Genetics of Postharvest Longevity and Quality Traits in Late Generation Crosses of *Antirrhinum majus* L.

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ABSTRACT. Progeny of 158 $F_5 \times F_5$ crosses of *Antirrhinum majus* (snapdragon) selected within and among cut flower postharvest longevity (PHL) categories (long = 12.6–16.8 days, middle = 9.3–12.1 days, and short = 4.8–8.9 days) were evaluated for PHL and quality traits. Results were compared with previous studies involving $F_2 \times F_2$ progeny, and F_3 , F_4 , and F_5 inbred lines. Heritability of PHL in $F_5 \times F_5$ progeny (0.77 ± 0.11) agrees with that of inbred lines (0.79 to 0.81) but is higher than in $F_2 \times F_2$ progeny (0.41). Therefore, selection for increased PHL should progress more rapidly and predictably through application of inbred lines rather than F_2 individuals. Significant differences between $F_5 \times F_5$ progeny PHL categories confirm PHL is heritable with a significant additive component. Heritabilities of quality traits in *A. majus* are high, suggesting selection for quality traits should progress without difficulty. Phenotypic and genotypic correlations of PHL with quality traits are not consistently significant across PHL studies in *A. majus*. Discrepancies between studies suggest most traits may not be correlated to PHL or are subject to strong environmental influence.

United States cut flower sales are \$1.1 billion of the nearly \$5.1 billion floriculture industry (Jerardo, 2004). Imported cut flowers are 61% of U.S. sales while domestic cut flower production is declining. The reliance on international cut flowers reinforces the importance of postharvest longevity. Prolonged PHL may also increase consumer demand for cut flowers (Reid et al., 1995; Rogers, 1963).

Cut flower PHL is affected by genetic and nongenetic components (Halevy and Mayak, 1979). Conditions preharvest and especially postharvest like temperature, light and humidity affect cut flower PHL (Halevy and Mayak, 1979; Holley, 1963; Urban et al., 1995). Postharvest techniques focus on minimizing water loss, respiration rate, microbial infection, and ethylene production and sensitivity (Goszczyńska and Rudnicki, 1988) and affect PHL more than preharvest conditions. Effectiveness of postharvest treatments and handling techniques vary by species and cultivar (Halevy and Mayak, 1979; Holley, 1963; Urban et al., 1995). Chemical treatments like silver thiosulfate (STS), an ethylene inhibitor (Coorts, 1973), and 8-hydroxyquinoline (8-HQ), a microbial growth inhibitor (Rogers, 1973), are used commercially to increase cut flower PHL. However, neurotoxic STS and carcinogenic 8-HQ may be banned (Nell, 1992; Ohkawa et al., 1999), making research on genetic improvement of PHL imperative.

Genetic variability in PHL exists in *Dendrobium* Sw. (Bobisud and Kamemoto, 1982) and *Rosa ×hybrida* L. (De et al., 1999). PHL is heritable with significant additive gene effects in *Cal-*

listephus chinensis (L.) Nees (Patil and Rane, 1995), *Dianthus caryophyllus* L. (Burchi et al., 1999), *Gerbera* Gmel. (de Jong and Garretsen, 1985; Harding et al., 1981; Wernett et al., 1996a, 1996b), *Lilium* L. (van der Meulen-Muisers et al., 1999), *Rosa* L. (De et al., 1999), and *Tulipa* L. (van Eijk and Eikelboom, 1980). Selection increased PHL ≈ 3.5 d in both *D. caryophyllus* (Onozaki et al., 2001) and *Gerbera ×hybrida* Hort. (Wernett et al., 1996a). Successful PHL selection in *G. ×hybrida* and *D. caryophyllus* along with the additive gene effects and moderate to high heritabilities for PHL found in various species suggest selection of prolonged PHL in cut flower crops is promising.

Antirrhinum majus is valued eighth in the U.S. cut flower market, with sales of \$14.6 million in 2003 (Jerardo, 2004). Difficulties in shipping and ethylene sensitivity decrease quality and PHL in *A. majus*. Cut flower PHL is increased by pulsing cut stems with STS and holding cut stems in sucrose and 8-hydroxyquinoline citrate (HQC) solutions (Rogers, 1992). Genetic PHL improvement would decrease dependence on these toxic chemical compounds and improve *A. majus* cut flower quality, which may increase consumer demand.

Studies in *A. majus* suggest PHL is a quantitative trait with significant additive and dominant components (Martin and Stimart, 2003, 2005; Schroeder, 2000; Schroeder and Stimart, 2001). A minimum of two to four genes appear to control the trait (Schroeder, 2000). PHL heritability estimates were 0.30 in F_2 , BC_1 , and BC_2 generations (Schroeder, 2000), 0.41 in $F_2 \times F_2$ progeny (Martin and Stimart, 2003), 0.79 in F_3 inbred lines, and 0.81 in F_4 and F_5 inbred lines (Martin and Stimart, 2005). The increase in heritability with further inbreeding suggests genetically pure breeding material will provide a better prediction of progeny performance. Although PHL is an important trait, cut flowers must possess additional quality traits for consumers (van der Meulen-Muisers and van Oeveren, 1997). Significant phenotypic (Martin and Stimart, 2003 and 2005; Schroeder and Stimart, 2001) and genotypic (Martin and Stimart, 2005) correlations of PHL with quality traits of *A. majus* are found in early generation crosses, backcrosses and inbred lines.

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This study used $F_5 \times F_5$ progeny of *A. majus* to estimate heritability for PHL and quality traits; to estimate phenotypic and genotypic correlation coefficients of quality traits with PHL; and to compare results with previous studies.

Materials and Methods

Commercial inbred lines of cut flower *A. majus* were evaluated in 1991 and 1992 for cut flower postharvest longevity (PHL). P1, 16.3 d PHL, was crossed with P2, 3.0 d PHL, to produce an F_1 (Stieve and Stimart, 1994). The F_1 was self-pollinated to produce an F_2 population in Fall 1998. Four hundred eighty-five plants were selected randomly and self-pollinated to create F_3 families. Of these families, 155 were selected randomly and advanced to the F_5 generation through single-seed descent. In fall, winter, and spring of 2001–02, F_3 , F_4 , and F_5 generations of 105 inbred lines were evaluated for PHL and quality traits in replicated plantings (Martin and Stimart, 2005).

To more accurately select lines for the current study, a PHL index (Falconer and Mackay, 1996) was calculated utilizing expected intergenerational genetic correlations and determined heritability estimates from F_3 , F_4 , and F_5 generations (Martin, 2002). Thirty-eight F_5 inbred lines were selected randomly: 14 lines within the 25% highest indices (12.99 to 15.58), 10 within the 50% of indices about the mean (10.19 to 11.54), and 14 within the 25% lowest indices (5.28 to 9.45). Selected lines were re-categorized into F_5 PHL categories for statistical analysis: 15 lines within the 25% longest lived (12.6 to 16.8 d), 12 within 1.5 d about the mean (9.3 to 12.1 d) and 11 within the 25% shortest lived (4.8 to 8.9 d). The selected F_5 inbreds were intermated in a half-diallel mating scheme to create $F_5 \times F_5$ progeny in Spring and Summer 2002.

Not all cross combinations could be evaluated due to resource limitations. Thus, a sample of 158 $F_5 \times F_5$ progeny was chosen among and within PHL categories for evaluation of PHL and quality traits in Fall 2002 and 2003. In Fall 2002, 79 $F_5 \times F_5$ progeny, P1, P2, and F_1 ($P1 \times P2$) were grown under standard forcing procedures (Rogers, 1992) in a polyethylene greenhouse at the Univ. of Wisconsin–Madison using a randomized complete-block design (eight blocks, three replications/genotype/block). Due to low seed production, crosses were recreated for the 79 previously evaluated $F_5 \times F_5$ progeny using remnant F_5 seed in Spring and Summer 2003 for Fall 2003 evaluation. Seventy-nine additional $F_5 \times F_5$ progeny along with 20 $F_5 \times F_5$ progeny evaluated in Fall 2002, P1, P2, and F_1 ($P1 \times P2$) were grown in three adjacent sections of a glasshouse at the Univ. of Wisconsin–Madison using a randomized complete block design (six blocks, three replications/genotype/block) in Fall 2003.

In both plantings, seeds were germinated in cells of 96-cell (65 cm^3) flats using a growing medium of equal volumes peat, perlite and composted soil. Seedlings were transplanted into single cells of 96-cell (65 cm^3) flats when the first true leaves appeared. After the third set of true leaves developed, seedlings were transplanted into 1250 cm^3 plastic pots and spaced on 22-cm centers. Supplemental lighting from 1000-W high-pressure sodium lamps, $27 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at bench level, was provided from 0600 through 2400 HR. Two hundred $\text{mg} \cdot \text{L}^{-1}$ N of Peter's fertilizer (20N–8.7P–16.6K) was applied every other week (Scott's Sierra Horticultural Products Co., Marysville, Ohio).

Plants were harvested at the soil line when five florets opened and transported in distilled water to the laboratory. Buds at harvest was recorded as the number of florets showing color prior to an-

thesis. Plant height, distance from inflorescence tip to stem base, and plant height nonfloral, distance from lowest floret to stem base, were measured, and floral region size was calculated from their difference. Floral region density was calculated by dividing the number of buds and florets open at harvest by the floral region size. Floral region uniformity was determined on a visual scale (1 = excellent to 5 = poor; Martin and Stimart, 2005). Floret size was recorded as the average distance between the tips of the upper and lower petals of the three lowest florets. Stems were cut to 40 cm below the lowest floret and the leaves from the bottom 15 cm of the stem were removed, hereafter termed cut flower. Cut flower weight and stem base diameter were recorded. Cut flower strength was measured as the deviation in cm at the cut flower tip when held horizontally by the stem's lowest 5 cm.

Cut flowers were held 7.5 cm apart in a three by five grid placed over a plastic storage container (34 cm long $\times$ 22 cm wide $\times$ 15 cm high) holding 3 L of distilled H_2O , a depth of 4 cm. The H_2O level was maintained daily. Containers were placed under constant cool-white fluorescent lighting at 23 °C. Cut flowers were discarded when 50% of the open florets displayed either a browning/drying or wilting senescence symptom (Marousky and Raulston, 1970). Presence of bentneck was determined by collapse of the floral region. Number of buds and open florets were recorded at discard. Degree of leaf wilt was determined on a visual scale (1 = zero to slight wilt, 2 = moderate wilt, 3 = high degree of wilt). Days to flower was calculated by the difference between dates of harvest and seed sowing. PHL was calculated by the difference between dates of harvest and discard.

Population statistics for traits, including means, minimums, maximums, and standard deviations; and phenotypic and genotypic correlation coefficients between traits were determined using SAS (Littell et al., 1996). All traits were tested for normal distributions. To account for repetition of some genotypes across years, estimates of genotypic means were made using Best Linear Unbiased Prediction (Bernardo, 2002). Variance components were estimated using SAS mixed model analysis assuming a completely random design with Satterthwaite corrections for degrees of freedom (Satterthwaite, 1946). Narrow-sense heritability estimates for traits were derived from both midparent-offspring regression and analysis of variance (ANOVA) (Falconer and Mackay, 1996; Hallauer and Miranda, 1988). As all genotypes were not repeated and block number varied across plantings, harmonic means were calculated for block ($b = 6.75$) and planting ($p = 1.06$) for use in ANOVA estimates of heritability. ANOVA removes environmental and genotype $\times$ environmental error as well as differences in evaluation technique between researchers (Falconer and Mackay, 1996). Thus, ANOVA-derived heritabilities are used for discussion unless otherwise noted. As a large number of genotypes were evaluated, the correlation value required for significance at $P \leq 0.01$ with ≈ 150 df was low at $r = 0.21$. Therefore, discussion will focus on traits that are still significant at $r = 0.21$ when the standard error of each trait's correlation coefficient is included.

Results and Discussion

Regression of $F_5 \times F_5$ progeny PHL means on midparent value reveals clustering within cross categories (Fig. 1). Transgressive segregants exist within cross categories; a trend also seen in crosses of Asiatic *Lilium* (van der Meulen-Muisers et al., 1999).

Midparent-offspring regression resulted in a heritability estimate for PHL of 0.54 (Fig. 1 and Table 1), slightly higher than previous ANOVA-derived estimates of 0.41 (Martin and Stimart,

Fig. 1. Regression of $F_5 \times F_5$ progeny on midparent values for postharvest longevity of *Antirrhinum majus* cut flowers. Progeny derived from crosses within and among categories of F_5 parents for postharvest longevity: long = 12.6–16.8 d, middle = 9.3–12.1 d, short = 4.8–8.8 d. **Significant at $P \leq 0.01$

Table 1. Heritability estimates from midparent-offspring regression and analysis of variance (ANOVA) for quality traits of $F_5 \times F_5$ progeny^a of *Antirrhinum majus*.

Phenotypic quality trait	Midparent-offspring regression derived h^2 and corresponding R^2	ANOVA derived h^2 and corresponding standard errors ^x
Bentneck ^w	---	0.44 0.13
Buds at discard (no.) ^v	0.48 0.04*	0.65 0.12
Buds at harvest (no.) ^v	0.24 0.12**	0.67 0.12
Cut flower diameter (cm) ^u	0.67 0.31**	0.87 0.11
Cut flower strength (-cm) ^t	0.33 0.34**	0.70 0.12
Cut flower weight (g) ^s	0.55 0.21**	0.79 0.11
Days to flower (d) ^r	0.23 0.22**	0.36 0.13
Floral region density ^q	0.03 0.06**	0.16 0.15
Floral region size (cm) ^p	0.14 0.02 ^{ns}	0.58 0.12
Floral region uniformity ^o	1.24 0.50**	0.71 0.12
Floret size (cm) ⁿ	---	0.74 0.12
Florets open at discard (no.)	0.29 0.24**	0.70 0.12
Leaf wilt ^m	---	0.75 0.12
Plant height (cm)	0.54 0.42**	0.84 0.11
Plant height nonfloral (cm) ^j	0.62 0.51**	0.82 0.11
Postharvest longevity (d) ^k	0.54 0.30**	0.77 0.11
Senescence symptom ^l	0.42 0.15**	0.65 0.12

^aBased on means of 158 $F_5 \times F_5$ crosses.

^b $h^2 = (\sigma^2_g) / (\sigma^2 / pbr + \sigma^2_{gb(p)} / pb + \sigma^2_{gp} / p + \sigma^2_e)$, derived from ANOVA.

^cSE $h^2 = [\text{var}(\sigma^2_g)]^{1/2} / (\sigma^2 / pbr + \sigma^2_{gb(p)} / pb + \sigma^2_{gp} / p + \sigma^2_e)$.

^dVisual rating on date of discard (0 = no, 1 = yes).

^eUnopened florets with visible color.

^f40 cm below lowest floret.

^gDeviation in cm from horizontal position.

^hStem cut 40 cm below lowest floret with lowest 15 cm of leaves removed.

ⁱ(Date of harvest – date of planting).

^jAt harvest, (number of buds + number of open florets) / (plant height – plant height nonfloral).

^k(plant height – plant height nonfloral).

^lVisual rating (1 = excellent uniformity, 5 = very poor uniformity).

^mBottom of lowest petal to top of highest petal on a single floret.

ⁿVisual rating (1 = little or no wilt, 2 = moderate wilt, 3 = extreme wilt).

^oSoil line to lowest floret.

^p(date of discard – date of harvest).

^qVisual rating taken on date of discard (browning/drying = 0, wilting = 1).

^r^{ns}, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

2003), and 0.30 (Schroeder and Stimart, 2001). Heritability of $F_5 \times F_5$ progeny PHL derived from ANOVA was 0.77 ± 0.11 (Table 1) and comparable to *A. majus* inbred lines (0.79 to 0.81; Martin and Stimart, 2005), *Lilium* (0.74; van der Meulen-Muisers et al., 1999), and *R. xhybrida* (0.80; De et al., 1999). Lower estimates are reported in *C. chinensis* (0.59; Patil and Rane, 1995), *D. caryophyllus* (0.51 to 0.59; Burchi et al., 1999), *Gerbera jamesonii* Bol. ex Adlam. (0.00 to 0.38; Harding et al., 1981), and *G. xhybrida* (0.28; Wernett et al., 1996b). The above studies estimate PHL heritability using different population structures and experimental designs, both of which affect heritability. Therefore, it is difficult to compare heritability estimates from other species and studies.

The PHL heritability estimate for $F_5 \times F_5$ progeny suggests strong additive genetic variance (Falconer and Mackay, 1996). Regression of repeated $F_5 \times F_5$ progeny from 2002 and 2003 plantings strengthens this assertion (Fig. 2). PHL values were slightly lower in 2003 supporting a significant genotype $\times$ planting interaction in ANOVA. Furthermore, significant differences exist between PHL cross categories with exception of the long $\times$ short and long $\times$ middle, and the long $\times$ short and middle $\times$ short (Fig. 3). The significant differences between cross categories additionally reinforce the significant additive component for *A. majus* PHL reported previously (Martin and Stimart, 2003, 2005; Schroeder and Stimart, 2001).

Distributions of $F_5 \times F_5$ and $F_2 \times F_2$ crosses are similarly normal implying that variation for PHL present in the F_2 remains in the F_5 (Fig. 4). Further, $F_5 \times F_5$ progeny variability confirms selection for increased PHL using the F_5 generation remains possible. The higher PHL heritability estimate in $F_5 \times F_5$ progeny (0.77, Table 1), vs. $F_2 \times F_2$ (0.41; Martin and Stimart, 2003), suggests inbreeding increases predictability and success of selection for PHL. Early vs. late generation testing has been discussed in *Zea mays* L. since 1935 (Hallauer, 1990). Theoretical calculations conclude correlation between parents and progeny should increase as parents become increasingly inbred (Bernardo, 1991). However, inbreeding beyond the S_3 (F_5) generation does not sufficiently increase correlation to justify further inbreeding (Bernardo, 1991). In addition, if heritability is low in the S_0 (F_2) generation, more families must be selected in early generations to obtain the best family (Bernardo, 1992). Similarly, PHL heritability estimates derived from $F_2 \times F_2$ (0.41) and $F_5 \times F_5$ (0.77) predict increased progeny correlation with parental value in later vs. earlier generations. However, the resources required for inbreeding one or two generations beyond the F_3 , with PHL heritability estimates of 0.79 in the F_3 and 0.81 in the F_4 and F_5 , may not warrant inbreeding beyond the F_3 .

Heritabilities of quality traits derived from midparent-offspring regression ranged from 0.03 to 1.24, while heritabilities derived from ANOVA ranged from 0.16 to 0.87 (Table 1). Heritabilities of quality traits were higher when derived from ANOVA than from parent-offspring regression agreeing with previous estimates (Martin and Stimart, 2005). The midparent-offspring derived heritability estimate of 1.24 for floral region uniformity is likely

Fig. 2. Regression of cut flower postharvest longevity in $F_5 \times F_5$ progeny of *Antirrhinum majus* grown in Fall 2002 and Fall 2003.

Fig. 3. Average postharvest longevity of cut flowers for $F_5 \times F_5$ progeny of *Antirrhinum majus*. Cross categories derived from crosses within and among categories of F_5 parents for postharvest longevity: long = 12.6–16.8 d, middle = 9.3–12.1 d, short = 4.8–8.8 d. Numbers in parentheses represent number of genotypes evaluated. Letters represent mean separation of cross categories, $LSD_{0.05} = 0.62$ d.

an overestimate due to differences between subjective individual rating techniques. This variability is eliminated when estimating heritabilities from ANOVA and therefore, estimates from ANOVA are more accurate.

ANOVA derived heritability estimates of traits evaluated in $F_5 \times F_5$ progeny (Table 1) and inbred lines (Martin and Stimart, 2005) agree except for buds at discard, days to flower, and floral region density. The heritability estimate for buds at discard (0.65) is slightly higher in $F_5 \times F_5$ progeny than in inbreds (0.20 to 0.48). Floral region density (0.16) has a much higher heritability in inbred lines, 0.69 to 0.80 (Martin and Stimart, 2005). However, one parent involved in crosses between F_5 lines had a much higher

floral region density which may have influenced heritability of the trait by skewing data in the $F_5 \times F_5$ progeny. Additionally, heritability of floral region density may be affected by the multiple, environmentally sensitive traits involved in its calculation including buds at harvest, plant height, and plant height nonfloral. Finally, heritability of days to flower is lower in $F_5 \times F_5$ progeny (0.36) than inbred lines, 0.63 to 0.72 (Martin and Stimart, 2005). This is likely due to photoperiodic differences between the four response groups of *A. majus* (Dole and Wilkins, 2005). Inbred lines were evaluated in fall, winter and spring, but both populations in this study were evaluated in fall.

Heritability estimates for quality traits of $F_5 \times F_5$ progeny are similar to estimates for *C. chinensis* for plant height (0.75), nonfloral height (0.75), cut flower weight (0.67), and buds at harvest (0.65) (Patil and Rane, 1995). Conversely, days to flower in *C. chinensis* (0.64) agrees with that of inbred lines of *A. majus* (Martin and Stimart, 2005) rather than that in $F_5 \times F_5$ progeny. The high heritabilities found in this and other studies for quality traits suggest selection for most quality traits in *A. majus* is possible and should proceed without difficulty.

Phenotypic traits are significantly correlated with PHL except floral region density (0.22 ± 0.08), floral region size (0.22 ± 0.07), and plant height (0.26 ± 0.08) (Table 2). Some traits are autocorrelated to PHL or confounded into the definition of PHL and have been disregarded. These include florets open at discard, buds at discard, and buds at harvest. Florets open at discard (0.66 ± 0.06) is incorporated into the definition of PHL; buds at discard (0.75 ± 0.05) is inversely proportional to florets open at discard; and buds at harvest (-0.34 ± 0.08) influences the potential number of florets opening. Previously unevaluated traits in *A. majus*, bentneck (-0.60 ± 0.06), floret size (-0.31 ± 0.08), and leaf wilt (-0.76 ± 0.05) are significantly correlated to PHL.

Traits highly correlated with PHL are related to water balance (Table 2). Bentneck (-0.60 ± 0.06), leaf wilt (-0.76 ± 0.05), and wilting senescence symptom (-0.58 ± 0.07) are signs of greater water loss through transpiration than uptake through the cut stem. Water imbalance may be due to multiple causes such as microbial plugging of conducting vessels (van Doorn et al., 1989; van Doorn and de Witt, 1991; Zagory and Reid, 1986), physiological stem embolism (Burge et al., 1998; Dai and Paull, 1991; Ichimura et al., 1998; Nakahara et al., 1998; van Doorn et al., 1989), or water loss through dysfunctional stomata (van Doorn, 1997). PHL is increased in wilting *A. majus* lines when transpiration is reduced (Martin, 2002). Also, recutting *A. majus* cut flower stems leads to greater and prolonged water uptake and

Fig. 4. Distribution of cut flower postharvest longevity in 68 $F_2 \times F_2$ progeny (—) and 158 $F_3 \times F_3$ progeny (----) of *Antirrhinum majus*.

significantly extended PHL (Martin, 2002). The high correlations between traits relating to water balance and PHL, considered along with extended PHL by recutting stems or reducing transpiration, suggest water balance plays a crucial role in PHL of *A. majus*. Comparison with previously reported phenotypic correlations between PHL and quality traits shows senescence symptom is the only trait consistently correlated in all studies (Martin and Stimart, 2003, 2005; Schroeder and Stimart, 2001).

Genotypic correlation coefficients estimate the level of genetic correlation between two traits, removing the environmental correlation found in phenotypic correlations (Falconer and Mackay, 1996). Autocorrelated traits were disregarded as described previously. Genotypic correlations of quality traits with PHL are highly significant for bentneck (-0.74 ± 0.13), cut flower stem diameter (-0.41 ± 0.13), floral region density (-0.52 ± 0.30), floral region size (-0.50 ± 0.14), floral region uniformity (-0.52 ± 0.13), floret size (-0.57 ± 0.12), and senescence symptom (-0.69 ± 0.11) (Table 2). F_3 inbred line PHL was significantly correlated with cut flower strength (-0.44 ± 0.04) and days to flower (-0.43 ± 0.04) (Martin and Stimart, 2005). The lack of similar genotypic correlations between PHL and quality traits in the two studies suggests traits may not be as correlated as it appears from correlation coefficient estimation. However, inbred lines have lower dominance and environmental variance, providing more precise correlations (Falconer and MacKay, 1996). Furthermore, all inbred lines were grown over three seasons, which may result in more precise genotypic correlation estimates by accurate removal of environmental influence.

Heritability estimates for PHL and quality traits are high and agree with those of inbred lines of *A. majus*. Therefore, selection for PHL and quality traits is possible and should proceed rapidly and without difficulty. Higher heritability for PHL is estimated in $F_3 \times F_3$ progeny than in $F_2 \times F_2$ progeny, which confirms the easier prediction of hybrid performance based on crossing later generation inbreds of *A. majus*. Thus, selection for increased PHL should progress more easily when utilizing genetically pure germplasm, but the time and resources required for inbred development must be considered. Genotypic and phenotypic correlation coefficients

of PHL with quality traits in *A. majus* are not consistently significant between studies. Population structure influences correlations which could lead to differences between studies. The only quality trait of *A. majus* significantly correlated with PHL in this and previous studies is senescence symptom. In addition, traits not previously studied, leaf wilt and bentneck, are highly correlated with PHL, strengthening the importance of water balance in PHL of *A. majus*.

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Table 2. Phenotypic and genotypic correlation coefficients and respective SES of phenotypic quality traits with postharvest longevity of *Antirrhinum majus*.

Phenotypic quality trait	Phenotypic correlation coefficient ^z	SE ^y	Genotypic correlation coefficient ^x	SE ^w
Bentneck (%) ^v	-0.60**	0.06	-0.74**	0.13
Buds at discard (no.) ^u	-0.75**	0.05	-0.80**	0.09
Buds at harvest (no.) ^u	-0.34**	0.08	-0.34**	0.15
Cutflower stem diameter (cm) ^t	-0.30**	0.08	-0.41**	0.13
Cutflower stem strength (-cm) ^s	0.35**	0.08	0.18*	0.15
Cutflower weight (g) ^r	-0.52**	0.07	-0.26**	0.14
Days to flower (d) ^q	0.36**	0.07	0.03	0.23
Floral region density ^p	0.22**	0.08	-0.52**	0.30
Floral region size (cm) ^o	0.22**	0.07	-0.50**	0.14
Floral region uniformity ⁿ	-0.45**	0.07	-0.52**	0.13
Floret size (cm) ^m	-0.31**	0.08	-0.57**	0.12
Florets open at discard (no.)	0.66**	0.06	0.60**	0.12
Leaf wilt ^l	-0.76**	0.05	-0.24**	0.15
Plant height (cm)	0.26**	0.08	-0.11	0.14
Plant height nonfloral (cm) ^k	0.40**	0.07	0.10	0.14
Senescence symptom ^j	-0.58**	0.07	-0.69**	0.11

^zPearson's correlation coefficient ($r_{xy} = \Sigma (x_i - \bar{x})(y_i - \bar{y}) / [\Sigma (x_i - \bar{x})^2 (y_i - \bar{y})^2]^{1/2}$), determines phenotypic correlation coefficients.

^ySE(r_p) = $((1 - r_p^2) / (n - 2))^{1/2}$.

^x $r_A = \text{cov}_{xy} / (\sigma_x^2 \sigma_y^2)^{1/2}$.

^wSE(r_A) = $[(1 - r_A^2) / (2)]^{1/2} [(\sigma_{h2x} \sigma_{h2y}) / (h_x^2 h_y^2)]^{1/2}$.

^vVisual rating on date of discard (0 = no, 1 = yes).

^uUnopened florets with visible color.

^t40 cm below lowest floret.

^sDeviation in cm from horizontal position.

^rStem cut 40 cm below lowest floret with lowest 15 cm of leaves removed.

^q(date of harvest – date of planting).

^pAt harvest, (number of buds + number of open florets) / (plant height – plant height nonfloral).

^o(Plant height – plant height nonfloral).

ⁿVisual rating (1 = excellent uniformity, 5 = very poor uniformity).

^mBottom of lowest petal to top of highest petal on a single floret.

^lVisual rating (1 = little or no wilt, 2 = moderate wilt, 3 = extreme wilt).

^kSoil line to lowest floret.

^jVisual rating on date of discard (browning/drying = 0, wilting = 1).

*, **Significant at $P \leq 0.05$ or 0.01, respectively.

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