Genetic Analysis of Advanced Populations in *Antirrhinum majus* L. with Special Reference to Cut Flower Postharvest Longevity

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ADDITIONAL INDEX WORDS. vase life, postharvest keeping quality, narrow-sense heritability, genetic correlation, phenotypic correlation, selection

ABSTRACT. Narrow-sense heritabilities and genetic correlations of ornamental quality traits of *Antirrhinum majus* (snapdragon) were evaluated with special reference to cut flower postharvest longevity (PHL). Inbreds P1 (16 days PHL) and P2 (3 days PHL) were hybridized to produce an F_1 ($P1 \times P2$) that was self-pollinated to produce an F_2 population. The F_2 were self-pollinated to produce F_3 families and advanced through single-seed descent by self-pollination to the F_5 generation. P1, P2, F_1 , F_3 , F_4 , and F_5 were evaluated for ornamental quality traits. Quality traits were found to be quantitative and normally distributed. Narrow-sense heritability (h^2) estimates were high and consistent across generations examined; PHL h^2 ranged from 0.79 to 0.81 ± 0.06 . Phenotypic and genotypic correlations revealed underlying physiological and pleiotropic interactions relevant to breeding programs aimed at simultaneous improvement of ornamental quality traits. PHL is inversely related to cut flower strength and days to flower, -0.44 ± 0.04 and -0.43 ± 0.44 . Buds at discard is positively correlated to cut flower and plant diameter, cut flower weight and days to flower, 0.77 ± 0.05 , 0.58 ± 0.06 , 0.71 ± 0.06 , and 0.77 ± 0.07 , respectively. Gain from selection for quality traits of interest can be rapid.

Crop quality is usually complexly defined and component traits are often quantitative in nature. In ornamentals, cut flower quality is defined by characteristics of plant and floral architecture as well as cut flower postharvest longevity (PHL). Reports attempt to alter architecture and PHL through chemical remediation but are often met with limited success. In addition, chemicals available to industry are becoming limited due to safety concerns (Nell, 1992; Ohkawa et al., 1999). Classic breeding techniques provide an alternative to chemical remedies for advancement of quantitative trait quality in ornamentals.

Quantitative trait heritability information is useful to breeding programs to best design evaluation and selection strategies. Common in agronomic crops, this information is rare in ornamentals. Variability within quantitative quality traits has been noted in many ornamental species, but application of this information in breeding programs is limited. Recent breeding advances in cut flower quality include selection response against stem bending, folding and wilting (Wernett et al., 1996a) and for an increase in number of flowering stems (Harding et al., 1981). Successful selection in *Dianthus caryophyllus* L. (carnation) for PHL was recently described by Burchi et al. (1999) and Onozaki et al. (2001).

Antirrhinum majus is an important cut flower, however, little is known about genetics of its ornamental quality traits. Preliminary work in *A. majus* revealed PHL as quantitative with significant additive and dominant genetic variance components (Schroeder and Stimart, 2001). In addition, PHL can be manipulated in populations (Schroeder, 1995).

Inheritance of ornamental quality traits and correlations between traits were investigated to provide a foundation to advance quality in *A. majus* cut flowers through classic breeding methodology with a goal of expanding crop market share. Work presented here provides trait heritability and correlational information relevant to breeding for plant architectural, production, and cut flower quality traits. Emphasis is placed on PHL and correlated traits.

Materials and Methods

Commercial inbred lines of *Antirrhinum majus* cut flower types were evaluated for cut flower PHL in 1991 and 1992 at the Univ. of Wisconsin–Madison (Stieve and Stimart, 1994). Two white-flowered lines selected represented observed extremes in PHL, P1 (16.3 d PHL) and P2 (3.0 d PHL) (Stieve and Stimart, 1994). P1 and P2 were self-pollinated for five generations and hybridized to produce F_1 ($P1 \times P2$). The F_1 was self-pollinated to produce an F_2 in Fall 1998. From the F_2 , 485 plants were randomly selected and self-pollinated to produce F_3 families. A total of 155 randomly selected F_3 families were advanced through single-seed descent to the F_5 . Seed set and germination failures resulted in loss of 19 families, 12% of the population, by the F_4 ; and 4 families, 3% of the population, by the F_5 . Thus, 132 F_3 , F_4 , and F_5 families remained with 110 randomly selected for evaluation. Poor germination in the 110 families being evaluated resulted in 4% reduction of the population.

$P1$, $P2$, F_1 , F_3 , F_4 , and F_5 plants were grown in Fall, Winter, and Spring 2001–2002 in three replicated plantings using a randomized complete-block design (six blocks fall and spring, nine blocks winter, one rep/genotype/block) in a polyhouse at the Univ. 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 as the first pair of true leaves emerged. Seedlings were trans-

Received for publication 3 June 2004. Accepted for publication 19 Aug. 2004. A note of gratitude to Dr. Erik Nordheim, Univ. of Wisconsin–Madison, for statistical consultation during preparation of this manuscript. Use of trade names does not imply endorsement of the products named or criticism of similar ones not named.

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planted to square plastic pots (1250 cm³) when the third to fourth set of true leaves appeared and grown through anthesis. Growing medium was equal volumes of 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, Marysville, Ohio) and provided supplemental light of 27 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at bench level using 1000-W high-pressure sodium lamps from 0600 through 2400 HR.

Whole plants were harvested for evaluation when the first five florets opened thereby equalizing developmental stage. Plants were immediately placed in distilled water (dH₂O) and transported to the laboratory. Plant height and lowest floret height, termed plant height nonfloral, were noted and floral region size was derived from their difference. Plant weight and basal plant diameter were recorded. Plant architecture, termed branching habit, was evaluated on a numeric scale based on commercial preference (L. Laughner, personal communication). Branching habit score was obtained by taking the sum of branching habit code multiplied by the number of nodes where branching occurred, $\sum k_i n_i$; where $k = 1$ (side branching <10 cm in length), 2 (basal branching), 3 (side branching >10 cm in length), 4 (crown branching), or 5 (branching with buds), and $n =$ number of nodes where branching occurred. Number of florets at harvest showing color before anthesis, termed buds at harvest, was recorded. At harvest, floral region uniformity was rated on a visual scale (1 = excellent to 5 = very poor, Fig. 1), and floral region density was derived by adding number of open florets and buds and dividing by floral region size. The width of a leaf from ≈ 40 cm below lowest floret was recorded.

Stems were adjusted to a length of 40 cm below the lowest floret and the bottom 15 cm of leaves from the stem were removed; the inflorescence and supporting stem are hereafter termed cut flower. Cut flower weight and basal cut flower diameter were recorded. Cut flower strength was assessed as deviation in cm at cut flower tip when holding the basal 5 cm of cut flower stem horizontal. Fifteen cut flowers were arranged in a three by five rectangular arrangement, stems placed 7.5 cm apart, supported upright with a wire mesh in plastic storage containers 34 $\times$ 22 $\times$ 15 cm (L $\times$ W $\times$ H) containing, at a depth of 4 cm, 3 L of dH₂O. Holding solutions were maintained daily by addition of dH₂O. PHL evaluation utilized a completely random design. Cut flowers 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. Cut flower senescence was defined as 50% of the florets browning/drying or wilting (Marousky and Raulston, 1970). At cut flower discard, numbers of buds, defined above, and open florets were recorded. Number of florets opening after harvest was derived by subtracting florets open at harvest, five, from number of open florets at discard. Dates of seed sowing, plant harvest, and cut flower senescence were recorded; days to flower and cut flower PHL were derived from their differences.

Due to logistic limitations, cut flower leaf area, stoma per area and stomatal index, $\{[(\text{number of stoma} / \text{number of stoma} + \text{number of epidermal cells}) \text{ per area}] \times 100\}$

(Salisbury, 1927 as referenced by Lea et al., 1977), were obtained from the winter planting on cut flowers from three blocks. Cut flower leaf area was determined using a LI-COR 3100 area meter (LI-COR, Lincoln, Nebr.) by destructively sampling three cut flowers of each genotype. Stoma per area and stomatal index were assessed by using abaxial leaf imprints created in super glue on glass microscope slides (Sampson, 1961). Fully expanded leaves from the third node above soil line were sampled destructively 8 weeks after seed sowing from three plants of F₃, F₄, and F₅ families. One image, 0.24 μm^2 , was collected digitally from the distal one-third of each imprint using iMovie (Apple Computer, Cupertino, Calif.) and analyzed using Adobe Photoshop 5.5 (Adobe Systems, San Jose, Calif.).

Population statistics, including generational means, minimums, maximums, and standard deviations; data transformations; and generation mean separations by LSD were generated by the SAS statistical package (Littell et al., 1996). Resolution of components of variance was completed assuming a completely random design in SAS mixed models analysis with Satterthwaite corrections for degrees of freedom (Satterthwaite, 1946). Narrow-sense heritability estimates for traits measured in three plantings were calculated (Hallauer and Miranda, 1988) with 95% confidence intervals (CI) calculated according to Knapp et al. (1985). Narrow-sense heritability estimates for traits measured in three plantings were confirmed via parent-offspring regression (Falconer and Mackay, 1996). Narrow-sense heritability and standard error estimates of traits measured in one planting were determined via parent-offspring regression (Falconer and Mackay, 1996).

Phenotypic and genotypic correlation coefficients were calculated utilizing the SAS statistical package (Littell et al., 1996). Trait correlations from inbred lines are considered most accurate due to minimal effects of dominance and environmental variance bias (Falconer and Mackay, 1996). Therefore, F₅ genotypic and phenotypic correlation coefficients are presented. Phenotypic correlations can be subject to large environmental correlations (Falconer and Mackay, 1996), therefore, focus will be on signifi-

Fig. 1. Visual scale of floret uniformity for *Antirrhinum majus*.

cant genotypic correlations with values of $r > 0.35$. This value is conservatively chosen as the minimum level of significant correlation with 100 df (0.25) plus the largest standard error observed among the genetic correlations, + 0.10. Genotypic correlations between traits measured in one planting and traits measured in three plantings were inestimable (Falconer and Mackay, 1996).

Results and Discussion

Cut flower and whole plant distributions for 22 evaluated traits are continuous and normal with exception of cut flower senescence symptom. Transformations of cut flower senescence symptom data had no effect upon subsequent analysis; therefore, raw data results are presented. Generation means are not significantly different for all traits examined with exception of days to flower (Fig. 2, Table 1). Mean days to flower for F_5 is significantly later than for F_3 while the F_4 mean, intermediate to F_3 and F_5 , is not significantly different from either (Fig. 2, Table 1). A significant shift in population mean signifies associated inbreeding depression with the trait (Falconer and Mackay, 1996).

Inbreeding depression, due to exposure of deleterious reproductive fitness alleles in the population, is expected if dominance exists for the trait but is rarely seen in naturally selfing species (Falconer and Mackay, 1996). Days to flower; and flower number, size, and nectar production directly affect reproductive fitness in *Penstemon centranthifolius* Benth. (scarlet bugler) (Mitchell and Shaw, 1993) a member of same plant family (Scrophulariaceae) as *A. majus*. Nectar production and flower size were not analyzed in *A. majus* and non-flowering genotypes were eliminated during population development. Dominance for days to flower has been reported in *Helianthus annuum* L. (sunflower) cultivars (Virk and Pooni, 1994) and *A. majus* days to flower inbreeding depression

supports existence of dominance variance. Lack of inbreeding depression in *A. majus* is expected because the species can naturally self-pollinate and the examined traits in this study, with the exception of days to flower, do not affect reproductive biology. Inbreeding depression has been reported for quantitative traits in outcrossing species including *Dendrobium* sp. Sw. (orchid) (Bobisud and Kamemoto, 1982), *Solanum tuberosum* L. (potato) (Bradshaw et al., 2000), and *Zea mays* L. (maize) (Hallauer and Sears, 1973); however, inbreeding depression was not found in naturally self-pollinating *Lupinus harvardii* Wats. (bluebonnet) (Mackay and Davis, 1998).

Dominance in *A. majus* PHL has been shown by analyses of generation means and hybrid populations (Martin, 2000; Schroeder and Stimart, 2001) but was not confirmed by analysis of this recombinant inbred population. Loss of families during population development could cause lack of observed inbreeding depression by purging deleterious alleles. Exploitation of dominance variance may be beneficial to hybrid production (Schroeder and Stimart, 2001). However, if released cultivars are inbred lines, exploitation of dominance variance may not be as important as previously thought for commercially important plant and cut flower traits.

Narrow-sense heritabilities, h^2 , and respective confidence intervals for F_3 , F_4 , and F_5 family traits measured in three plantings range from 0.20 (CI = -0.05 to 0.39) to 0.88 (CI = 0.85 to 0.91) (Table 2). All traits were highly heritable in F_5 families, ranging from 0.63 to 0.88 (± 0.10) with exceptions of branching habit (0.41, CI = 0.23 to 0.55) and buds at discard (0.20, CI = -0.05 to 0.39). Heritabilities for cut flower leaf area, stoma and stomatal index, each examined in the winter planting, are moderate to low for F_3 , F_4 , and F_5 families. Narrow-sense heritability estimates from parent-offspring regression for traits measured in three plantings are lower than estimates derived from analy-

Fig. 2. Days to flower for inbred lines P1 and P2, F_1 ($P1 \times P2$), and 105 F_3 (—), F_4 (---) and F_5 (····) families of *Antirrhinum majus*. $\bar{x}$ = group mean. Mean separation by LSD, $P < 0.05$.

Table 1. Population statistics for phenotypic traits of F₃, F₄, and F₅ families in *Antirrhinum majus*.

Phenotypic trait	F ₃				F ₄				F ₅			
	Mean ^z	Min.	Max.	SD	Mean ^z	Min.	Max.	SD	Mean ^z	Min.	Max.	SD
Branching habit ^y	15.0	6.3	25.3	4.1	14.1	3.8	29.1	4.5	14.7	2.3	29.9	5.2
Buds at discard (no.) ^x	4.5	1.4	12.4	1.5	4.4	1.1	9.4	1.5	4.2	0.6	7.7	1.4
Buds at harvest (no.) ^x	17.0	11.2	22.8	2.3	16.6	8.9	24.4	2.9	16.4	7.8	25.9	3.2
Cut flower diameter (mm) ^w	4.2	3.2	5.9	0.6	4.2	2.7	6.2	0.7	4.1	2.7	6.2	0.8
Cut flower leaf area (cm ²) ^v	130.2	50.3	273.0	51.6	135.6	24.2	461.0	70.4	134.1	26.0	450.4	64.0
Cut flower strength (-cm) ^u	9.4	2.9	20.9	3.4	9.1	1.3	20.3	3.9	9.2	0.5	17.2	3.9
Cut flower weight (g) ^v	18.6	12.2	28.2	3.3	18.7	11.1	35.2	4.3	18.5	12.1	39.0	4.8
Days to flower (d) ^t	91.5 a	81.7	107.0	5.2	93.1 ab	79.6	111.1	5.6	96.0 b	80.7	114.4	6.8
Floral region density ^s	0.9	0.6	1.4	0.1	0.9	0.6	2.1	0.2	1.0	0.6	2.9	0.3
Floral region size (cm) ^r	19.3	12.7	26.8	2.6	18.9	11.2	27.4	3.3	18.0	8.2	27.1	3.7
Floral region uniformity ^q	3.1	1.8	4.1	0.4	3.1	1.6	4.4	0.5	3.1	1.8	4.1	0.4
Florets open at discard (no.)	14.2	9.5	17.8	1.7	13.7	7.3	20.6	2.3	13.5	7.2	19.7	2.4
Florets opening (no.) ^p	9.3	4.8	13.7	1.7	8.9	2.4	15.6	2.2	8.6	3.2	14.7	2.3
Leaf width (cm) ^w	2.2	1.6	4.0	0.4	2.3	1.2	3.7	0.4	2.3	1.3	3.8	0.5
Plant diameter (mm) ^o	4.1	3.1	5.4	0.5	4.0	2.8	5.5	0.6	3.9	2.5	6.7	0.7
Plant height (cm) ⁿ	90.0	58.3	122.2	11.3	88.5	56.1	128.5	14.4	86.5	55.6	124.4	15.1
Plant height nonfloral (cm) ^m	70.7	44.6	102.8	10.5	69.6	42.1	109.0	12.6	68.5	42.5	101.8	13.3
Plant weight (g) ⁿ	49.0	27.5	66.5	8.9	48.5	26.1	74.0	10.1	48.9	20.0	84.1	11.2
Postharvest longevity (d) ^l	11.5	6.1	16.1	2.1	10.9	4.9	16.4	2.5	10.8	4.8	16.8	2.7
Senescence symptom ^k	0.8	0.2	1.0	0.2	0.7	0.0	1.0	0.3	0.7	0.2	1.0	0.3
Stoma (no.)	42.4	22.0	70.0	9.0	40.4	22.7	62.0	9.4	39.9	23.3	62.3	8.7
Stomatal index ^j	23.0	19.5	27.4	1.9	23.0	18.0	27.2	2.0	22.2	17.3	26.8	2.0

^zMean separation by LSD, $P \leq 0.05$. Mean values without letters are not significantly different.

^yBranching habit: $\sum k_i n_i$; where $k = 1$ (side branching <10 cm in length), 2 (basal branching), 3 (side branching >10 cm in length, usually singular), 4 (crown branching), or 5 (branching with floral buds) and $n =$ number of nodes where branching occurred.

^xFlorets showing color before anthesis.

^wAt 40 cm below lowest floret.

^vOf 40 cm stem below lowest floret with bottom 15 cm of leaves removed.

^uDeviation in cm from horizontal position.

^t(Date of plant harvest – date of seed sowing).

^s[(Number of buds + number of open florets) / (plant height – plant height nonfloral) at harvest].

^r(Plant height – plant height nonfloral).

^qVisual scale (1 = excellent, 5 = very poor).

^p(Florets open at discard – florets open at harvest).

^oAt soil line.

ⁿSoil line to plant tip.

^mSoil line to lowest floret.

^l(Date of cut flower senescence – date of plant harvest).

^kWilting = 0 or browning/drying = 1.

^j[Number of stoma / (number of stoma + number of epidermal cells) per area] $\times$ 100.

sis of variance (ANOVA) (Table 2). For ANOVA derivation of h^2 from data collected on repeated plantings, formulas include mathematical corrections for environmental and genotype-by-environmental error estimates thereby increasing h^2 (Falconer and Mackay, 1996). With this correction, h^2 estimates from ANOVA are considered more accurate.

Reduction in heritability with inbreeding may be due to reduced upward bias of dominance variance (Falconer and Mackay, 1996), and significant dominance variance in *A. majus* was concluded above for days to flower. Therefore, stability of heritability values across generations evaluated is expected and was observed with exceptions of buds at discard and cut flower

Table 2. Narrow-sense heritability estimates (h^2) and confidence intervals (CI) or standard errors (SE) for phenotypic traits.

Phenotypic trait	F ₃ h^2 ^z	CI ^y	F ₄ h^2	CI	F ₅ h^2	CI
Branching habit ^x	0.49	(0.33, 0.61)	0.42	(0.24, 0.56)	0.41	(0.23, 0.55)
Buds at discard (no.) ^w	0.48	(0.32, 0.60)	0.46	(0.29, 0.59)	0.20	(-0.05, 0.39)
Buds at harvest (no.) ^w	0.73	(0.65, 0.79)	0.74	(0.66, 0.80)	0.69	(0.60, 0.77)
Cut flower diameter (mm) ^v	0.81	(0.75, 0.86)	0.73	(0.65, 0.80)	0.77	(0.70, 0.82)
Cut flower strength (-cm) ^u	0.75	(0.67, 0.81)	0.72	(0.64, 0.79)	0.69	(0.60, 0.77)
Cut flower weight (g) ^t	0.85	(0.80, 0.88)	0.76	(0.69, 0.82)	0.80	(0.74, 0.85)
Days to flower (d) ^s	0.72	(0.63, 0.79)	0.63	(0.52, 0.72)	0.68	(0.58, 0.75)
Floral region density ^r	0.69	(0.59, 0.76)	0.80	(0.73, 0.84)	0.77	(0.69, 0.82)
Floral region size (cm) ^q	0.74	(0.65, 0.80)	0.73	(0.65, 0.79)	0.63	(0.51, 0.72)
Floral region uniformity ^p	0.76	(0.69, 0.82)	0.78	(0.71, 0.83)	0.73	(0.65, 0.80)
Florets open at discard (no.)	0.63	(0.51, 0.72)	0.75	(0.67, 0.81)	0.72	(0.63, 0.79)
Florets opening (no.) ^o	0.66	(0.56, 0.74)	0.75	(0.67, 0.81)	0.71	(0.63, 0.78)
Leaf width (cm) ^v	0.73	(0.64, 0.79)	0.67	(0.57, 0.75)	0.85	(0.80, 0.88)
Plant diameter (mm) ⁿ	0.83	(0.78, 0.87)	0.73	(0.65, 0.80)	0.81	(0.76, 0.86)
Plant height (cm) ^m	0.78	(0.71, 0.83)	0.84	(0.79, 0.88)	0.84	(0.79, 0.88)
Plant height nonfloral (cm) ^l	0.82	(0.76, 0.86)	0.87	(0.82, 0.90)	0.88	(0.85, 0.91)
Plant weight (g) ^m	0.77	(0.70, 0.82)	0.65	(0.54, 0.73)	0.73	(0.64, 0.79)
Postharvest longevity (d) ^k	0.79	(0.73, 0.84)	0.81	(0.75, 0.86)	0.81	(0.75, 0.86)
Senescence symptom ^j	0.61	(0.49, 0.70)	0.75	(0.67, 0.81)	0.70	(0.61, 0.77)
Cut flower leaf area (cm ²) ^t	0.58	± 0.08	0.33	± 0.08	0.28	± 0.08
Stoma (no.)	0.21	± 0.07	0.33	± 0.08	0.28	± 0.08
Stomatal index ^g	0.21	± 0.07	0.14	± 0.07	0.21	± 0.08

$h^2 = (\sigma^2_g) / (\sigma^2_{re} + \sigma^2_{ge} + \sigma^2_e)$, derived from ANOVA.

^y95% CI: $1 - [(F_{dfG, dfG \times E}) \times ((MS_G / MS_{G \times E}) F_{1 - \alpha/2, dfG \times E, dfG})]^{-1}$ and $1 - [(F_{dfG, dfG \times E}) \times ((MS_G / MS_{G \times E}) F_{\alpha/2, dfG \times E, dfG})]^{-1}$.

^xBranching habit: $\sum k_i n_i$; where $k = 1$ (side branching <10 cm in length), 2 (basal branching), 3 (side branching >10 cm in length, usually singular), 4 (crown branching), or 5 (branching with buds) and $n =$ number of nodes where branching occurred.

^wFlorets showing color before anthesis.

^vAt 40 cm below lowest floret.

^uDeviation in cm from horizontal position.

^tOf 40 cm stem below lowest floret with bottom 15 cm of leaves removed.

^s(Date of plant harvest – date of seed sowing).

^r $[(\text{Number of buds} + \text{number of open florets}) / (\text{plant height} - \text{plant height nonfloral}) \text{ at harvest}]$.

^q(Plant height – plant height nonfloral).

^pVisual scale (1 = excellent, 5 = very poor).

^o(Florets at cut flower senescence – florets at harvest).

ⁿAt soil line.

^mSoil line to plant tip.

^lSoil line to lowest floret.

^k(Date of cut flower senescence - date of harvest).

^jWilting = 0 or browning/drying = 1.

ⁱDerived by parent-offspring regression.

^h $\{k[1 + (n-1)t]/nN\}$; $k =$ number of parents of each family, $N =$ number of families giving paired observations, $n =$ number of offspring observed for each family, $t =$ intraclass correlation of siblings.

^g $[(\text{Number of stoma}) / (\text{number of stoma} + \text{number of epidermal cells}) \text{ per area}] \times 100$.

leaf area, which dropped from 0.48 and 0.58 in the F₃ to 0.20 and 0.28 in the F₅, respectively.

Environmental sensitivity can reduce heritabilities (Falconer and Mackay, 1996). Leaf area has been shown to vary with soil moisture in *Pelargonium hortorum* Ait. (geranium) (Metwally et al., 1971), light intensity in *Sinapsis alba* L. (white mustard) (Wild and Wolf, 1980), and was one of the most environmentally sensitive traits to date of seed sowing in *A. majus* (Rabinowitch

et al., 1977). Ornamental quality is known to be environmentally sensitive to production (Rabinowitch et al., 1977) and post-production conditions (Halevy and Mayak, 1979; van der Meulen-Muisers and van Oeveren, 1997). Traits measured in *A. majus* were affected by production conditions; however, buds at discard, PHL, and senescence symptom were affected by both production and post-production conditions. This experiment was designed to provide maximum resolution between genotypes for the later two

Table 3. Phenotypic correlation coefficients^z (above diagonal) and genotypic correlation coefficients^y with respective standard errors^x (below diagonal) between phenotypic traits in F₅ families of *Antirrhinum majus*.

	Cut			Cut			Cut			Floral			Floral			Florets			Plant			Post-			Senesc-			Cut		
	Buds at	Buds at	flower	flower	flower	Days to	Floral	region	region	open at	Florets	Leaf	Plant	Plant	height	Plant	harvest	ence	flower				harvest	ence	flower					
Branching	discard	harvest	diameter	strength	weight	flower	region	size	uniform-	discard	opening	width	diameter	height	nonfloral	weight	longevity	symp-	leaf area	Stoma	Stomatal									
habit ^w	(no.) ^y	(no.) ^y	(mm) ^a	(-cm) ^j	(g) ^k	(d) ^l	density ^d	(cm) ^g	ity ^o	(no.)	(no.) ^p	(cm) ^m	(mm) ^j	(cm) ^k	(cm) ^j	(g) ^k	(d) ^j	tom ^h	(cm ²) ^f	(no.)	index ^t									
Branching	-0.08	-0.08	0.18	-0.19	0.02	0.18	-0.17	0.10	0.07	-0.05	-0.06	-0.20 [*]	0.29 ^{**}	0.14	0.13	0.38 ^{**}	-0.07	0.01	0.00	0.24 [*]	0.23 [*]									
habit																														
Buds at	-0.51 ^{**}																													
discard (no.)	(0.10)	0.59 ^{**}	0.48 ^{**}	-0.30 ^{**}	0.48 ^{**}	0.03	0.24 [*]	0.24 [*]	-0.38 ^{**}	0.30 ^{**}	0.28 ^{**}	-0.01	0.30 ^{**}	0.04	-0.02	0.22 [*]	-0.28 ^{**}	-0.30 ^{**}	0.15	0.20 [*]	0.26 ^{**}									
Buds at	-0.11	1.10 ^{**}																												
harvest (no.)	(0.06)	(0.01)	0.44 ^{**}	-0.17	0.41 ^{**}	-0.29 ^{**}	0.16	0.50 ^{**}	-0.55 ^{**}	0.86 ^{**}	0.85 ^{**}	-0.18	0.14	0.30 ^{**}	0.20 [*]	0.13	0.11	0.06	-0.11	0.19	0.13									
Cut flower	0.22	0.77 ^{**}	0.40 ^{**}																											
diameter	(0.06)	(0.05)	(0.04)	-0.68 ^{**}	0.86 ^{**}	0.33 ^{**}	0.32 ^{**}	0.24 [*]	-0.23 [*]	0.35 ^{**}	0.36 ^{**}	0.04	0.80 ^{**}	0.17	0.12	0.78 ^{**}	-0.21 [*]	-0.12	0.16	0.03	0.10									
Cut flower	-0.09	-0.35 ^{**}	-0.09	-0.72 ^{**}																										
strength (-cm)	(0.06)	(0.08)	(0.05)	(0.03)	-0.58 ^{**}	-0.43 ^{**}	-0.44 ^{**}	0.19	0.12	0.00	-0.02	-0.09	-0.60 ^{**}	0.18	0.15	-0.59 ^{**}	0.36 ^{**}	0.27 ^{**}	-0.26 ^{**}	0.08	-0.01									
Cut flower	-0.01	0.71 ^{**}	0.35 ^{**}	0.88 ^{**}	-0.66 ^{**}																									
weight (g)	(0.06)	(0.05)	(0.04)	(0.02)	(0.03)	0.21 [*]	0.47 ^{**}	0.13	-0.27 ^{**}	0.34 ^{**}	0.35 ^{**}	0.37 ^{**}	0.69 ^{**}	-0.14	-0.19	0.64 ^{**}	-0.20 [*]	-0.14	0.34 ^{**}	-0.03	0.02									
Days to	0.18	0.77 ^{**}	-0.26 ^{**}	0.47 ^{**}	-0.54 ^{**}	0.35 ^{**}																								
flower (d)	(0.06)	(0.07)	(0.04)	(0.04)	(0.04)	(0.04)	0.30 ^{**}	-0.37 ^{**}	0.15	-0.33 ^{**}	-0.31 ^{**}	-0.18	0.61 ^{**}	0.08	0.20 [*]	0.61 ^{**}	-0.39 ^{**}	-0.01	0.12	-0.10	0.06									
Floral region	-0.40 ^{**}	0.42 ^{**}	0.26 ^{**}	0.29 ^{**}	-0.54 ^{**}	0.41 ^{**}	0.34 ^{**}																							
density	(0.05)	(0.08)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	-0.62 ^{**}	-0.34 ^{**}	0.06	0.10	0.23 [*]	0.39 ^{**}	-0.39 ^{**}	-0.28 ^{**}	0.32 ^{**}	-0.10	0.00	0.26 ^{**}	-0.19	-0.15									
Floral region	0.24 [*]	0.31 ^{**}	0.41 ^{**}	0.19	0.29 ^{**}	0.06	-0.31 ^{**}	-0.68 ^{**}																						
size (cm)	(0.06)	(0.09)	(0.04)	(0.05)	(0.05)	(0.05)	(0.05)	(0.03)	0.07	0.09	0.50 ^{**}	0.46 ^{**}	-0.22 [*]	-0.04	0.58 ^{**}	0.38 ^{**}	0.00	0.09	0.00	-0.33 ^{**}	0.32 ^{**}									
Floral region	-0.57 ^{**}	-0.64 ^{**}	-0.62 ^{**}	0.03	-0.68 ^{**}	0.03	0.16	-0.52 ^{**}																						
uniformity	(0.05)	(0.06)	(0.03)	(0.04)	(0.03)	(0.04)	(0.05)	(0.04)	(0.05)	-0.53 ^{**}	-0.52 ^{**}	-0.04	-0.10	0.09	0.08	-0.06	-0.24 [*]	-0.14	-0.13	-0.01	0.06									
Florets open	-0.06	0.61 ^{**}	0.90 ^{**}	0.32 ^{**}	0.09	0.31 ^{**}	-0.30 ^{**}	0.19	0.43 ^{**}	-0.56 ^{**}																				
at discard	(0.06)	(0.07)	(0.02)	(0.04)	(0.05)	(0.04)	(0.04)	(0.04)	(0.03)	0.99 ^{**}	-0.11	0.12	0.36 ^{**}	0.27 ^{**}	0.17	0.46 ^{**}	0.39 ^{**}	-0.13	0.08	-0.06										
Florets	-0.06	0.70 ^{**}	0.91 ^{**}	0.34 ^{**}	0.09	0.34 ^{**}	-0.29 ^{**}	0.36 ^{**}	0.41 ^{**}	-0.50 ^{**}	1.06 ^{**}																			
opening (no.)	(0.06)	(0.06)	(0.02)	(0.04)	(0.05)	(0.04)	(0.04)	(0.04)	(0.04)	(0.01)																				
Leaf	-0.31 ^{**}	-0.12	-0.20 [*]	0.02	-0.03	0.37 ^{**}	-0.18	0.17	-0.36 ^{**}	-0.06	-0.10	0.01																		
width (cm)	(0.05)	(0.08)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)																			
Plant	0.38 ^{**}	0.58 ^{**}	0.13	0.85 ^{**}	-0.60 ^{**}	0.76 ^{**}	0.84 ^{**}	0.48 ^{**}	-0.08	0.13	0.16	0.19	-0.02																	
diameter	(0.05)	(0.06)	(0.04)	(0.02)	(0.03)	(0.02)	(0.02)	(0.03)	(0.05)	(0.04)	(0.04)	(0.04)	(0.04)	0.16	0.19	0.92 ^{**}	-0.25 ^{**}	-0.17	0.17	-0.10	0.04									
Plant	0.20 [*]	0.18	0.27 ^{**}	0.11	0.31 ^{**}	-0.19	-0.18	-0.52 ^{**}	0.59 ^{**}	-0.35 ^{**}	0.37 ^{**}	0.36 ^{**}	-0.68 ^{**}	0.14																
height (cm)	(0.05)	(0.08)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.03)	(0.03)	(0.04)	(0.04)	(0.04)	(0.04)																	
Plant height	0.16	0.07	0.19	0.08	0.26 ^{**}	-0.24 [*]	0.27 ^{**}	-0.02	0.42 ^{**}	-0.29 ^{**}	0.29 ^{**}	0.28 ^{**}	-0.70 ^{**}	0.18	1.01 ^{**}															
nonfloral (cm)	(0.05)	(0.08)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.02)	(0.04)	(0.01)	0.30 ^{**}														
Plant	0.49 ^{**}	0.41 ^{**}	0.10	0.83 ^{**}	-0.55 ^{**}	0.73 ^{**}	0.83 ^{**}	0.27 ^{**}	-0.06	0.18	0.22 [*]	0.25 ^{**}	-0.01	1.04 ^{**}	0.25 [*]															
weight (g)	(0.05)	(0.08)	(0.05)	(0.02)	(0.04)	(0.03)	(0.02)	(0.04)	(0.05)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)															
Postharvest	-0.04	-0.47 ^{**}	0.12	-0.27 ^{**}	0.44 ^{**}	-0.24 [*]	-0.43 ^{**}	-0.08	0.04	-0.24 [*]	0.49 ^{**}	0.51 ^{**}	0.05	-0.23 [*]	0.15	0.14	-0.11													
longevity (d)	(0.06)	(0.07)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)	(0.05)	(0.04)	(0.04)	(0.03)	(0.04)	(0.04)	(0.04)															
Senescence	-0.07	-0.52 ^{**}	0.22 [*]	-0.15	0.12	-0.17	-0.34 ^{**}	-0.03	-0.13	-0.23 [*]	0.61 ^{**}	0.77 ^{**}	-0.07	0.01	0.19	0.18	0.01	0.32 ^{**}												
symptom	(0.06)	(0.07)	(0.05)	(0.04)	(0.05)	(0.04)	(0.04)	(0.04)	(0.05)	(0.04)	(0.03)	(0.03)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)													
Cut flower																														
leaf area																														
Stoma (no.)																														

^zPearson's r calculated by $r_{xy} = \Sigma (x_i - \bar{x})(y_i - \bar{y}) / [\Sigma (x_i - \bar{x})^2 (y_i - \bar{y})^2]^{1/2}$.

^y $r_A = (\text{cov}_{xy} / \text{G}^2_x + \text{G}^2_y)^{1/2}$.

^x $\text{SE}(r_A) = 1 - r_A^2 / (2)^{1/2} [\{(\sigma_{h2x})(\sigma_{h2y}) / h^2_x h^2_y\}^{1/2}]$.

^wBranching habit: $\Sigma k_i n_i$; where k = 1 (side branching < 10 cm in length), 2 (basal branching), 3 (side branching > 10 cm in length, usually singular), 4 (crown branching), or 5 (branching with buds) and n = number of nodes where branching occurred.

^yFlorets showing color before anthesis.

^aAt 40 cm below lowest floret.

^jDeviation in horizontal position.

^{*}Of 40 cm stem below lowest floret with bottom 15 cm of leaves removed.

^l(Date of harvest – date of seed sowing).

^q[(Number of buds + number of florets) / (plant height – plant height nonfloral) at harvest].

^r(Plant height – plant height nonfloral).

^oVisual scale (1 = excellent, 5 = very poor).

^p(Florets open at discard – florets at harvest).

^mAt 40 cm below lowest floret.

^lAt soil line.

^kSoil line to plant tip.

^jSoil line to lowest floret.

ⁱ(Date of cut flower senescence – date of harvest).

^hWilting = 0 or browning/drying (1).

^gOf 40 stem below lowest floret with bottom 15 cm of leaves removed.

^f[(Number of stoma) / (number of stoma + number of epidermal cells) per area] × 100.

^{*,**}Significant at $P < 0.05$ or $P < 0.01$, respectively.

traits by minimizing the expected standard errors; no such consideration was given for buds at discard. Therefore, experimental control of error may partially explain the stability of heritability for PHL and senescence symptom and the drop in heritability for buds at discard. Environmental sensitivity of branching habit in *A. majus* (Rabinowitch et al., 1977) and lack of accuracy and/or consistency in trait quantification can also reduce heritabilities (Falconer and Mackay, 1996). Subjective quantification of the environmentally sensitive branching habit likely caused moderate h^2 for F_5 families (0.41 , $CI = 0.23-0.55$).

Narrow-sense heritability estimates for *A. majus* PHL, ranging 0.79 to 0.81 (Table 2), are higher than previously reported, 0.30 (Schroeder, 2000) and 0.41 (Martin, 2000); however, the estimates are considered more representative of genetic potential due to evaluation of larger and more genetically pure populations and more generations being utilized for derivation. Narrow-sense heritabilities for PHL reported here, though population specific, agree with estimates in *Lilium* L. (lily) 0.74 (van der Meulen-Muisers et al., 1999) and *Rosa* L. (rose) 0.80 (De et al., 1999), but are higher than those reported for *Gerbera* Gmel. (gerbera daisy) 0.00 to 0.38 (Harding et al., 1981) and 0.28 (Wernett et al., 1996b). Moderate h^2 for PHL are reported for F_1 hybrids of *Callistephus chinensis* Nees (China aster) 0.59 (Patil and Rane, 1995), and backcrosses of *D. caryophyllus*, 0.51 to 0.59 (Burchi et al., 1999). PHL h^2 disparity supports expected species and population variability and additionally, that estimate variability may be due to inbreds being evaluated in *A. majus* and clones in *Lilium* spp. and *Rosa* spp. vs. full- and half-sib families in *Gerbera* spp.

Narrow-sense heritability estimates reported here (Table 2) for plant phenotypic traits of this population of *A. majus* are similar to those found for *C. chinensis* for branching habit (0.47), days to flower (0.64), plant and floret height (0.75), buds at harvest (0.65), and plant and cut flower weight (0.67) (Patil and Rane, 1995). Narrow-sense heritability estimates reported here for plant height and days to flower agree with broad sense heritabilities given for *H. annuum*, 0.41 to 0.93 and 0.81 to 0.95 (Virk and Pooni, 1994) and for *Cicer arietinum* L. (chickpea) 0.62 and 0.71 (Moussa et al., 2000). Relatively high heritabilities suggest predictability of progeny from crosses of characterized parentage and that selection is possible and should be successful (Falconer and Mackay, 1996). Heritability estimates can be affected by species, population, environment, experimental design, sampling techniques, and complex interactions of these factors (Falconer and Mackay, 1996). Quality trait h^2 estimates are presented acknowledging parental lines were not selected to deviate specifically for the examined quality traits. Information on h^2 of ornamental quality traits is generally lacking in the literature; therefore, the information presented here on *A. majus* is to serve as a basis for future work and meanwhile as a guide to ornamental breeders.

Genotypic correlations between trait combinations vary from highly significant to nonexistent (Table 3). Utility of genetic correlations can be limited due to some traits being autocorrelated and subsequently these combinations show high and likely false correlations. Examples of suspect correlations include plant height and plant height nonfloral (1.01 ± 0.01), buds at discard and buds at harvest (1.10 ± 0.01), and florets open at discard with florets opening (1.06 ± 0.01). Less obvious examples confounded not by autocorrelations but by definition include buds at harvest with floral region uniformity, 0.62 ± 0.03 , and florets open at discard,

0.56 ± 0.03 . Correlations of florets opening with PHL, 0.51 ± 0.03 , and with senescence symptom, 0.77 ± 0.03 , provide two more examples of definitional nonindependence. Finally, the negative correlations of cut flower strength with floral region density, -0.54 ± 0.04 , and with floral region uniformity, -0.68 ± 0.03 , are likely due to more buds and florets in the floral region putting comparatively unequal strain on the stem and, therefore, are autocorrelated.

Plant architecture traits including branching habit, cut flower weight, floral region size, plant height, plant height nonfloral, plant weight, cut flower diameter, and cut flower strength are often significantly and positively correlated suggesting an underlying pleiotropic consequence of plant vigor. Floral region density is inversely correlated with floral region size, -0.68 ± 0.03 , suggesting increased internode length may reduce plant and floral quality characteristics. Inverse correlations between leaf width and plant height nonfloral, -0.70 ± 0.02 , as well as the inverse correlation of branching habit with buds at discard, -0.51 ± 0.10 , with floral region density, -0.40 ± 0.05 , and with floral region uniformity, -0.57 ± 0.05 , may reflect carbon and energy partitioning that subsequently detracts from ornamental cut flower quality.

PHL is of primary interest to this research and several correlations suggest plant architecture may have impacts upon PHL. Buds at discard is positively correlated to cut flower and plant diameter, cut flower weight and days to flower, 0.77 ± 0.05 , 0.58 ± 0.06 , 0.71 ± 0.06 , and 0.77 ± 0.07 , respectively. Interpreted, these positive correlations suggest increased stem diameter increases the number of florets failing to open postharvest. In addition, cut flower strength and days to flower are inversely related to PHL, -0.44 ± 0.04 and -0.43 ± 0.44 , respectively, while cut flower diameter, strength, and weight are increased by days to flower, 0.47 ± 0.04 , 0.54 ± 0.04 , and 0.35 ± 0.04 , respectively. Woodier plant stems are more prone to wilt (Jones et al., 1993) and likely contain more secondary growth including development of secondary xylem (Raven et al., 1992). Canny (1995, 1997a, 1997b, 1998) has shown that secondary xylem is less stable in water balance, being more prone to vascular occlusions and/or cavitations due to its larger interior diameter. These inverse correlations between PHL and other quality traits of interest may provide challenges to breeders as selection performed on PHL will lead to negative correlated responses in other traits (Falconer and Mackay, 1996). Populations can be screened for exceptions to negative correlations. Rare favorable combinations were found in evaluated *A. majus* populations.

Simultaneous selection for multiple quality traits is more effective than independent culling or tandem selection (Baker, 1986). Correlated response to selection addresses changes in trait values when a separate trait is selected (Falconer and Mackay, 1996). Due to the complex definition of quality and exhibited genetic correlations among ornamental quality traits, correlated response to selection is of concern when selecting for PHL (Falconer and Mackay, 1996). With PHL positively correlated to evaluated quality traits (Table 3) and existing population variability (Table 1), a simplistic situation for simultaneous selection for PHL and other traits exists. In other situations with negative genetic correlations, analogous variation is found within quality traits; therefore, simultaneous selection remains reasonable though caution is advised. Selection for simultaneous improvement of quality traits should be effective.

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