Genotypic Variation in Postharvest Flower Longevity of Asiatic Hybrid Lilies

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ABSTRACT. Genotypic variation in postharvest flower longevity was determined for 63 Asiatic lily hybrids (*Lilium* L.). The reliability of standardized test conditions for longevity screening was also examined. Improvement of lily flower longevity by breeding appears feasible. Considerable genotypic variation in individual flower longevity was obtained and estimates of the degree of genotypic determination were high. The rank order of the genotypes with respect to individual flower longevity was similar between years using standardized test conditions. Screening results for flowers forced in a growth chamber were similar to those obtained in a greenhouse. No plant traits suitable for indirect selection on flower longevity were detected.

Asiatic hybrids represent a major part of the commercially important lilies for cut flower production in The Netherlands. These hybrids originate from interspecific crosses between species of the *Sinomatragon* section, one of the seven sections of the genus *Lilium* (Van Creijl et al., 1993). Longevity of cut flowers is an important quality factor since it affects consumer satisfaction. To prolong the longevity of Asiatic hybrids, pretreatment with silver thiosulfate (STS) is obligatory at Dutch auctions. However, the extension of flower longevity is still restricted by genetic factors. Thus, breeding and selection techniques that improve lily flower longevity can eliminate the use of chemicals such as STS.

Flower longevity can be influenced by growing conditions, developmental stage of the flowers at harvest, and environmental conditions after harvest (Halevy and Mayak, 1979). To reduce undesirable nongenotypic variation, breeding cultivars with long-lasting flowers requires the availability of a reliable screening test. Standardized conditions with sufficient sensitivity to discriminate between various longevity levels in Asiatic hybrid lilies have been developed (Van der Meulen-Muisers and Van Oeveren, 1997).

In The Netherlands, Asiatic hybrid lilies are forced year-round, and interactions between the environment and genotype longevity are expected (Swart, 1980). Therefore, in breeding experiments, using growth chambers for forcing is preferred, since it eliminates the environmental variation encountered in greenhouse trials. To establish reliable results in a standardized screening test, the influence of forcing conditions on the cultivar ratings must be determined. Screening results obtained after forcing in a growth chamber using standard conditions must be similar to results obtained with greenhouse forcing.

To ascertain the possibility of improving lily flower longevity by breeding, knowledge of the genotypic variation within the Asiatic hybrids is required. Genotypic variation is expected, because the Asiatic hybrids possess complex parentage. Hybrids are derived from interspecific hybridization of at least 12 different *Lilium* species (Marshall, 1981).

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The objectives of this research were to 1) evaluate the genotypic variation in flower longevity in Asiatic hybrid lilies and 2) test the reliability of the conditions used. With regard to the possibility of indirect screening and selection, it was also ascertained to which extent flower longevity is correlated with other plant characters.

Materials and Methods

PLANT MATERIALS. Bulbs of Asiatic hybrid lilies, 12 to 16 cm in circumference, were obtained from commercial growers in The Netherlands and from the CPRO–DLO lily collection in 2 successive years. Before planting, the bulbs were stored in moist peat at –2 °C for ≈5 months. Evaluated for individual flower longevity were 63 genotypes consisting of 56 cultivars, 2 *Lilium* species, and 5 seedling clones (Table 1) that were selected based on their broad genetic backgrounds; thus, differences in individual flower longevity could be expected. All cultivars except ‘Prominence’ are listed in The International Lily Register (Leslie, 1982). All genotypes are diploid, except for ‘Compass’, which is triploid, and ‘Avignon’, ‘GranParadiso’, ‘Tetra Aristo’, ‘Tetra Bicolito’, ‘Tetra Orlito’, CPRO-85598.2, CPRO-85702.5, CPRO-85710.2, CPRO-85774.2, and CPRO-82297.2, which are tetraploid.

Three experiments were conducted in 2 successive years. In the first year (1991) all 63 lily genotypes were evaluated for individual flower longevity (Expt. 1). In the second year (1992) a subset of the genotypes consisting of 47 diploid cultivars was evaluated in two experiments using different forcing conditions (Expts. 2 and 3). ‘Ballade’, ‘Rolito’, and ‘Sylvester’ were excluded from the 1992 experiments because no bulbs were obtained.

FORCING CONDITIONS. Bulbs were weighed and individually planted in 2.5-L plastic pots using a prefertilized standard commercial potting medium. In Expts. 1 and 2, plants were forced in a growth chamber of the CPRO–DLO Selektion (Smeets, 1986), with a constant 17 °C air temperature, 60% relative humidity (RH), and a 16-h photoperiod. Photosynthetically active radiation (PAR) (400 to 700 nm) at the top of the plants, was kept at a photosynthetic photon flux density (PPFD) of ≈112 μmol·m⁻²·s⁻¹, using high-pressure metal halide lamps (HPI-T 400W, Philips). In Expt. 3, plants were forced in a greenhouse at CPRO–DLO during spring 1992 (March–May) using natural light conditions and minimum day/night temperatures of ≈18/14 °C.

HARVESTING CONDITIONS. Inflorescences were harvested at anthesis of the most mature floral bud by cutting the stems at soil level. This occurred within 4 h after the onset of the light period

(Expts. 1 and 2) or from 0800 to 1100 HR (Expt. 3). The harvest dates of the genotypes fell within the period of 6 weeks. The data recorded were 1) the number of flower buds, 2) stem weight, 3) stem length (the distance between the cut stem base and the pedicel base of the basal flower bud), and 4) inflorescence length (the distance between the pedicel base of the basal and apical flower bud). The leaves on the basal 15 cm were removed and individual inflorescences were placed in 1-L glass flasks containing ≈500 mL tap water.

POSTHARVEST CONDITIONS. Cut inflorescences were held at a constant air temperature of 17 °C, 60% RH, and a 12-h photoperiod. PAR (400 to 700 nm) at the top of the inflorescences was kept at a PPFD of ≈14 μmol·m⁻²·s⁻¹ using fluorescent lamps (TL-D84 36W, Philips). Each individual flower was observed daily and within 4 to 6 h after the onset of the photoperiod. Flower longevity was recorded as the time between bud anthesis and deformation of the flower, the visual withering of the petals. Individual flower longevity, calculated as the mean flower longevity per stem, was used as a parameter for screening (Van der Meulen-Muisers and Van Oeveren, 1996).

INDIRECT SELECTION. To examine the suitability of other plant characteristics for indirect selection on individual flower longevity, bulb weight at the planting time, stem length, inflorescence length, stem weight and the number of buds at harvest, and the number of flowers were used. Forcing period (the time between planting and harvest), inflorescence longevity (the time between anthesis of the first floral bud and deformation of the last flower), and the percentage of floral buds that reached anthesis were also examined for their suitability for indirect selection.

STATISTICS. Experiments consisted of three blocks with three plants of each genotype per block. For practical reasons, the genotypes evaluated in 1991 (Expt. 1) were divided into two groups that were planted 11 weeks apart. Both groups contained the genotypes 'Orange Aristo', 'Connecticut King', 'Enchantment', 'Harmony', 'Monte Rosa', and 'Orlito', which were used as controls to determine the influence of the planting date on flower longevity. In 1992, bulbs were planted with a time interval of 11 weeks between both experiments (Expts. 2 and 3).

Data were analyzed by analysis of variance, and variance components were estimated using the Genstat 5 statistical package (Rothamsted, U.K.). Ratios of genotypic variance and phenotypic variance were calculated to measure the degree of genotypic determination (R^2). Predicted estimates of R^2 were obtained to determine the accuracy gained by repetition of measurements. The degree of genotypic determination was calculated as $R^2 = s_g^2 / (s_g^2 + s_e^2)$, where s_g^2 and s_e^2 denote genotypic variance and environmental variance, respectively. Environmental variances were calculated as $s_e^2 = (s_i^2 + (s_i^2/n_i)) / n_i$, with s_i^2 denoting the variance between inflorescences, s_i^2 denoting the variance between flowers within inflorescences, n_i being the number of flowers, and n_i the number of inflorescences.

To compare the ranking of the genotypes between experiments, correlation coefficients (r) were calculated. To examine the suitability of other plant characteristics for indirect selection on individual flower longevity, regression coefficients were calculated and multiple regression was carried out.

Results

GENOTYPIC VARIATION. The analysis of variance gave highly significant differences ($P < 0.001$) between genotypes in all experiments. Effects of blocks and interactions between genotypes and blocks were also significant but small compared to genotypic effects.

Table 1. Individual flower longevity (days) of Asiatic hybrid lilies after growth chamber forcing in 1991 (Expt. 1) and 1992 (Expt. 2) and after greenhouse forcing in March–May in 1992 (Expt. 3), using standardized harvest and postharvest conditions; $n = 9$ inflorescences. Genotypes are sorted toward increasing flower longevity (Expt. 2).

Genotype	Flower longevity		
	Expt. 1	Expt. 2	Expt. 3
Red Night	5.2	4.0	5.0
Prominence	5.3	4.9	5.3
Corina	5.8	4.9	5.3
Bright Beauty	5.2	5.0	6.1
Harmony	4.9	5.1	5.0
Ladykiller	5.6	5.2	6.1
Sirocco	5.6	5.3	5.1
Enchantment	5.6	5.3	6.0
Sterling Star	4.8	5.6	6.6
Lavender Dream	5.8	5.6	5.9
Whilite	6.2	5.8	6.7
Yellow Blaze	6.0	5.8	7.0
Jolanda	7.0	5.8	7.0
Apeldoorn	6.0	6.0	6.7
Monte Negro	6.3	6.1	7.0
Concorde	6.9	6.2	6.4
Pollyanna	6.2	6.3	8.3
Roma	6.4	6.3	9.2
Dreamland	6.5	6.4	7.4
Figaro	5.5	6.6	7.1
Montreux	5.6	6.6	7.4
Mona	6.2	6.6	8.0
Sarina	6.7	6.6	8.1
Eurovision	6.4	6.7	7.0
Orange Mountain	6.9	6.8	7.0
Adelina	7.2	7.0	7.8
Sahara	5.6	7.1	6.8
Orange Aristo	6.9	7.1	7.4
Napoli	7.0	7.2	8.1
Connecticut King	7.4	7.4	9.1
Bora	7.8	7.4	7.7
Fair	8.1	7.4	8.9
Crescendo	---	7.6	8.9
Revival	8.6	7.6	9.1
Orlito	6.7	7.7	7.3
Gran Sasso	7.9	7.7	8.3
Pirate	6.9	7.9	7.0
Snowstar	7.5	7.9	8.7
Yellito	8.2	7.9	9.8
Mont Blanc	7.5	8.0	8.4
Monte Rosa	7.3	8.2	8.2
Bicolito	6.8	8.3	9.0
Fashion	7.6	8.3	8.4
Corsica	8.8	8.4	11.0
Crete	7.9	8.5	9.9
Fuego	8.2	8.7	9.7
Commodore	7.9	8.9	9.1
Sylvester	6.6	---	---
Ballade	8.4	---	---
Rolito	8.8	---	---
Compass (3n)	7.4	---	---
Gran Paradiso (4n)	6.0	---	---
Tetra Aristo (4n)	6.3	---	---
CPRO-85774.2 (4n)	6.3	---	---
CPRO-85702.5 (4n)	6.4	---	---
Tetra Orlito (4n)	6.8	---	---
CPRO-82297.2 (4n)	7.1	---	---
Avignon (4n)	7.2	---	---
Tetra Bicolito(4n)	7.6	---	---
CPRO-85598.2 (4n)	8.6	---	---
CPRO-85710.2 (4n)	9.2	---	---
CPRO-77643.6 <i>L. concolor</i>	7.1	---	---
CPRO-73139 <i>L. dauricum</i>	7.5	---	---
Mean	6.7	6.8	7.6
SED [†]	0.26	0.26	0.27
n_f^*	6.9	7.8	8.9
R^{2w}	0.97	0.98	0.98

[‡]Missing values.

[†]Standard error of differences between genotype means.

^{*}Mean number of flowers per inflorescence.

^wDegree of genotypic determination (genotypic variation/phenotypic variation).

Fig. 1. Relation between the degree of genotypic determination (genotypic variation/phenotypic variation), the number of inflorescences (n) and the number of flowers per inflorescence in Asiatic hybrid lilies.

When forced under standardized conditions in a growth chamber, variation in longevity levels among genotypes ranged from 4.8 to 9.2 d per individual flower in Expt. 1 and from 4.0 to 8.9 d in Expt. 2. After being forced in a greenhouse during spring (Expt. 3), longevity levels ranged from 5.0 to 11.0 d per flower (Table 1). In Expt. 1, longevity values of the six genotypes used as controls did not significantly differ between the two planting dates (data not shown). Thus, longevity data of genotypes from different planting dates were considered comparable. Of the 63 genotypes, 46 were evaluated in all three experiments (Table 1). In Expt. 1, longevity data of 'Crescendo' were discarded from the analyses. The quality of the inflorescences was poor, since flowering was strongly reduced by bud abortion.

When forced in a greenhouse (Expt. 3), open flowers at harvest differed in their longevity between inflorescences of the same genotype depending on the date of harvest (anthesis of the most mature floral bud). Differences could be due to different temperatures from anthesis to harvest between dates. Therefore, in Expt. 3 open flowers at the time of harvest were excluded from the analysis.

In all three experiments, >90% of the floral buds reached anthesis except for 'Bright Beauty', 'Harmony', 'Montreux', and 'Sahara'. They had an average flowering percentage ranging from 67% ('Harmony') to 89% ('Bright Beauty'). In general, the percentage of floral buds that reached anthesis and flower size were improved by greenhouse forcing compared to growth chamber forcing.

Comparisons of diploid and tetraploid genotypes (Expt. 1) showed no specific influence of ploidy level on the level of flower longevity (Table 1). Between the diploid genotypes 'Bicolito', 'Orange Aristo', 'Orlito' and their corresponding mitotic tetraploid genotypes 'Tetra Bicolito', 'Tetra Aristo', and 'Tetra Orlito',

differences in longevity level did not exceed 0.8 d, either in favor of the diploid genotype in the case of 'Orange Aristo' or the tetraploid genotype in the case of 'Bicolito'. The two species *L. concolor* Salisb. and *L. dauricum* Ker-Gawl. tested in Expt. 1 showed only an average longevity compared to the cultivars and seedling clones tested (Table 1). Because of their moderate longevity, those species and polyploid genotypes were excluded from the second year experiments.

DEGREE OF GENOTYPIC DETERMINATION. The s^2_e estimates were small compared to s^2_g . This resulted in large R^2 estimates for flower longevity in all three experiments (Table 1).

Predicted estimates of R^2 were calculated for 1, 2, 4, 6, 8, and 9 inflorescences per genotype in combination with 1, 2, 4, 6, and 8 flowers per inflorescence using the mean genotypic variance ($s^2_g = 1.42$) and the mean environmental variances ($s^2_i = 0.20$, $s^2_f = 0.58$) over the three experiments (Fig. 1). Increasing the number of measurements per genotype reduced the amount of environmental variance that contributed to the total phenotypic variance, which improved the degree of genotypic determination. Increasing the number of inflorescences per genotype appeared to be more effective in reducing environmental variance than increasing the number of flowers per inflorescence. The degree of genotypic determination based on a single measurement per genotype was moderately high ($R^2 = 0.64$).

RELIABILITY OF TEST CONDITIONS. High correlations ($r = 0.83$) were found between longevity values of 46 diploid cultivars tested in 2 successive years after forcing under controlled conditions in a growth chamber (Fig. 2). The average longevity levels of 47 diploid cultivars forced under standardized conditions in a growth chamber was improved by ≈ 1 d when forced in a greenhouse during spring in the same year (Fig. 3). High correlations ($r = 0.84$) were found between longevity values of those 47 diploid cultivars comparing different forcing conditions, although some deviating genotypes ('Corsica', 'Pirate', and 'Roma') were present (Table 1).

INDIRECT SELECTION. Only small correlation coefficients up to $r = 0.42$ were found between flower longevity and other plant characteristics studied (data not shown). Bulb mass, stem length, stem mass, inflorescence longevity, and forcing period had little association with individual flower longevity. Significant, but

Fig. 2. Correlation between longevity levels (days) of individual flowers of 46 lily genotypes evaluated in 1991 and 1992 using standardized forcing, harvest and postharvest conditions; $r = 0.83$.

Fig. 3. Correlation between longevity levels (days) of individual flowers of 47 lily genotypes either forced in a growth chamber using standardized conditions or in a greenhouse during spring. Standardized harvest and postharvest conditions were used; $r = 0.84$.

small associations of number of floral buds and flowers per inflorescence and percentage of floral buds that reached anthesis with individual flower longevity were detected in all three experiments (Table 2). These three plant characteristics accounted for only 15% to 21% of the total variance in individual flower longevity using multiple regression. The strongest association with flower longevity was found for the number of floral buds. An increase of one additional bud per inflorescence led to a decrease in the average longevity of ≈ 0.2 d in all three experiments (Table 2).

Discussion

GENOTYPIC VARIATION. The genotypic variation in flower longevity (Table 1), in combination with a large R^2 for this characteristic indicates that flower longevity in Asiatic hybrid lilies can be improved by breeding and selection. Knowledge of this variation and reliable test conditions are beneficial to breeding programs directed on the improvement of lily flower longevity.

Comparisons of diploid and tetraploid cultivars showed no influence of ploidy level on the level of flower longevity. Chromosome doubling (polyploidy) is known to be effective in the improvement of quality characteristics in lily, such as flower size and morphology and stem firmness (Schenk, 1987; Van Tuyl, 1989), and in the improvement of flower longevity in *Tulipa* (Van Eijk and Eikelboom, 1986). The polyploid genotypes evaluated (Table 1) did not provide an additional genetic source for the improvement of flower longevity in lily.

DEGREE OF GENOTYPIC DETERMINATION. Quantitative traits, such as flower longevity, are expected to be influenced by environmental effects to a large extent. Our environmental variances, however, accounted for only 3% (Expt. 1) or 2% (Expts. 2 and 3) of the total variance in this study. While the controlled environment in the growth chamber can explain the low estimates of environmental variance in Expts. 1 and 2, we also found a low estimate of environmental variance in the greenhouse experiment (Expt. 3). Although environmental variances increased, when the number of measurements per genotype decreased, the estimation of the degree of genotypic determination was moderately high only when

one flower per genotype was used in the analysis (Fig. 1). These results suggest that flower longevity is controlled to a large extent by genetic effects.

From the predicted estimates of R^2 (Fig. 1), it could be concluded that the gain in accuracy for determining longevity levels of genotypes by their phenotypes was all the higher when the number of inflorescences used for evaluation was increased, rather than by increasing the number of flowers per inflorescence. However, the production of a large number of flowering bulbs per genotype involves vegetative propagation followed by cultivation over at least 2 years (Beattie and White, 1993). In breeding trials it would be preferable to carry out initial selection at the individual plant level to speed up the breeding progress. Since the estimation of R^2 based on a single measurement per genotype was moderately high ($R^2 = 0.64$), selection based on one plant per genotype is possible. In the case of selection at individual plant level, it would be advisable to evaluate as many flowers as possible to get a maximal reduction of the environmental variance.

RELIABILITY OF TEST CONDITIONS. Replications carried out under controlled forcing conditions in 2 successive years had similar results, indicating that test results were reproducible under standardized conditions. Some variation between the replicates was, however, detected. This could be due to differences in bulb age or bulb quality. Differences due to bulb age were small for the six cultivars used as replications in time (Expt. 1). Bulbs of the same genotype used in different years originated from different bulb growers and could, therefore, be of different quality (Van der Boon and Niers, 1986). Although bulb origin has been reported to be only a minor source of nongenotypic variation in individual flower longevity of Asiatic hybrid lilies, differences up to 1 d within a genotype have been found (Van der Meulen-Muisers and Van Oeveren, 1997). This could account for part of the variation between the different years (Expts. 1 and 2).

Although flower longevity generally increased after greenhouse forcing in spring, compared to growth-chamber forcing under standardized conditions, longevity data of experiments carried out under different forcing conditions were highly correlated. Therefore, the ranking of the genotypes based on their longevity values is reliable even after greenhouse forcing. Some deviations, however, were detected. Variation between experiments due to quality and age of the bulbs was unlikely. Bulbs used in both 1992 experiments originated from the same bulb grower per genotype and the 11 weeks difference in planting dates produced no significant differences in longevity as stated before

Table 2. Regression coefficients and corresponding standard errors (SE) for the relationship between changes in individual flower longevity (days) per additional floral bud, per additional open flower, and per additional percent of floral buds that reached anthesis of Asiatic hybrid lilies. Lilies were forced in a growth chamber in 1991 (Expt. 1) and 1992 (Expt. 2) and in a greenhouse in 1992 (Expt. 3) using standardized harvest and postharvest conditions.

Plant characteristic	Expt. 1	Expt. 2	Expt. 3
Floral bud	-0.177**	-0.228**	-0.193*
SE	0.054	0.073	0.076
Open flower	-0.165**	-0.192*	-0.162*
SE	0.059	0.081	0.081
Anthesis (%)	0.088**	0.071**	0.087*
SE	0.030	0.025	0.036
Degrees of freedom	60	45	45

* ** Significant at $P = 0.05$ and 0.01 , respectively.

(Expt. 1). Therefore, deviations between Expts. 2 and 3 were probably due to differences in genotype response to varying forcing conditions.

The controlled conditions used as a standard for forcing were generally suboptimal for flower longevity. Longevity increased with ≈ 1 d on average after greenhouse forcing in spring, the optimal season for forcing of Asiatic hybrids in The Netherlands (Fig. 3). In practice, screening and selection will probably take place after forcing under nonstandardized conditions. To make sure results are comparable year-round, some cultivars might be used as a control to correct for general seasonal effects. It should be taken into account that specific genotype $\times$ environment interactions can occur. Thus, selections must be tested for year-round performance using a range of forcing environments. Due to time differences in flowering dates, the condition of open flowers at the time of harvest could be influenced by temperature fluctuations during forcing under greenhouse conditions. Such fluctuations are likely to account for longevity differences between open flowers at the time of harvest in Expt. 3. It is known (Van der Meulen-Muisers and Van Oeveren, 1997) that lily flower life is highly influenced by temperature after anthesis. In practice, evaluation of lily flower longevity should be carried out using controlled post-harvest conditions. Also, open flowers at the time of harvest should be excluded from the analyses. This will avoid large environmental variances within inflorescences due to temperature fluctuations before harvest. Discarding one or a few flowers per stem will not influence the accuracy of the longevity level determined per genotype (Fig. 1).

INDIRECT SELECTION. Since only small correlation coefficients between plant characters and flower life were detected, none seemed suitable for indirect selection on flower longevity. The small effects found could be due to the influence of bulb mass on other plant characters (Van der Meulen-Muisers and Van Oeveren, 1996). However, only a relatively small variation in bulb mass was introduced because of the limited range of bulb sizes used. Another explanation could lie in the cultivars used in our experiments. Within cultivars, many traits are combined which were selected to obtain the desired lily. This preselection could disturb the natural correlation between flower longevity and other plant characteristics. Useful associations are more likely to appear when seedling populations are used.

Because of the relatively narrow range of bulb sizes used, the number of floral buds did not vary per genotype, and differences in number of buds between genotypes could be ascribed to genetic

differences in the ability to produce buds. Within genotypes, no significant influence of number of flower buds on individual flower longevity has been found (Van der Meulen-Muisers and Van Oeveren, 1996). In the present study, an increase in number of flower buds between genotypes caused a small but significant reduction in the individual flower longevity independently of the forcing conditions used. These results indicate that two desirable characteristics—the potential for the formation of a large number of floral buds per inflorescence and a long individual flower longevity—are negatively correlated.

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