 stems in preference to one F_2 stem (Fig. 2A and B) (Schroeder and Stimart, 2001).

Matings of $F_2 \times F_2$, within and among short, middle and long PHL categories, generated progeny with PHL values reflecting parental origin (Fig. 4). Crosses within PHL categories generated progeny that clustered in the respective categories. Matings among parental categories resulted in progeny of intermediate PHL. Regression of $F_2 \times F_2$ progeny PHL values on midparent PHL values demonstrates a significant positive correlation, $R^2 = 0.71$ (Fig. 4). Multiple matings created for each cross category bolster the strong correlation. A narrow sense heritability estimate for PHL of 0.41 agrees with the narrow sense heritability of 0.30 obtained by Schroeder (2000). Based on a strong correlation, moderate heritability, and visual clustering of the data, prediction of

$F_2 \times F_2$ progeny PHL appears feasible if genotypic PHL value of F_2 individuals is known. Similar results have been shown with intermating of *Lilium* cultivars (van der Meulen-Muisers et al., 1999).

Average $F_2 \times F_2$ progeny PHL are a day, ≈ 24 h, greater than respective midparent values without significant deviation across categories (Fig. 5, Table 1). Midparent PHL values for middle

Fig. 4. Regression of cutflower postharvest longevity of $F_2 \times F_2$ progeny on midparent value in *Antirrhinum majus* L. Crosses made within and among cutflower postharvest longevity categories: short = 4.7–6.9 d, middle = 7.2–8.4 d, and long = 9.0–11.0 d. Solid line represents linear regression across categories, **Significant at $P \leq 0.01$.

x middle and short x long categories do not deviate significantly from each other nor do progeny from these groups deviate significantly; all other deviations are significant (Fig. 5). Significant differences among progeny of PHL cross categories (Fig. 5) suggest a significant additive component to PHL agreeing with the significant additive variance reported by Schroeder and Stimart (2001). No significant differences across categories in deviation from midparent values (Fig. 5, Table 1) suggest a simple additive genetic model with partial dominance approximates the observed heterotic trend (Falconer and Mackay, 1996). A genetic model for *A. majus* PHL with additive and dominance components agrees with previous reports (Schroeder and Stimart, 2001).

Average deviations from high parent PHL varied ± 1 d and were significantly different across categories (Table 1). Average high parent deviations of progeny involving all PHL categories differ significantly among and within categories (Table 1). Lack of a simple trend in deviations from high parent PHL suggests genetic control of PHL is more complex than explained by a simple additive genetic model with partial dominance.

Prediction of $F_2 \times F_2$ progeny PHL was most accurately based on respective F_3 family PHL values. Based on data presented, selection of breeding lines for extended PHL is best completed after some form of multiple cutflower evaluation using F_3 (F_2 self-pollinated) families,

$F_2 \times F_2$ progeny, or F_2 clones. Evaluation of these generations should provide an effective means of predicting value of individuals or families per se and in cross combinations. Initial evaluation for PHL may be completed using F_2 on-plant floret longevity and PHL of a single cutflower.

The quantitative nature and narrow sense heritability estimate

Fig. 5. Average midparent (unshaded bars) and $F_2 \times F_2$ progeny (shaded bars) cutflower postharvest longevity in *Antirrhinum majus* L. for crosses made within and among cutflower postharvest longevity categories: short = 4.7–6.9 d, middle = 7.2–8.4 d, and long = 9.0–11.0 d. Numbers in parenthesis represent number of crosses evaluated per cross category. Letters above columns represent mean separation of $F_2 \times F_2$ progeny by LSD. Letters in columns represent mean separation of midparent and respective $F_2 \times F_2$ progeny within a cross category by pair-wise t test, $P \leq 0.05$.

Table 1. Average deviations of *Antirrhinum majus* L. $F_2 \times F_2$ progeny from midparent and high parent cutflower postharvest longevity calculated as days and percentage.

Cross category ^a	N ^w	Midparent ^z		High parent ^y	
		Days	Percentage	Days	Percentage
Short x short	10	1.1 a ^v	17.8	0.8 ab ^v	13.1
Short x middle	18	0.6 a	8.9	–0.2 c	–2.0
Middle x middle	9	0.9 a	10.7	–1.1 d	–11.3
Short x long	6	0.7 a	8.7	0.5 abc	6.4
Middle x long	7	1.0 a	11.1	0.1 bc	0.7
Long x long	9	1.4 a	13.4	1.0 a	9.7

^a(Parent A cutflower postharvest longevity + Parent B cutflower postharvest longevity)/2.

^zGreatest of Parent A or Parent B cutflower postharvest longevity in any given cross.

^yCrosses between cutflower postharvest longevity categories: short = 4.7–6.9 d, middle = 7.2–8.4 d, and long = 9.0–11.0 d.

^wNumber of $F_2 \times F_2$ progeny evaluated per cross category with 25–30 plants evaluated per progeny.

^vMean separation by LSD, $P \leq 0.05$.

for PHL in *A. majus* (Schroeder, 2000) are reinforced with our data. Significant additive and dominance genetic variance components detected here in early generations agree with results obtained by Schroeder and Stimart (2001) using a generation means analysis population. Inconsistent magnitudes of heterotic deviation, from high parent PHL, suggest complex inheritance of the trait. Future work will attempt to resolve the complex inheritance patterns observed.

Literature Cited

- Bicknell, R. 1995. Breeding cut flower cultivars of *Leptospermum* using interspecific hybridisation. N.Z. J. Crop Hort. Sci. 23:412–421.
- Bobisud, C.A. and H. Kamemoto. 1982. Selection and inbreeding in *Dendrobium* (Orchidaceae). J. Amer. Soc. Hort. Sci. 107:1024–1027.
- Burchi, G., C. Bianchini, A. Mercuri, G. Foglia, D. Rosellini, and T. Schiva. 1999. Analysis of post-harvest flower life in a cross between carnation cultivars with different ethylene responses. J. Genet. Breeding 53:301–306.
- Burge, G.K., E.R. Morgan, I. Konczak, and J.F. Seelye. 1998. Postharvest characteristics of *Limonium* 'Chorus Magenta' inflorescences. N.Z. J. Crop Hort. Sci. 26:135–142.
- De, L.C., S.D. Wahi, and S.K. Bhattarcharjee. 1999. A post-harvest study of genetic divergence in cut roses. Indian J. Genet. 59:351–356.
- Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Addison Wesley Longman Ltd., Edinburgh Gate, Harlow Essex, England.
- Halevy, A.H. and S. Mayak. 1975. Interrelationships of several phytohormones in the regulation of rose petal senescence. Acta Hort. 41:403–416.
- Hallauer, A.R. and J.B. Miranda. 1988. Quantitative genetics in maize breeding. 2nd ed. Iowa State Univ. Press, Ames.
- Harding, J.T., T. Byrne, and R.L. Nelson. 1981. Estimation of heritability and response to selection for cut-flower yield in *Gerbera*. Euphytica 30:313–322.
- Heuser, C.W. and K.B. Evensen. 1986. Cut flower longevity of peony. J. Amer. Soc. Hort. Sci. 111:896–899.
- Hvoslef-Eide, A.K., T. Fjeld, and J.W. Einset. 1995. Breeding Christmas begonia (*Begonia* $\times$ *cheimanthus* Everett) for increased keeping quality by traditional and biotechnological methods. Acta Hort. 405:197–204.
- Joyce, D.C. and P.R. Beal. 1999. Cutflower characteristics of terminal flowering tropical *Grevillea*: A brief review. Austral. J. Expt. Agr. 39:781–794.
- Krahl, K.H. and W.M. Randle. 1999. Genetics of floral longevity in *Petunia*. HortScience 34:339–340.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS system for mixed models. SAS Inst. Inc., Cary, N.C.
- Mackay, W.A. and T.D. Davis. 1998. 'Texas Sapphire' and 'Texas Ice' long-stem bluebonnets (*Lupinus havardii*). HortScience 33:348–349.
- Marousky, F. J. and J.C. Raulston. 1970. Interaction of flower preservative components and light on fresh weight and longevity of snapdragon cut flowers. Proc. Fla. State. Hort. Soc. 27-29:445–448.
- Muceniece, G.Y., I.D. Rasals, and V.Y. Dislers. 1978. Investigation of the inheritance of quantitative characteristics of *Gerbera* in diallel crosses. I. Productivity of the plants. Soviet Genet. 14:160–162.
- Nell, T.A. 1992. Taking silver safely out of the longevity picture. Grower Talks (June):35, 37, 39, 41–42.
- Nyquist, W.E. 1991. Estimation of heritability and prediction of selection response in plant populations. Critical Rev. Plant Sci. 10:235–322.
- Ohkawa, K. and E. Sasaki. 1999. *Eustoma* (Lisianthus) — Its past, present and future. Acta Hort. 482:423–426.
- Ohkawa, K., K. Youichi, and J.S. Suh. 1999. Mobility and effects on vase life of silver-containing compounds in cut rose flowers. HortScience 34:112–113.
- Onozaki, T., H. Ikeda, and T. Yamaguchi. 2001. Genetic improvement of vase life of carnation flowers by crossing and selection. Scientia Hort. 87:107–120.
- Patil, S.S.D. and D.A. Rane. 1999. Studies on heritability estimates in China aster. J. Maharashtra Agr. Univ. 20:137–138.
- Rogers, M.N. 1992. Snapdragons, p. 93–112. In: R.A. Larson (ed.). Introduction to floriculture. Academic Press, New York.
- Satterthwaite, F.E. 1946. An approximate distribution of estimates of variance components. Biometrics Bul. 2:110–114.
- Schroeder, K.R. 1995. Inheritance of postharvest longevity of cut stems in *Antirrhinum majus* L., snapdragon. MS thesis. Univ. Wis.—Madison, Madison, Wis.
- Schroeder, K.R. 2000. A study on the genetics and physiology of cut flowers postharvest longevity in *Antirrhinum majus* L. PhD diss. Univ. Wis.—Madison, Madison, Wis.
- Schroeder, K.R. and D.P. Stimart. 2001. Genetic analysis of cut-flower longevity in *Antirrhinum majus*. J. Amer. Soc. Hort. Sci. 126:200–204.
- Steel, G.D. and J.H. Torrie. 1980. Principles and procedures of statistics. 2nd ed. McGraw-Hill Inc., New York.
- Stieve, S.M. and D.P. Stimart. 1994. Genetic analysis of postharvest longevity in *Antirrhinum majus* L. HortScience 29:435 (abstr.).
- van der Meulen-Muisers, J.J.M. and J.C. van Oeveren. 1996. Influence of variation in plant characteristics caused by bulb weight on inflorescence and individual flower longevity of asiatic hybrid lilies after harvest. J. Amer. Soc. Hort. Sci. 121:33–36.
- van der Meulen-Muisers, J.J.M., J.C. van Oeveren, and J.M. van Tuyl. 1997. Breeding as a tool for improving postharvest quality characters in lily and tulip flowers. Acta Hort. 430:569–575.
- van der Meulen-Muisers, J.J.M., J.C. van Oeveren, and J.M. van Tuyl. 1998. Genotypic variation in postharvest flower longevity in Asiatic hybrid lilies. J. Amer. Soc. Hort. Sci. 123:283–287.
- van der Meulen-Muisers, J.J.M., J.C. van Oeveren, J. Jansen, and J.M. van Tuyl. 1999. Genetic analysis of postharvest flower longevity in asiatic hybrid lilies. Euphytica 107:149–157.
- van Eijk, J.P. and W. Eikelboom. 1980. Methods of selection in tulip breeding. Acta Hort. 109:217–225.
- Wernett, H.C., G.J. Wilfret, T.J. Sheehan, P.M. Lyrene, F.G. Martin, T.L. White, G.L. Powell, and C.J. Wilcox. 1996a. Postharvest longevity of cut-flower *Gerbera*. II. Heritability of vase life. J. Amer. Soc. Hort. Sci. 121:222–224.
- Wernett, H.C., T.J. Sheehan, G.J. Wilfret, F.J. Marousky, P.M. Lyrene, and D.A. Knauff. 1996b. Postharvest longevity of cut-flower *Gerbera*. I. Response to selection for vase life components. J. Amer. Soc. Hort. Sci. 121:216–221.