Genetic Analysis of Cut-flower Longevity in *Antirrhinum majus*

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ABSTRACT. Genetics of *Antirrhinum majus* L. (snapdragon) cut flower postharvest longevity (PHL) was investigated by generation means analysis using a white short-lived inbred (WS) and white long-lived inbred (WL) to determine mode of inheritance and heritability. Broad and narrow sense PHL heritability was estimated at 78% and 30%, respectively. Scaling tests for adequacy of an additive-dominance model in explaining PHL inheritance suggested absence of epistasis. However, joint scaling indicated digenic or higher order epistatic interactions. Fitting of a digenic epistatic model revealed significant additive effects and nonsignificant dominance and epistatic interactions. Additionally, based on sequential model fittings all six parameters [mean, additive (a), dominance (d), $a \times a$, $d \times d$, and $a \times d$] proved necessary to explain observed PHL variation. Continuous variation for PHL observed in the F_2 and backcross generations suggests PHL is quantitative. Assessment of associated traits revealed a positive relationship between number of flowers opening postharvest on a cut flower and PHL. In addition, floret wilting led to short PHL while floret browning was associated with long PHL.

Exploiting natural genetic variability of cut flower postharvest longevity (PHL) may prove a good alternative to chemical enhancement of PHL. However, information on genetics and heritability of cut flower PHL is lacking. Observations of natural genetic variability in PHL have been found in *Gerbera* sp. L. (Smith and Nelson, 1967; van Meeteren, 1978; Wilberg, 1973), *Rosa* $\times$ *hybrida* L. (Mayak et al., 1974; Zieslin et al., 1978), and *Tulipa* $\times$ *hybrida* L. (van Eijk and Eikelboom, 1976). Recent research has redirected selection and breeding to improve cut flower PHL. Studies on *Gerbera* (De Jong and Garretsen, 1985; Harding et al., 1981; Wernett et al., 1996a, 1996b), *Lilium* L. Asiatic hybrids (van der Meulen-Muisers et al., 1998), *Petunia* $\times$ *hybrida* Vilm. (Krahl and Randle, 1999), and *Tulipa* $\times$ *hybrida* (van Eijk and Eikelboom, 1980) have implied cut flower PHL is a heritable trait with moderately low narrow sense heritability and significant additive gene effects.

Postharvest longevity studies with *Antirrhinum majus*, snapdragon, [Stimart and Stieve, 1993, (unpublished data)] involved cut flower evaluation of commercial inbreds and F_1 hybrids in deionized water (dH_2O). PHL of inbreds ranged from 3 to 18 d with an average of 7.5 d. Generally, inbreds with white flowers had longest PHL and inbreds of other colors had shortest PHL. Upon evaluation, an F_2 population ranged from 1 to 21 d with a continuous normal distribution, which suggested selection for improved PHL should be possible. Therefore, the objective of this study was to evaluate inheritance of PHL of *A. majus* by generation means analysis.

Materials and Methods

Seeds of *A. majus* were germinated and plants grown through flowering in the greenhouse according to established procedures (Ball, 1998; Larson, 1992). Briefly, seeds were germinated in 48 cell (144 cm^3) flats. Seedlings were transplanted into 72 cell (72

cm^3) flats with one plant per cell when the first set of true leaves appeared and into plastic pots (1,100 cm^3) when the third to fourth set of true leaves appeared. Plants were then grown through flowering. The growing medium was 1 soil : 1 perlite : 1 sphagnum peat (by volume). Plant spacing on benches was on 22-cm centers. Plants were fertilized biweekly with N at 200 $mg \cdot L^{-1}$ using Peter's 20N–8.7P–16.5K water soluble fertilizer (Scott's Sierra Horticultural Products Co., Marysville, Ohio). Supplemental light from 1000 W high-pressure sodium lamps (27 $\mu mol \cdot m^{-2} \cdot s^{-1}$ measured at bench level) was provided daily from 0600 through 2400 HR.

Flowers were harvested for postharvest longevity (PHL) evaluation when the first five florets opened. PHL was defined as the number of days from harvest until 50% of open florets browned or wilted. Stem lengths were cut to 40 cm measuring from the bottom floret down. Leaves were removed from the basal 15 cm of each stem, henceforth referred to as cut flowers. Cut flowers were placed randomly in a 7 $\times$ 9 cm grid and held vertically by wire mesh supports placed on plastic storage containers 35 $\times$ 23 $\times$ 14 cm (L $\times$ W $\times$ H). Holding solution was 2.5 L dH_2O maintained daily by adding water. Containers with flowers were placed on lab benches under continuous cool white fluorescent light (9 $\mu mol \cdot m^{-2} \cdot s^{-1}$) at 24 °C measured at bench level.

Two white-flowered inbreds of *A. majus* were selected for further study since they exhibited the shortest and longest PHL of 40 commercial inbreds evaluated by the authors: a short-lived (WS) 3 d PHL and a long-lived (WL) 18 d PHL. Twenty-five WS and 35 WL plants were grown and self-pollinated for four generations by single-seed descent to reduce heterozygosity at loci affecting PHL. The S_4 lines were grown and evaluated for PHL to identify the shortest WS and longest WL lines for use in developing a generation means analysis population. Six generations for analysis of variation were developed: parent 1 (WS) at S_5 ; parent 2 (WL) at S_5 ; F_1 (WS $\times$ WL); F_2 (self-mating of F_1); backcross to parent 1 (BC_{WS}) = WS $\times$ (WS $\times$ WL); and backcross to parent 2 (BC_{WL}) = WL $\times$ (WS $\times$ WL). Seeds from the six generations were sown 21 Aug., 1997 and seedlings transplanted to final containers 22 Sept. 1997. Plants were arranged in greenhouses at the University of Wisconsin, Madison, in randomized complete block designs. Three blocks were used at each of two locations. Each block contained 10 plants for WS, WL, and F_1 generations, 40 plants for the BC_{WS} and BC_{WL} generations, and 60

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F₂ plants. Location one was a glasshouse with fan and pad cooling and temperature set at 19 °C. Location two was a double-walled, polyethylene covered house (polyhouse) equipped with air circulation tubes and exhaust fan ventilation. Day/night temperatures in the polyhouse were set at 24/18 °C. Harvesting of flowers began 30 Oct. and spanned 5 weeks. Data were recorded on days to flower (seed sowing until harvest), plant height (soil surface to plant top), flower spike length (bottom floret to shoot tip), leaf length and width, total shoot fresh weight (FW, entire above ground shoot), FW of cut flower (22 cm stem portion as described previously), total flowers and buds, PHL, number of flowers opened postharvest, and senescence symptom (1 = petal browning and 2 = petal wilting).

Data were analyzed with the SAS MIXED procedure (Littell et al., 1996). Locations and generations were considered fixed effects while replications within locations were treated as random effects. Generation variance estimates were obtained from independent analyses for each generation. Heritability estimates, based on the variances of the three segregating generations (Warner, 1952), were calculated using the following formulas where P₁, P₂, F₁, F₂, B₁, and B₂ are PHL means of WS, WL, F₁, F₂, BC_{WS}, and BC_{WL}, respectively, for narrow sense estimates (Mather, 1949): $h^2 = [2(V_{F2} - (V_{B1} + V_{B2})/2)]/V_{F2}$ and broad sense estimates (Allard, 1960): $H^2 = [V_{F2} - (V_{P1} + V_{P2} + V_{F1})/3]/V_{F2}$.

Estimate of minimum number of genes controlling PHL was calculated from Wright (1968): $n_{min} = [1.5 - 2h(1 - h)](P_2 - P_1)^2 / 8(V_{F2} - V_E)$, where $h = (F_1 - P_1)/(P_2 - P_1)$ and $V_E = (V_{P1} + V_{P2} + 2V_{F1})/4$.

Scaling tests for adequacy of the additive-dominance model were used to calculate quantities of: $A = 2B_1 - P_1 - F_1$, $B = 2B_2 - P_2 - F_1$, $C = 4F_2 - 2F_1 - P_1 - P_2$, $D = 2F_2 - B_1 - B_2$. When $A = B = C = D = 0$, additive and dominance gene effects fully account for the observed variation. A joint scaling test (Cavalli, 1952) was used to further test goodness-of-fit of the observed mean, additive, and dominance values with expected values. When the additive-dominance model proved inadequate, a digenic epistatic model (Mather and Jinks, 1982), based on generation means and weighted least square analysis, was used to fit and estimate the six parameters [mean, additive (a), dominance (d), $a \times a$, $a \times d$, $d \times d$]. Sequential model fitting (Mather and Jinks, 1982) was used to further analyze the significance of individual parameters in the model. One parameter at a time was deleted from the six parameter model to allow for a one degree of freedom χ^2 goodness-of-

fit test to determine the necessity of that parameter in the model. If nonsignificant, the parameter was eliminated from the model.

Results

Broad and narrow sense heritability for PHL was estimated at 0.78 and 0.30, respectively. Estimate of minimum number of loci controlling PHL was two. All generation means were significantly different except the F₁ and BC_{WL} (Table 1). The F₁ generation exhibited midparent heterosis of 1.5 d. One backcross to WS lowered mean PHL to 7.4 d near the midpoint (7.3) between the F₁ and WS (Fig. 1). One backcross to WL exhibited a mean of 11.2 d, one day less than the midpoint (12.3) between F₁ and WL. PHL ranged from 3 to 8 d for WS, 8 to 18 d for WL, and 8 to 13 d for the F₁. Variation was continuous in the F₂ and BC generations ranging from 3 to 23 d for the F₂, 3 to 13 d for BC_{WS}, and 3 to 24 d for BC_{WL}.

Scaling tests for adequacy of the additive-dominance model in explaining PHL inheritance suggested absence of epistasis since quantities for A, B, C, and D were not different from zero (Table 2). Further analysis through joint scaling indicated a highly significant χ^2 (85.9, df 3) for goodness-of-fit of the observed mean, additive, and dominance values with expected values suggesting epistatic interactions are important. Generation means and variances (Table 1) were used to fit a digenic epistatic model. Estimates of gene effects indicated a significant additive effect while dominance and epistatic interactions were all nonsignificant (Table 3). However, all six parameters proved necessary to explain the observed variance based on sequential model fitting.

Correlations of PHL with the data parameters taken as described previously were low, inconsistent, and generation and location dependent (Table 4). Number of flowers opened postharvest exhibited significant positive correlations with PHL ranging from 0.22 to 0.73 in all generations except WL and F₁. Senescence symptom was negatively correlated with PHL ranging from -0.48 to -0.71 in all cases except the F₁ generation grown in the glasshouse.

Discussion

Postharvest longevity of *A. majus* cut flowers is heritable based on estimates of 78% broad sense heritability, 30% narrow sense heritability, and significant additive gene effects. Midparent

Table 1. Generation means and variances influenced by location and replication within location on *Antirrhinum majus* cut flower postharvest longevity from six generations.

Generation ^z	n ^y	Postharvest longevity (d) ^x	Variance	Location ^v	Rep(loc) ^u
WL	60	14.0 a	3.6	NS	NS
WS	60	4.1 e	0.7	NS	NS
F ₁	60	10.5 b	1.5	****	NS
F ₂	360	8.1 c	8.8	****	NS
BC _{WL}	240	11.2 b	8.2	NS	*
BC _{WS}	240	7.4 d	6.9	NS	NS

^zInbreds white short-lived = WS and white long-lived = WL, WS x WL = F₁, F₁ self-mated = F₂, and F₁ backcrossed to each parent = BC_{WS} or BC_{WL}.

^yNumber evaluated.

^xMean separation by pairwise *t* tests.

^vVariances obtained from independent analyses of variance for each generation.

^uGlass and polyhouse.

^uReplication within location.

NS, *, **** Nonsignificant or significant at $P \leq 0.05$ or 0.0001, respectively.

Fig. 1. Cut flower postharvest longevity of *Antirrhinum majus* within six generations. Inbreds white short-lived = WS and white long-lived = WL, WS $\times$ WL = F_1 , F_1 self-mated = F_2 , and F_1 backcrossed to each parent = BC_{ws} or BC_{wl} . Arrows indicate generation means.

heterosis of 1.5 d indicates PHL is partially dominant. Epistatic interactions, continuous variation, estimates of a minimum of two genes controlling the trait, and significant environmental variation suggest selection for increased PHL would be successful but slow. The broad sense heritability estimates for *A. majus* were slightly lower than the 97 % and 98% estimates of genotypic determination for individual flower PHL of *Lilium* Asiatic hybrids (van der Meulen-Muisers et al., 1998) and higher than the 28% to 46% heritability estimates on *Gerbera* cut flowers post-harvest (Harding et al., 1981; Wernett et al., 1996b). Narrow sense heritability estimate of 30% on *A. majus* is within the range of the 15% to 38% narrow sense heritability estimates reported on *Gerbera* cut flowers (Harding et al., 1981, 1987; Serini and De Leo, 1978; Tesi, 1978; Wernett et al., 1996b). Thus, one should be able to make gains from selection; however, gains will likely be small and progress slow.

Existence of significant additive gene effects on *A. majus* cut flower PHL is in agreement with findings on *Gerbera* (De Jong and Garretsen, 1985; Wernett et al., 1996b); *Petunia* $\times$ *hybrida*

(Krahl and Randle, 1999), and *Tulipa* (van Eijk and Eikelboom, 1980). Although scaling tests (Table 2) indicate an additive-dominance model is adequate to explain the observed variation in PHL of *A. majus*, there is strong evidence of digenic or higher order epistatic interactions. The highly significant χ^2 from joint scaling analysis indicates additive-dominance model inadequacy. Furthermore, sequential model fitting of the six parameters [mean, additive (a), dominance (d), $a \times a$, $a \times d$, $d \times d$] proved all were necessary to explain observed variation. Due to limits of the generations available (six generations and six variables), a χ^2 test for goodness-of-fit was not possible. Additional generations such as an F_3 and/or additional backcross generations are necessary to test the fit of the full digenic model. Failure of scaling tests to detect overall nonallelic interactions is not unlikely and can occur if the signs of $a \times a$, $a \times d$, and $d \times d$ interaction effects differ from one pair of interacting genes to another when more than two genes interact (Mather and Jinks, 1982).

Continuous variation for PHL in the F_2 generation of the WS $\times$ WL cross (Fig. 1) provides further evidence that PHL is quantitative. A minimum of two genes control PHL based on generation means and variances from the generation means study. However, this method assumes no dominance, linkage, or epistasis and any or all of these factors would bias outcome.

Environmental factors accounted for 22% of PHL variation in the generation means study. Significant variation for location was observed in the F_1 and F_2 generations (Table

1). Increased PHL in the glasshouse may be due to higher natural light levels. Other studies have found similar environmental effects. Variation due to environmental conditions were found on individual cut flower PHL of *Lilium* (van der Meulen-Muisers et al., 1998). Flowers open at harvest exhibited significantly more variation in longevity than those opened after harvest in a more constant environment. van der Meulen-Muisers and van Oeveren (1997) reported strong influences of temperature after anthesis on *Lilium* flower PHL. De Jong and Garretsen (1985) reported

Table 2. Scaling tests for adequacy of the additive-dominance model in explaining inheritance mode for *Antirrhinum majus* cut flower postharvest longevity.^z

Scaling test ^y	Quantity	SE
$A = 2BC_{wl} - WL - F_1$	-2.1 ^{NS}	6.1
$B = 2BC_{ws} - WS - F_1$	0.2 ^{NS}	5.4
$C = 4F_2 - 2F_1 - WL - WS$	-6.7 ^{NS}	12.3
$D = 2F_2 - BC_{wl} - BC_{ws}$	-2.4 ^{NS}	7.1

^zInbreds white short-lived = WS and white long-lived = WL, WS $\times$ WL = F_1 , F_1 self-mated = F_2 , and F_1 backcrossed to each parent = BC_{ws} or BC_{wl} .

^yIf $A = B = C = D = 0$, then additive-dominance model is adequate.

^{NS}Not significantly different from 0.

Table 3. Estimates of gene effects for *Antirrhinum majus* cut flower postharvest longevity.

Effect	Parameter estimate	SE	t value
Mean	4.215	0.813	5.18 ^{NS}
Additive (A)	4.958	0.133	37.21*
Dominance (D)	9.261	2.003	4.62 ^{NS}
A x A	4.794	0.802	5.98 ^{NS}
A x D	-2.128	0.567	-3.75 ^{NS}
D x D	-2.976	1.252	-2.38 ^{NS}

^{NS}, *Nonsignificant or significant at $P \leq 0.05$.

seasonal effects on cut flower PHL in *Gerbera*; vase life was shorter and stems weaker in winter than in summer. Research involving *Dendrobium* sp. Sw. cut flower production in the warm season resulted in a 30% to 35% reduction in PHL (Dai and Paull, 1991). In addition, Tesi (1978) identified strong environmental factors affecting PHL of *Gerbera jamesonii* Bol. Ex Adlam. 'Bolus' cut flowers.

The importance of endogenous carbohydrates to cut flower PHL has been reported by several authors (Celikel and Karacaly, 1995; Coorts, 1973; Halevy and Mayak, 1979). In addition, studies have demonstrated the importance of carbohydrate metabolism and source-sink relationships to PHL (Coorts, 1973; Marissen and La Brijn, 1995; Nichols, 1973). Positive correlations of PHL with number of flowers opened postharvest in the F_2 segregating population suggest long PHL is associated in part with more florets opening on a cut flower stem postharvest. This result suggests endogenous carbohydrate levels and source-sink relationships influence *A. majus* cut flower PHL. However, one can not rule out water stress as a factor in reducing flower opening on short PHL genotypes. Further study is warranted to determine the extent to which endogenous carbohydrates influence *A. majus* cut flower PHL and underlying possible genetic associations.

Consistent negative correlations of senescence symptom with PHL indicate short *A. majus* cut flower PHL is associated with wilting, while floret browning leads to longer PHL. In the segregating F_2 population, significant correlation coefficients of -0.52 and -0.56 suggest floral senescence symptoms may explain 25% or more of the PHL variability observed. This result points to postharvest water relations of *A. majus* cut flower longevity. The importance of cut flower water status to PHL is well known (Halevy and Mayak, 1981; van Doorn, 1997). Additional studies on transpiration and water uptake of *A. majus* cut flowers are needed to better understand the causes of this negative relationship and possible solutions to the problem leading to extended cut flower PHL.

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Table 4. Postharvest longevity of *Antirrhinum majus* cut flowers as correlated with days to flower, plant height, flower spike length, leaf length, and width, total shoot weight, weight of cut flower, total flowers and buds, flowers opened postharvest, and senescence symptom as influenced by location and generation.

Parameter	Location											
	Glasshouse						Polyhouse					
	Generation ^z											
	WS	WL	F ₁	F ₂	BC _{WS}	BC _{WL}	WS	WL	F ₁	F ₂	BC _{WS}	BC _{WL}
Days to flower ^y	0.035 ^{NS†}	0.065 ^{NS}	0.073 ^{NS}	-0.285 ^{****}	-0.128 ^{NS}	-0.186 [*]	0.292 ^{NS}	0.143 ^{NS}	-0.133 ^{NS}	-0.012 ^{NS}	-0.362 ^{****}	0.314 ^{***}
Plant height ^x	0.232 [*]	-0.010 ^{NS}	0.118 ^{NS}	0.008 ^{NS}	0.200 [*]	0.222 [*]	0.325 ^{NS}	-0.194 ^{NS}	-0.382 [*]	0.052 ^{NS}	0.042 ^{NS}	-0.042 ^{NS}
Flower spike length ^w	0.063 ^{NS}	0.035 ^{NS}	-0.40 ^{NS}	-0.164 [*]	0.114 ^{NS}	0.075 ^{NS}	-0.110 ^{NS}	-0.200 ^{NS}	0.285 ^{NS}	-0.031 ^{NS}	0.148 ^{NS}	-0.204 [*]
Leaf length ^v	0.497 ^{**}	0.175 ^{NS}	0.282 ^{NS}	0.017 ^{NS}	0.224 [*]	0.200 [*]	0.485 ^{**}	0.253 ^{NS}	0.311 ^{NS}	0.144 ^{NS}	0.262 ^{**}	0.152 ^{NS}
Leaf width ^v	0.318 ^{NS}	-0.111 ^{NS}	0.197 ^{NS}	0.099 ^{NS}	0.201 [*]	0.223 [*]	0.203 ^{NS}	0.566 ^{**}	0.131 ^{NS}	0.147 [*]	0.210 [*]	0.162 ^{NS}
Total shoot weight ^x	0.081 ^{NS}	0.163 ^{NS}	0.151 ^{NS}	0.088 ^{NS}	-0.025 ^{NS}	0.249 ^{**}	-0.051 ^{NS}	0.217 ^{NS}	0.350 ^{NS}	0.081 ^{NS}	-0.009 ^{NS}	-0.028 ^{NS}
Weight of cut flower ^w	0.242 ^{NS}	0.122 ^{NS}	0.055 ^{NS}	-0.125 ^{NS}	-0.327 ^{***}	-0.026 ^{NS}	-0.191 ^{NS}	0.038 ^{NS}	0.566 ^{***}	-0.067 ^{NS}	0.002 ^{NS}	-0.155 ^{NS}
Total flowers and buds	0.476 ^{**}	-0.210 ^{NS}	0.125 ^{NS}	-0.055 ^{NS}	-0.307 ^{***}	-0.133 ^{NS}	-0.211 ^{NS}	-0.197 ^{NS}	-0.337 ^{NS}	-0.112 ^{NS}	-0.218 [*]	-0.134 ^{NS}
Flowers opened postharvest	0.731 ^{****}	-0.068 ^{NS}	0.026 ^{NS}	0.393 ^{****}	0.589 ^{****}	0.219 [*]	0.576 ^{***}	0.075 ^{NS}	0.053 ^{NS}	0.686 ^{****}	0.641 ^{****}	0.393 ^{****}
Senescence symptom ^u	-0.494 ^{**}	-0.714 ^{****}	0.225 ^{NS}	-0.524 ^{****}	-0.678 ^{****}	-0.590 ^{****}	NV	-0.695 ^{****}	-0.550 ^{***}	-0.559 ^{****}	-0.683 ^{****}	-0.477 ^{****}

¹Inbreds white short-lived = WS and white long-lived = WL, WS x WL = F₁, F₁ self-mated = F₂, and F₁ backcrossed to each parent = BC_{WS} or BC_{WL}.

²Seed sowing to harvest.

³Soil surface to plant top in cm.

⁴Forty centimeters from bottom floret down.

⁵Midstem leaf in cm.

⁶Grams.

⁷Visual scale 1 = browning and 2 = wilting.

⁸Correlation coefficient and level of significance.

NV = no variation.

NS, *, **, ****, ***** Nonsignificant or significant at $P \leq 0.05$, 0.01, 0.001, or 0.0001.

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