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Genetic analysis of postharvest flower longevity in Asiatic hybrid lilies

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Summary

To investigate the genetic regulation of postharvest flower longevity in Asiatic hybrid lilies (*Lilium* L.), 10 cultivars and 45 progenies were forced, harvested and evaluated under standardised conditions in growth chambers. Analysis of variance for individual flower longevity indicated highly significant ($p < 0.001$) variation among parents, among progenies and among descendants within progenies. High broad-sense heritability (0.79) calculated at the individual plant level indicated that selection for long individual flower longevity can be expected to be very effective. General combining ability (GCA) effects were highly significant ($p < 0.001$), and the estimated narrow-sense heritability was high (0.74). Therefore, individual flower longevity of a genotype can be used as an indication for its breeding value. Although deviating results can be expected as specific combining ability (SCA) effects were also significant ($p = 0.046$). Small, but significant correlations between individual flower longevity and other plant characters were found. The impact of these correlations on the selection efficiency for improved postharvest performance of lily inflorescences is discussed.

Introduction

In the Netherlands *Lilium* is economically the second bulb-flower crop after *Tulipa* for cut flower production. In 1996 about 36 percent of the turnover of the lily cut flowers at the Dutch auctions is accounted for by the Asiatic hybrids, which have been developed from interspecific hybridisation within the *Sinomartagon* section, one of the seven sections of the genus *Lilium* (Van Creij et al., 1993).

Postharvest treatments with silver thiosulphate (STS) are commonly used to enhance the vase life of Asiatic hybrid lilies (e.g., Nowak & Mynett, 1985; Swart, 1980) but the extent to which these treatments can improve flower longevity is limited and is dependent on the genotype. Developing cultivars with genetically improved postharvest longevity may provide the consumer with a more reliable expectation for postharvest quality. Therefore, research to evaluate the potential of plant breeding as a method for genetically improving longevity in lily is important.

Postharvest inflorescence longevity of lilies is complex because it is a function of the number of buds per inflorescence, of the expansion and opening of the buds and of the life-span of the individual flowers. Large environmental variances due to forcing conditions, harvest stage and postharvest conditions can be expected (Halevy & Mayak, 1979; Swart, 1980). By using standardised conditions for screening as developed by Van der Meulen-Muisers & Van Oeveren (1997), that variation is strongly reduced.

Individual flower longevity has been found to be a stable parameter for screening (Van der Meulen-Muisers & Van Oeveren, 1996). Improving individual flower longevity would give the potential for an increment of the number of flowering buds at the same time, it would extend the longevity of the whole inflorescence and, therefore, improve the postharvest performance of the inflorescence. Knowledge about the inheritance of individual flower longevity is a prerequisite for the successful use of this trait as a selection criterion.

Genotypic variation in individual flower longevity has been found to be present (Van der Meulen-Muisers et al., 1998). When using standardised conditions during forcing, harvest and postharvest evaluation, the potential life of individual flowers on an inflorescence placed in water is about 4 to 9 days depending on the genotype. Individual flower longevity has been reported to have a high broad-sense heritability which should ensure effective selection in this vegetatively propagated crop (Van der Meulen-Muisers et al., 1998). Information on its narrow-sense heritability is lacking and the main objective of this study was to learn more about the inheritance of individual flower longevity.

Other important characters of lily postharvest performance are the number of buds per inflorescence and the percentage of flowering buds. Only small phenotypic associations between individual flower longevity and those two characters have been found (Van der Meulen-Muisers et al., 1998). However, that study was based on observations of vegetatively propagated material, mainly commercially grown cultivars. In the study reported here, unselected seedling progenies were screened to determine if there are favourable associations between individual flower longevity and other desirable plant characters. Such associations can lead to an improvement in selection efficiency for postharvest performance in Asiatic hybrid lilies.

Initial studies to improve lily flower longevity by cross breeding suggested an indirect linkage between the occurrence of male sterility and the improvement of flower longevity (Van der Meulen-Muisers et al., 1995a). Such an association could possibly be mediated by the absence of an ethylene peak which seems to occur in male fertile flowers at the end of the pollen meiosis as discussed by Van Tuyl et al. (1985). In the present study the association between male sterility and flower longevity was investigated in more detail.

Materials and methods

Plant material

In spring 1992, crosses were made using 10 Asiatic hybrid lilies (*Lilium* L.) (Table 1). Parents were chosen on the basis of differences in individual flower longevity. The parental combinations which gave the progenies were largely dictated by practical conditions; 'Yellito' could mainly be used as a female parent, 'Revival' could mainly be used as a male parent and, most important, some crosses gave few or no seed. Nevertheless, the progenies which were studied can reasonably be considered as a representative sample with regard to the individual flower longevity character. In December 1992, seeds of 45 populations (Table 1), including 12 pairs of progenies from reciprocal crosses, were sown in flat trays with peat. For each population, 125–250 seeds were used. Trays were placed in a greenhouse at $\pm$ 17/15°C (16h day/8h night). At the same time commercial bulbs of the 10 parents were vegetatively propagated by scaling. Scales were placed in perforated plastic bags with moist vermiculite at 26°C for 8 weeks to induce scale bulblets. This was followed by 4 weeks at 17°C and 8 weeks at 5°C. In May 1993, scale bulblets and seedling bulblets were planted simultaneously outdoors, using aphid-free facilities to prevent virus spread. Progenies and parental bulblets were cultivated for 2 years to obtain adult bulbs with the potential to flower. Bulbs harvested in autumn 1994 were rated and disinfected in captan (Captan Flow; 1.0%) and prochloraz (Sportak; 0.2%). Bulbs were stored at –2°C in plastic bags with moist peat for about 4 months until planted. To ensure flowering only bulbs $\geq$ 12 cm in circumference were used.

Experimental conditions

Cultivars and progenies were forced, harvested and evaluated for individual flower longevity utilising standardised conditions outlined by Van der Meulen-Muisers & Van Oeveren (1997). Plants were forced in a growth chamber at 17°C, 60% relative humidity (RH), 112 μmol.m^{-2}.s^{-1} using high pressure metal halide lamps (HPI-T 400W, Philips) during 16-h per day. Inflorescences were harvested at anthesis of the most mature floral bud. Cut inflorescences were placed in tap water without additives in a climate room at 17°C, 60% RH, 14 μmol.m^{-2}.s^{-1} using fluorescent lamps (TL-D84 36W, Philips) during 12-h per day.

Flower longevity

Individual flower longevity was defined as the time between bud anthesis and visual wilting (start of deformation) of the flower. Plant means were determined from data collected on all flowers evaluated per plant. Evaluation of flower longevity was carried out at the clonal level for the parental genotypes. Progeny means were determined for each cross from individual plant means.

Table 1. Parentage of 45 progenies studied from crosses between ten Asiatic hybrid lily cultivars. Parental cultivars are arranged in decreasing order of individual flower longevity as determined in the experiment (Table 2).

Cultivar ♀/♂	FA	YE	RE	OR	CO	MO	HA	PR	BR	ST
Fashion (FA)		*	*	*		*	*			
Yellito (YE)						*	*	*	*	*
Revival (RE)				*			*			
Orlito (OR)	*					*			*	*
Montreux (MO)		*		*			*	*		
Connecticut King (CO)	*					*		*	*	*
Harmony (HA)			*	*		*		*		
Prominence (PR)	*		*	*	*		*			
Bright Beauty (BR)	*		*	*	*		*			*
Sterling Star (ST)	*	*	*		*				*	

Indirect selection

To examine the suitability of other plant characters for indirect selection on individual flower longevity, bulb weight at planting time, inflorescence length, stem weight, tepal length at anthesis, number of buds and number of flowers were determined. The 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), percentage of floral buds that reached anthesis, and male sterility were also examined for their suitability for indirect selection. Male sterility (the complete absence of pollen production) was scored as present or absent.

Experimental design and statistics

Twenty-one descendants per cross and 24 inflorescences per parental clone were tested in 1995. They were forced in 3 blocks planted 3 weeks apart. Data were analysed by analysis of variance using the Genstat 5 Statistical Package (Rothamsted, U.K.). General combining ability (GCA) effects, specific combining ability (SCA) effects and reciprocal effects were calculated. Conclusions concerning GCA, SCA and reciprocal effects were assessed by analysis of variance.

Broad sense heritability (coefficient of genotypic determination) of individual flower longevity was estimated per progeny and as a composite estimate calculated over 45 progenies. In addition, broad sense heritability of the parental clones was estimated (based on a single plant level). Broad sense heritability (H^2) estimates were calculated from estimated variance components as $H^2 = s_g^2/(s_g^2 + s_e^2/n)$, where s_g^2 denotes genotypic variance, s_e^2 denotes environmental variance (determined on the basis of variation between replicate plots of vegetatively propagated parental cultivars), and n is the number of plants per genotype. All calculations were carried out for n = 1. The heritability in narrow-sense (h^2), as an estimation of the part of the phenotypic variance resulting from additive gene effects, was calculated as the regression coefficient of the offspring on mid-parent.

Correlation coefficients (r) were calculated between parents and offspring. To examine the suitability of other plant characters for indirect selection on individual flower longevity phenotypic correlation coefficients (r_p) based on progeny means and genetic correlation coefficients (r_g) based on parental GCA were calculated and multiple regression was carried out.

Results

Within the parental clones 3 significantly different groups were distinguished with a long (L), moderate (M) and short (S) individual flower longevity respectively (Table 2). Broad-sense heritability (H^2) for individual flower longevity of the parents was estimated to be 0.88 based on a single plant level.

The analysis of variance showed highly significant differences ($p < 0.001$) in individual flower longevity among crosses and among plants within crosses. Individual flower longevity did not segregate into discrete classes within the progenies. Transgressive segrega-

Table 2. Longevity levels of the ten parental clones (L = long, M = moderate, S = short), clonal flower longevity given as deviation from the grand mean across the ten parental clones, and parental GCA estimates given as deviation from the grand mean across the ten parents; parents are arranged in the order of decreasing flower longevity.

Cultivar	Longevity level	Flower longevity	GCA
Fashion	L	1.8	0.5
Yellito	L	1.6	0.7
Revival	L	1.2	0.5
Orlito	L	1.0	0.5
Montreux	M	0.2	0.1
Connecticut King	M	0.1	0.0
Harmony	S	–1.2	–0.6
Prominence	S	–1.4	–0.7
Bright Beauty	S	–1.5	–0.5
Sterling Star	S	–1.8	–0.5
Grand mean		6.0	5.7
SED[z]		0.17	0.14

[z] standard error of differences between parental means.

tion for long individual flower longevity occurred in all progenies except for MO × PR (data not shown).

In Figure 1 the mean longevity values of the parents per cross (mid-parent values) were plotted against the longevity levels of the progenies. In general, longevity levels of the progenies increased with an increase of the longevity levels of their parents (r = 0.87). All progenies obtained from two parents with a long (L) flower longevity had a longer flower life than progenies obtained from one L parent and one parent with a short (S) flower longevity, and the latter progenies had a longer flower life than progenies obtained from two S parents (Figure 1).

The composite broad-sense heritability for individual flower longevity was estimated to be 0.79 (coefficient of genetic variance based on progenies was 1.08, and coefficient of environmental variance calculated from parental clones was 0.29). In separate analyses, broad-sense heritabilities were calculated for each progeny. Broad-sense heritabilities appeared to be little influenced by the degree of similarity of the parents. Estimated heritabilities ranged from 0.31 to 0.89, reflecting varying levels of genetic variance within the individual progenies (Figure 2). The values obtained were mainly in the intermediate to high range although two deviating progenies (ST × BR, PR × HA) with relatively low heritabilities were present (Figure 2).

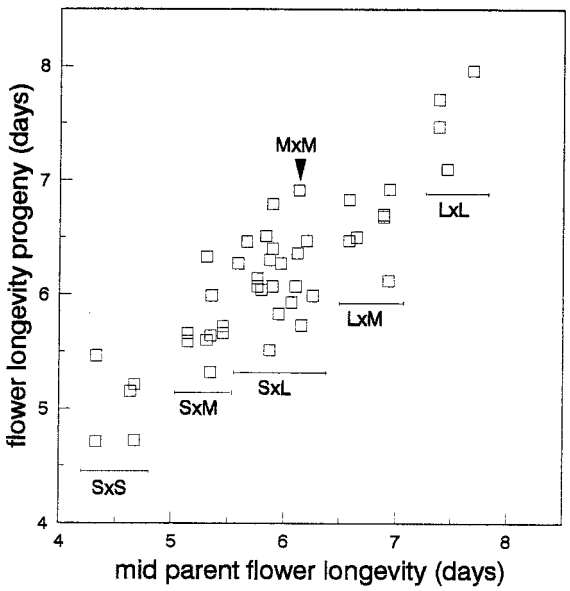

Figure 1. Association between longevity values obtained after testing 45 Asiatic hybrid lily progenies and their corresponding mid-parent longevities (r = 0.87). The six different longevity cross combinations are given. Longevity levels: L = long, M = moderate, and S = short.

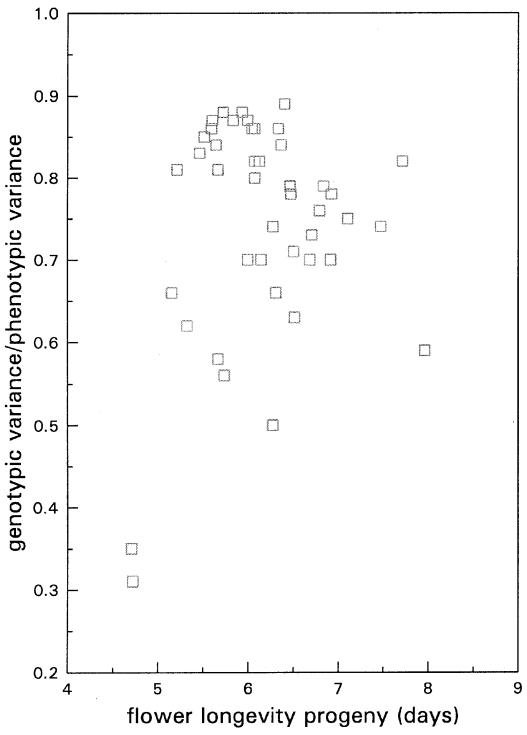

Figure 2. Association between longevity values obtained after testing 45 Asiatic hybrid lily progenies and their corresponding broad-sense heritabilities (genotypic variance/phenotypic variance).

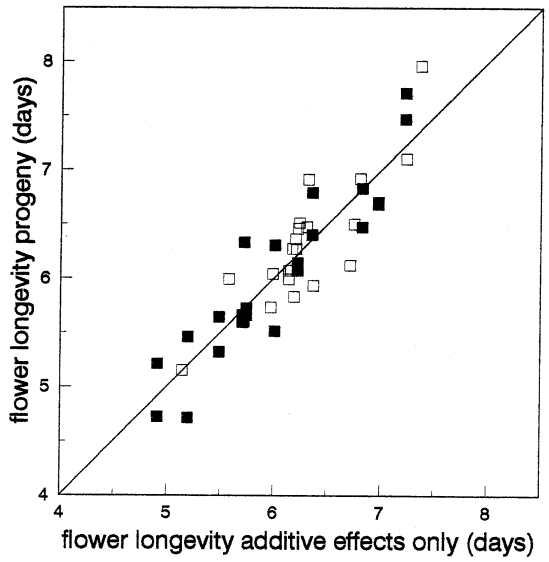

Figure 3. Association between longevity values obtained after testing 45 Asiatic hybrid lily progenies and the longevity values calculated with only additive (GCA) effects ($r = 0.90$). Vertical distances between each point and the given line x = y represent variances from additivity. Solid squares indicate reciprocal crosses.

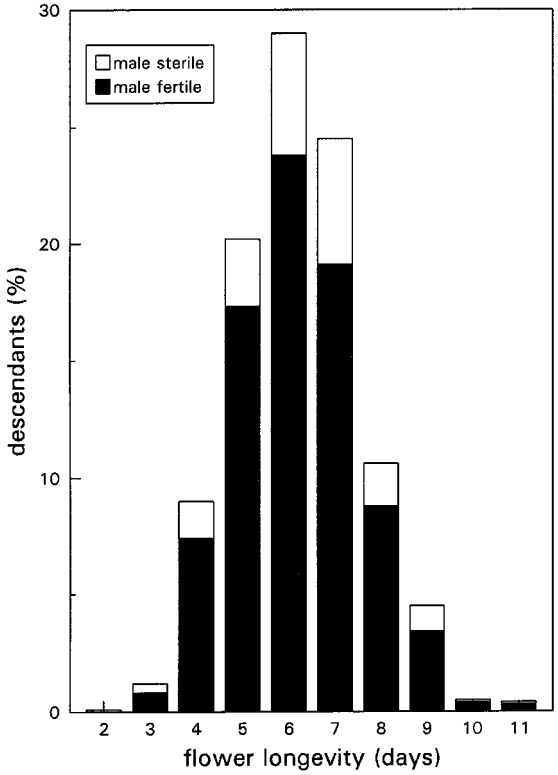

Figure 4. Segregation of individual flower longevity of male sterile and male fertile inflorescences within the descendants of 45 lily progenies evaluated at individual plant level.

Analysis of variance showed GCA effects to be highly significant ($p < 0.001$), 81% of the variation in individual flower longevity between progeny means could be attributed to parental effect. However, the effects of specific combining ability (SCA), although of smaller importance, were also significant ($p = 0.046$); whereas reciprocal effects were not significant ($p = 0.161$). Breeding values (GCA) of the parental clones are presented in Table 2. Longevity values and breeding values were highly correlated ($r = 0.98$).

Narrow-sense heritability for individual flower longevity was estimated to be 0.74, indicating a marked influence of additive genetic variance. In Figure 3 the longevity values of the progenies were plotted against the longevity value per progeny calculated with GCA effects only. Vertical distances between each point and the line x = y represent deviations from additivity. Although some deviations from the additive model were significant, the additive model explained almost all variation between crosses.

Longevity values of the descendants evaluated at individual plant level ranged from 2.0 to 10.8 days (Figure 4). Overall 11 percent of the seedlings had an improved longevity (better than 'Fashion' i.e., > 7.8 days, Table 2). Most of the descendants with an improved individual flower longevity were obtained in the L × L cross combinations, while in S × S combinations although descendants with a long (L) flower longevity were observed (between the longevity level of 'Orlito' and 'Fashion' i.e., 7.0 to 7.8 days, Table 2), no descendants with an improved flower longevity (> 7.8 days) were found (Figure 5).

In 33 of the progenies tested, male sterility occurred corresponding with 23% of all descendants tested. Many of the male sterile plants occurred in offsprings from four female cultivars: 'Bright Beauty', 'Connecticut King', 'Harmony', 'Yellito', whereas the breeding value for the occurrence of male sterility of those cultivars was considerably less when used as a male parent (data not shown).

A large segregation in flower longevity of male sterile descendants existed (Figure 4). In 21 populations the average individual flower longevity of the male sterile plants exceeded the average individual flower longevity of the male fertile plants of the same population. Overall, male sterile descendants and male fertile descendants did not significantly differ for individual flower longevity; whereas the tepal length at anthesis, the percentage of flowers that reached an-

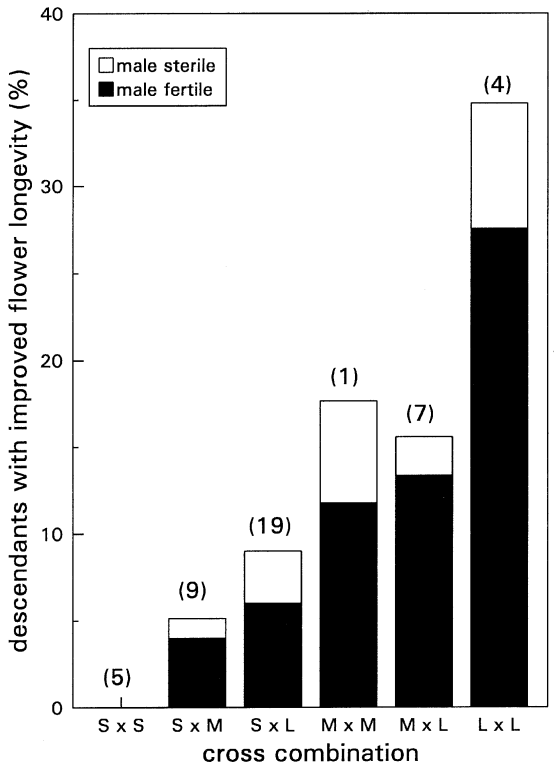

Figure 5. Distribution of improved longevity levels (better than 'Fashion', i.e., > 7.8 days, Table 2) of both male sterile and male fertile descendants between six different longevity cross combinations. Longevity levels: L = long, M = moderate, and S = short; number of crosses per cross combination in parentheses.

thesis, the stem weight, and the number of buds per stem within male sterile descendants were significantly ($p < 0.05$) reduced compared to male fertile descendants (data not shown).

Within the male sterile descendants roughly two plant types could be identified. The first plant type was mainly comparable with the male fertile plants, except for the production of pollen; whereas the second plant type showed more or less phenotypic aberrations (e.g., reduced plant weight, relatively small flowers, deviating flower shape), which did not occur in the male fertile plants. Within the latter plant type flower longevity tended to be reduced compared to flower longevity of inflorescences of the first plant type and compared to the longevity of male fertile flowers of the same population.

Significant but small phenotypic associations were found between progeny means of individual flower longevity and inflorescence longevity, forcing time, percentage of floral buds that reached anthesis and number of floral buds (Table 3). Inflorescence longevity, forcing time and number of floral buds accounted for about 64 percent of the total variance in individual flower longevity using multiple regression. Because percentage of floral buds that reached anthesis was correlated with inflorescence longevity ($r = 0.50$) the former was excluded from the multiple regression calculation. Except for number of floral buds all correlation coefficients were positive. Overall tepal length at anthesis, stem weight, bulb weight and number of flowers had little association with individual flower longevity. Genetic associations based on parental GCA values appeared to be comparable with their corresponding phenotypic associations. However, only the genetic association between individual flower longevity and inflorescence longevity was significant (Table 3).

Among progeny means based on male sterile plants only, significant positive phenotypic correlation coefficients (r_p) were found between flower longevity and inflorescence longevity, forcing time, tepal length at anthesis and stem weight (Table 3). Among overall progeny means (both male sterile and fertile plants) no significant associations between flower longevity and stem weight and between flower longevity and tepal length at anthesis were found (Table 3).

Discussion

The high value ($H^2 = 0.79$) for the broad-sense heritability of individual flower longevity, based on 45 progenies at individual plant level, confirms earlier estimations based on clonal material (Van der Meulen-Muisers et al., 1998). Phenotypic selection for long individual flower longevity in trials with one representative plant of each genotype ought, in consequence, to be very effective (Aikman & Langton, 1983).

The correspondence between the breeding value of the parents with their phenotypic performance as a clone was very close despite physiological differences in bulb material (seedling bulbs versus scale propagated bulbs). These results confirm earlier work comparing longevity data obtained from an individual plant test (seedling bulbs) with a clonal test (scale propagated bulbs) of the same progeny (Van der Meulen-Muisers et al., 1995a). This suggests an equal expression of flower longevity in inflorescences obtained from seedling bulbs and in inflorescences obtained from scale propagated bulbs. Therefore, initial

Table 3. Phenotypic correlation coefficients (r_p) based on overall progeny means and genetic correlation coefficients (r_g) based on GCA of associations between individual flower longevity and six other plant characters. In addition r_p based on progeny means calculated for sterile descendants only.

Character	Individual flower longevity (d)		
	Overall progeny means		Sterile descendants only
	r_p	r_g	r_p
Inflorescence longevity (d)	+0.62**	+0.81**	+0.62*
Forcing time (d)	+0.54**	+0.53	+0.34*
Flowering buds (%)	+0.31*	+0.61	+0.26
Number of floral buds	–0.29*	–0.38	–0.00
Tepal length at anthesis (mm)	+0.25	+0.41	+0.55**
Stem weight (g)	+0.23	+0.30	+0.45**
df	43	8	31

*, ** significant at 5 and 1 percent level, respectively.

selection for improved flower longevity can be carried out using seedling bulbs.

Knowledge of the way in which individual flower longevity is sexually inherited is important to the breeder. Individual progeny H^2 estimations show that similarities between parents in individual flower longevity do not necessarily indicate genetic homogeneity. This, together with the absence of discontinuous variation and the domination of transgressive segregation, suggests that individual flower longevity is inherited as a polygenic character. However, only by using genetic markers linked with loci involved in the encoding of flower longevity can a more explicit statement be given upon the course of the inheritance of flower longevity in lily. The relatively low H^2 found within two progenies, PR × HA and ST × BR, could indicate that per cross both parents are mainly homozygous for the longevity genes.

The highly significant GCA component and high narrow-sense heritability estimate indicate the importance of additive genetic variance in the transmission of parental individual flower longevity to the progeny. Therefore, the individual flower longevity of the genotype can be used as an indication for its breeding value in practical breeding.

Because of the importance of additive genetic variance in the inheritance of individual flower longevity, genotypes with a short individual flower longevity should, whenever possible, be excluded as parents in *Lilium* breeding programmes. However, since both SCA and transgressive segregation also play a role in the inheritance of individual flower longevity, high heritability in broad sense can occur even when both parents have a short individual flower longevity. So, even if two S parents are used, some descendants with a long individual flower longevity could still be obtained.

In a standardised screening test containing 63 Asiatic hybrids a variation in individual flower longevity of about 4 to 9 days was found (Van der Meulen-Muisers et al., 1998). Hybrids with a long individual flower longevity could be useful as parents in breeding programmes to produce cultivars with an improved individual flower longevity. Within the populations tested individual descendants occurred with longevity levels which exceeded the highest longevity level found within the Asiatic hybrids of the screening test. Because of the effective selection due to high broad-sense heritability and because of the way of inheritance which has been discussed before, genetic improvement for individual flower longevity in this vegetatively propagated crop can be expected to be relatively rapid.

Although significant correlation coefficients between individual flower longevity and other plant characters were found, they were only moderately high. Because of the absence of strong correlations none of the plant characters tested was found to be suitable for indirect selection on individual flower longevity. Ideally, indirect selection should be carried out by using genetic markers linked with flower longevity genes. The high GCA effects together with the large segregation of flower longevity found in our progenies provide good prospects for a successful use of genetic markers in the search for loci involved in the encoding of lily flower longevity.

On the other hand the associations found between flower longevity and other plant characters will have some impact on the selection efficiency. The association of a long individual flower longevity with a long inflorescence longevity and a high percentage flowering buds ought to simplify selection because these characters will all improve the postharvest performance of lily inflorescences. Although the underlying cause of these associations is not known, it is possible that these three characters might, in some manner, be regulated by the available amount of carbohydrates within the inflorescence. It has been suggested that failure of bud opening in lily may be caused by depletion of carbohydrates (Roh, 1990), leading to a reduction in inflorescence longevity. Furthermore, in preliminary research tepal carbohydrate level was found to be associated with individual flower longevity in lily (Van der Meulen-Muisers et al., 1995b).

The negative correlation between individual flower longevity and number of buds per inflorescence might also be regulated by the available amount of carbohydrates within the inflorescence as developing lily flower buds are known to have a large sink strength (Wang & Breen, 1986, 1987) and bud development has been reported to be at the expense of the longevity of accompanying flowers within the inflorescence (Van der Meulen-Muisers et al., 1995b).

Like in *Tulipa* (Van Eijk & Eikelboom, 1976) flower longevity was positively and significantly correlated with the forcing period. This association could cause some problems in selection, as a long forcing period is considered an undesirable character due to an increase in production costs as a consequence. Large numbers of plants must be available for selection on a long individual flower longevity combined with a short forcing period.

The association of male sterility with a longer flower longevity within about 64% of the progenies containing male sterile descendants, could be due to the possible absence of an ethylene peak, which occurs in male fertile flowers (Durieux et al., 1983; Van Meeteren & De Proft, 1982), and seems to coincide with the end of the pollen meiosis. Furthermore, in male sterile flowers a reduction of the ethylene precursor ACC, which is found in ripening pollen of many species (Spikman, 1987; Whitehead et al., 1983), might be expected. Influence of ethylene on longevity of lily flowers has been found by Woltering & Van Doorn (1988) and Van der Meulen-Muisers & Van Oeveren (1993). Also the beneficial effect of the ethylene retardant silver thiosulphate (STS) in Asiatic hybrid lilies is known (Nowak & Mynett, 1985; Swart, 1980).

The absence of a significant overall association between male fertility and individual flower longevity is likely caused by the appearance of two plant types within male sterile descendants. This might be due to the fact that male sterility and flower distortion often seem to be associated in lily breeding (Wadekamper, 1977). Also other factors concerning inflorescence and flower development might be involved in determining flower life in male sterile flowers. This is supported by the significant positive correlation between individual flower longevity and both stem weight and tepal length at anthesis within male sterile descendants.

The results of this study indicate that there are good prospects for the genetic improvement of individual flower longevity in Asiatic hybrid lilies. Because of the associations of individual flower longevity with other desired characters of postharvest performance of lily inflorescences, genetic improvement within this vegetatively propagated crop can be expected to be effective.

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