

## Postharvest flower development in Asiatic hybrid lilies as related to tepal carbohydrate status

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Received 16 March 2000; accepted 17 July 2000

### Abstract

For three Asiatic hybrid lily cultivars ('Bright Beauty', 'Fashion', 'Orlito') the potential postharvest performance of floral buds in terms of growth, anthesis and longevity was studied in relation to tepal carbohydrate status. To determine the importance of carbohydrate redistribution within lily inflorescences, the postharvest performance of several attached and detached buds was compared at the time of anthesis of the most mature floral bud of the inflorescence. Detachment of buds increased failure of opening in small buds, whereas in the largest buds tepal size at anthesis and longevity were improved. In lily inflorescences, postharvest translocation of substrate from the basal to the upper buds takes place. Five bud classes have been characterised, comparing the postharvest performance of attached and detached buds. Classes were based on differences in tepal growth rate, absolute growth and the potential to reach anthesis. A bud length of about 60 mm at harvest, appeared to be critical for reaching anthesis of detached buds. Comparable bud development and flower longevity of inflorescence-attached and inflorescence-detached floral buds was determined in buds of 70–75 mm. At this bud length the total carbohydrate content (fructose, glucose, glycerol glucoside, starch, sucrose) covered about three-fourths of the total tepal carbohydrate content found in the largest bud stage just prior to anthesis. Per cultivar, postharvest flower longevity after anthesis of detached buds was well correlated with total carbohydrate content of the tepals at harvest. Longevity of inflorescence-attached flowers remained constant within the inflorescence, likely due to postharvest redistribution of tepal carbohydrate. These findings indicate an important role for tepal carbohydrate content in postharvest bud development and flower longevity of Asiatic hybrid lilies. Carbohydrate redistribution is suggested to play a major role in the postharvest performance of Asiatic lily inflorescences. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* *Lilium* L.; Anthesis; Bud development; Carbohydrate; Flower longevity; Inflorescence

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\* 21 May 1997.

## 1. Introduction

Unlike most other horticultural crops, cut flowers are often harvested before full development. Particularly in case of inflorescence-type flowers, which consist of several buds differing in the stages of development, a large part of the floral buds is usually still in a premature developmental stage at harvest.

The formation of a mature flower depends on carbohydrate supply. Before harvest, inflorescences are supplied with carbohydrates by photosynthesis, which occurs in the green organs of the plant. After reaching the inflorescence these assimilates are distributed among the various floral buds. The proportion of assimilate uptake in each bud is correlated with the organ sink strength, which largely depends on the rate of utilisation of imported assimilates in the sink tissue (Ho, 1988).

Postharvest light intensity is usually low and, therefore, the production of carbohydrates by photosynthesis of cut flowers generally is negligible. Since the amount of carbohydrate in cut flowers is limited, competition for carbohydrate among developing buds within the inflorescence may occur. A deficiency in carbohydrate reserve in the inflorescence may result in the failure of bud opening, starting in the smallest bud stages as is hypothesised to take place in inflorescence-type bulbous species like freesia (Spikman, 1989) and *Gladiolus* (Serek et al., 1994). Therefore, understanding carbohydrate metabolism in the flower requires that the development of the surrounding floral buds in the inflorescence is taken into account in terms of competition for carbohydrate import.

In *Lilium*, flower buds express a high sink strength throughout their development until anthesis (Wang and Breen, 1986), probably correlated with the increase in growth of floral tissue, occurring after the anthers have reached the sporadic mitosis stage (Clément et al., 1996). Variation in individual flower longevity within the lily inflorescence is relatively small despite large differences in developmental stage of the floral buds at harvest (Van der Meulen-Muisers and Van Oeveren, 1996; Van der Meulen-Muisers et al., 1998). In a previous paper, it was demonstrated that

preharvest floral bud reduction increases individual flower longevity in *Lilium* after harvest (Van der Meulen-Muisers et al., 1995). The effects of preharvest floral bud reduction on flower longevity were probably mainly due to a reduction of the number of competitive sinks within the inflorescence after harvest. The role of carbohydrate redistribution in postharvest development of lily flowers might, therefore, be important.

The purpose of the present paper is to study flower carbohydrate metabolism during postharvest floral bud development by quantifying the development of the tepals and to correlate the results with their carbohydrate content. First the potential postharvest floral bud development was studied, and next, soluble and insoluble tepal sugar contents were assayed at several stages of bud development. Ultimately, we attempted to determine the importance of carbohydrate redistribution in relation to flower development by comparing the postharvest performance of inflorescence-attached buds and inflorescence-detached buds. To affirm our hypothesis about the importance of carbohydrate redistribution in inflorescence-type cut flowers, we focussed on the postharvest flower development of three lily cultivars differing in individual flower longevity.

## 2. Materials and methods

Bulbs of Asiatic lily hybrids (*Lilium* L.), 12–16 cm in circumference, were obtained from commercial growers in The Netherlands and from the lily collection of Plant Research International. Three cultivars, 'Bright Beauty', 'Fashion', and 'Orlito' were used. The choice of the cultivars is based on known differences in individual flower longevity (Van der Meulen-Muisers et al., 1998). Before planting, the bulbs were stored in moist peat at  $-2^{\circ}\text{C}$  for about 8 months.

Standardised conditions were used during forcing, harvest and postharvest (Van der Meulen-Muisers and Van Oeveren, 1997). Plants were forced in a growth chamber at  $17^{\circ}\text{C}$ , 60% relative humidity (RH), and a 16 h photoperiod. Photosynthetically active radiation (400–700 nm) (PAR) at the top of the plants, was kept at a

photosynthetic photon flux density (PPFD) of about  $112 \mu\text{mol m}^{-2} \text{s}^{-1}$  using high pressure metal halide lamps (HPI-T 400W, Philips).

Inflorescences were harvested at anthesis of the most mature floral bud by cutting the stems at the soil level within 4 h after the onset of the photoperiod. Tepal length was measured and subsequently, the buds were divided into groups differing by 5 mm increments in length. In addition, open flowers were included. When tepals were to be studied, they were excised from the inner whorl of the flower head at harvest.

Cut inflorescences and cut individual buds were both placed in glass flasks containing tap water, and were held at  $17^{\circ}\text{C}$ , 60% RH, and a 12 h photoperiod. PAR was kept at a PPFD of about  $14 \mu\text{mol m}^{-2} \text{s}^{-1}$  using fluorescent lamps (TL-D84 36 W, Philips).

Tepal length of both the inflorescence-attached and inflorescence-detached floral buds was recorded until anthesis, as a parameter for tepal growth. From each available developmental stage at harvest eight flowers were studied. Flower longevity was recorded as the time between anthesis and visual withering of the tepals. Each individual floral bud and flower was observed daily within 4–6 h after the onset of the photoperiod.

From each available developmental stage at harvest, 12 flowers were sampled. One tepal (inner whorl) of each flower was weighed to determine tepal fresh weight, immersed in liquid nitrogen, freeze-dried and reweighed to determine tepal dry weight. Fresh weight/dry weight ratios were calculated.

From the 12 samples per developmental stage four replicates were composed by pooling the freeze-dried tepals of three different flowers before grinding. Using 10 mg of the powder, sugars were extracted in 80% methanol ( $76^{\circ}\text{C}$ ) for 15 min. Before extraction raffinose was added to the 80% methanol as the internal standard. After centrifugation the pellet was stored for starch analysis. The supernatant was vacuum-evaporated and its residue was taken up in 1 ml purified water (Milli-Q purification system, Millipore, Molsheim, France). After proper dilution the samples were injected in a Dionex HPLC system (Dionex Corporation, Sunnyvale, CA). The HPLC was

equipped with a CarboPac PA1 column and a pulsed-amperometric detection system with an Au working electrode and an Ag/AgCl reference electrode. Peaks were identified by comparing their retention times with the retention times of a mixture of standard sugars (De Bruijn et al., 1997). A peak that eluted before glucose has been identified as glycerol glucoside, and could be quantified by using the response factor of glucose after dividing it by 1.5 (U. Van Meeteren and A.C. Van de Peppel, pers. commun.). Total soluble carbohydrate was calculated by summing glucose, fructose, sucrose and glycerol glucoside.

Preliminary analysis ascertained that Asiatic lily tepal tissue did not contain any fructans, and that the storage carbohydrate in the developing floral buds was starch. Starch determination was performed on the tissue pellet that remained after soluble carbohydrate extraction, using a commercial starch determination kit (Boehringer, Mannheim, Germany) according to the protocol of the supplier.

Completely randomised designs were used. Data were analysed by analysis of variance, using the Genstat 5 statistical package (Rothamsted, UK). Correlation coefficients of linear regression ( $r$ ) were calculated to look for associations between tepal carbohydrate content and flower longevity.

### 3. Results

#### 3.1. Bud growth

Postharvest growth of attached and detached buds was similar for the three cultivars tested, and is demonstrated for 'Orlito' in Fig. 1. In buds reaching anthesis postharvest bud growth proceeded nearly linear in time. In buds that failed to open, postharvest bud growth was halted prematurely. In both attached and detached buds, tepal length at anthesis slightly decreased with developmental stage at harvest. At anthesis, the tepal length exceeded 75 mm in all the three cultivars tested.

At harvest (at the time of anthesis of the most mature floral bud), tepal length distribution

within the inflorescences varied per cultivar, with a minimal length of 30 mm ('Bright Beauty', 'Orlito') or 45 mm ('Fashion') and a maximal tepal length in the open flower of 85 mm ('Bright Beauty', 'Fashion') or 90 mm ('Orlito'). The study of the postharvest development of detached and attached flower buds made it possible to determine five classes. Classes were based on differences in the tepal growth rate, absolute growth and the potential to reach anthesis (Fig. 1, Table 1).

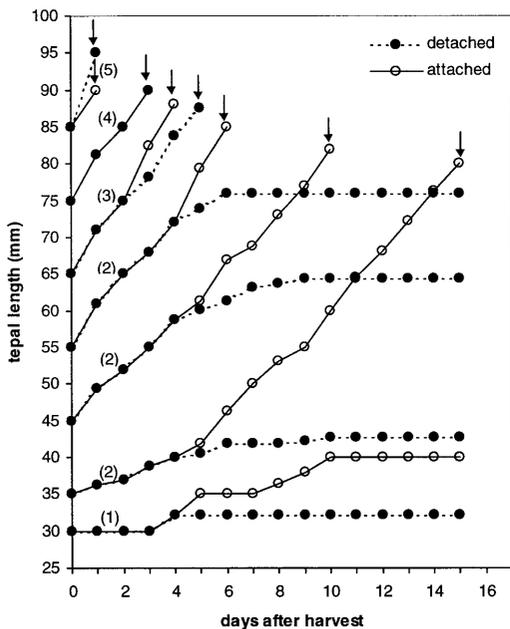


Fig. 1. Postharvest development of inflorescence-attached (open symbols) and inflorescence-detached (closed symbols) flower buds of the Asiatic hybrid cultivar Orlito, harvested at the time of anthesis of the most mature floral bud. Five bud classes were distinguished, comparing the postharvest performance of detached buds with attached buds of initially the same size. Class numbers are presented in parentheses; (1) both attached and detached buds: little tepal growth, no anthesis; (2) detached buds: lower tepal growth rate and smaller absolute growth than attached buds, no anthesis. Attached buds: anthesis; (3) detached buds: lower tepal growth rate and equal absolute growth compared to attached buds. Both attached and detached buds: anthesis; (4) both attached and detached buds: comparable tepal growth rate, anthesis, comparable absolute growth; (5) detached buds: higher tepal growth rate and greater absolute growth than attached buds. Both attached and detached buds: anthesis. Arrows indicate open flowers;  $n = 8$  flowers per treatment combination.

All the attached buds reached anthesis, except for buds of class 1. After detachment both buds of class 1 and 2 did not complete their development. Within buds of class 2 the growth rate of the tepals in detached buds was lower than the growth rate of attached buds, from three ('Bright Beauty') or four ('Fashion', 'Orlito') days after harvest. Of the detached buds reaching anthesis (class 3–5) only buds of class 4 completed their development in the same way as matching attached buds. Within class 3 anthesis occurred later in time, whereas in class 5 the tepals of the resulting flowers were larger in size. In class 3 the growth rate of the tepals of detached buds was lower compared with the growth rate of the tepals of attached buds, from two days after harvest independent of the cultivar tested (Fig. 1, e.g. 'Orlito').

### 3.2. Anthesis

In 'Fashion' and 'Orlito', respectively, 100 and 96% anthesis was obtained in attached flowers, whereas in attached flowers of 'Bright Beauty' 81% of the floral buds reached anthesis. After detachment, the percentage of floral buds that reached anthesis decreased 20 ('Fashion') to 48% ('Orlito'), (data not shown). For all three cultivars tested, a bud length of about 60 mm at harvest appeared to be critical for reaching anthesis for a bud detached from the inflorescence (Table 1).

### 3.3. Flower longevity

Longevity of attached flowers remained nearly constant within the inflorescence independent of the developmental stage of the floral bud at harvest. After anthesis, longevity of detached flowers increased with the progression of the stage of development at harvest (Fig. 2). Longevities of the two largest bud stages and of the open flower were significantly improved ( $P = 0.05$ ) in detached flowers compared with those of attached flowers in all three cultivars (Fig. 2). Detaching open flowers improved their longevity by about 14–18% depending on the cultivar.

Table 1

Distribution of five classes of flower buds (as defined in Fig. 1) and open flowers at harvest (OF), within lily inflorescences of 'Bright Beauty', 'Fashion' and 'Orlito'; classes were distinguished comparing the postharvest development of attached lily flower buds with detached buds of initially the same tepal length at harvest of the inflorescence

Genotype	Class number												
	Tepal length of floral buds at harvest (mm)												
	30	35	40	45	50	55	60	65	70	75	80	85	90
'Bright Beauty'	1	1	1	2	2	2	2/3	3	4	4	5	OF	. <sup>a</sup>
'Fashion'	.	.	.	2	2	2	2/3	3	4	5	5	OF	.
'Orlito'	1	2	2	2	2	2	2/3	3	3	4	5	5	OF

<sup>a</sup>., Tepal length not present at harvest of the inflorescence.

### 3.4. Tepal weight

Tepal fresh weight and dry weight increased almost proportionally with tepal length until the largest bud stage before anthesis. As a consequence, the tepal fresh weight/dry weight (fw/dw) ratio remained almost constant within the inflorescence (Fig. 3). Maximum fresh weight occurred in tepals of fully opened flowers in all the three cultivars tested. Maximum dry weight occurred at anthesis ('Orlito') or at the largest bud stage just before anthesis ('Bright Beauty', 'Fashion') (data not shown). Between the largest floral bud before anthesis and the open flower (a 24 h time lapse in development) an increase in the fw/dw ratio occurred (Fig. 3). Tepal fw/dw ratios were similar for the three cultivars tested (Fig. 3).

### 3.5. Tepal carbohydrate

The total carbohydrate content (soluble carbohydrate and starch) of lily tepals gradually increased with the developmental stage of the floral buds (Fig. 4, e.g. 'Orlito'). Glycerol glucoside was the major tepal carbohydrate in the smaller bud stages up to about 55 mm; it remained constant or slightly decreased through all the stages of bud development. From a bud length of about 55 mm, starch became the major tepal carbohydrate. Tepal starch content increased with bud development to a maximum value at the largest bud stage before anthesis and then declined to low levels at bud opening. Amounts of glucose and fructose

were nearly identical through all stages of bud development, and gradually increased with the developmental stage of the floral buds. When

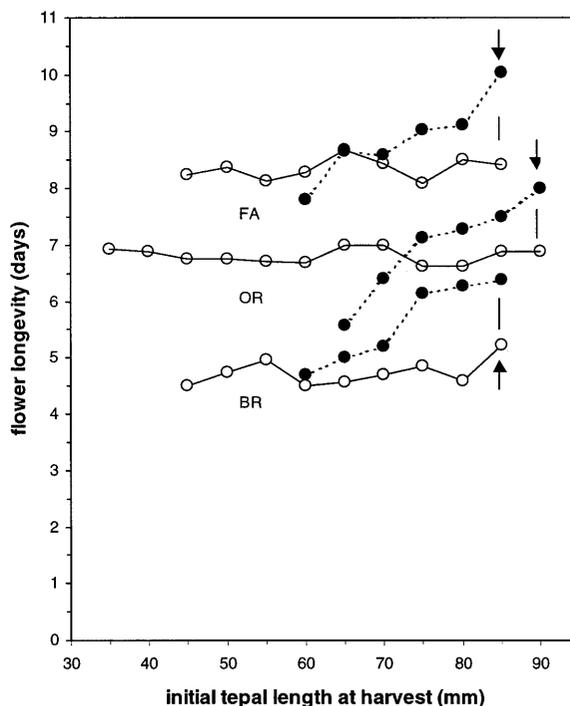


Fig. 2. Individual flower longevity (in days) of attached flowers (open symbols) and detached flowers (closed symbols) of 'Bright Beauty' (BR), 'Orlito' (OR) and 'Fashion' (FA), in relation to their initial tepal length (in mm) at harvest. Arrows indicate already open flowers at harvest per cultivar. Bars indicate least significant differences between means (LSD) at  $P = 0.05$ ;  $n = 8$  flowers per treatment combination.

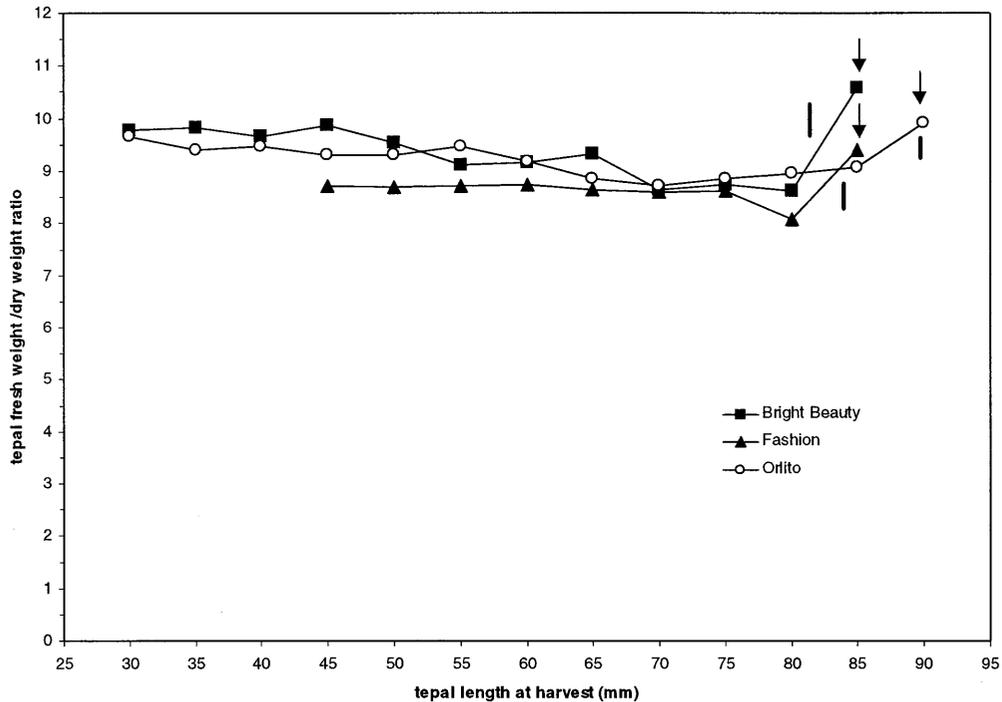


Fig. 3. Tepal fw/dw ratio of flower buds of 'Bright Beauty', 'Fashion' and 'Orlito' at the stages of development present at the time of anthesis of the most mature flower bud. Developmental stages are defined by the tepal length of the flower buds (in mm). Arrows indicate open flowers. Bars indicate least significant differences between means (LSD) at  $P=0.05$ ;  $n=12$  flowers per treatment combination.

starch content declined near anthesis, glucose and fructose content rapidly increased in 'Orlito' (Figs. 4 and 5). In 'Bright Beauty' and 'Fashion', the increase in glucose and fructose with the decrease of starch at bud opening was less profound, since total tepal carbohydrate content decreased (Fig. 5). Tepal sucrose content gradually increased with bud development, but remained at relatively low values (about 7% of the total tepal carbohydrate) for all the bud stages, with an increase to 12–15% in the open flower (Figs. 4 and 5).

### 3.6. Flower development as related to tepal carbohydrate content

At a bud length of about 60 mm, the critical stage of detached buds to reach anthesis (Table 1), the total carbohydrate content (soluble sugar

and starch) amounted to 12 ('Bright Beauty') to 14 mg ('Fashion') per tepal. At this bud length there was also a colour change from greenish to the true flower colour in each cultivar (data not shown). At a bud length of 70 mm ('Bright Beauty', 'Fashion') or 75 mm ('Orlito'), attached and detached buds showed a similar growth pattern towards anthesis and a comparable final tepal length (Table 1, group 4). After anthesis of those buds, longevities of attached and detached flowers were non-significantly different (Fig. 2). At this bud length total tepal carbohydrate content amounted to 21–25 mg, covering 68 ('Fashion') to 78% ('Bright Beauty') of the total tepal carbohydrate content found in the largest bud stage just prior to anthesis.

Total tepal carbohydrate expressed as a percentage of the dry-weight increased with the stage of development of the floral buds (Fig. 6). Be-

tween the largest bud stage and the open flower the percentage of total tepal carbohydrate increased in 'Orlito', and slightly decreased in 'Bright Beauty' and 'Fashion' (Fig. 6). At anthesis, carbohydrates accounted for 33–41% of the tepal dry weight depending on the cultivar (Fig. 6).

Flower longevity of detached buds that reached anthesis was positively correlated with the total carbohydrate content of the tepals at detachment, for all three cultivars tested (Fig. 7). For all the cultivars taken together, the association was moderately high ( $r = 0.62$ ). No association was found between longevity of the attached flowers and total carbohydrate content of the tepals at the stage the inflorescence was harvested, as flower longevity of attached flowers hardly changed within the inflorescence (Fig. 2).

#### 4. Discussion

The postharvest development of attached lily floral buds follows a clearly defined pattern that hardly changes with the position of the bud on the stem as illustrated for 'Orlito' in Fig. 1. Lily flower maturation is characterised by an increase in bud size (tepal length Fig. 1, fresh weight and dry weight), and a change in the pigmentation of the tepals (data not shown). Soluble carbohydrate levels and starch increase until anthesis (Fig. 4, e.g. 'Orlito'). At anthesis, tepal starch shows a decrease with a subsequent increase in the soluble carbohydrate levels (Fig. 5) and an increase in water content leading to an increase in the fw/dw ratio (Fig. 3). Within inflorescences harvested at anthesis of the most mature floral bud nearly all buds reach anthesis, as reported before (Van der Meulen-Muisers and Van Oeveren, 1997). After

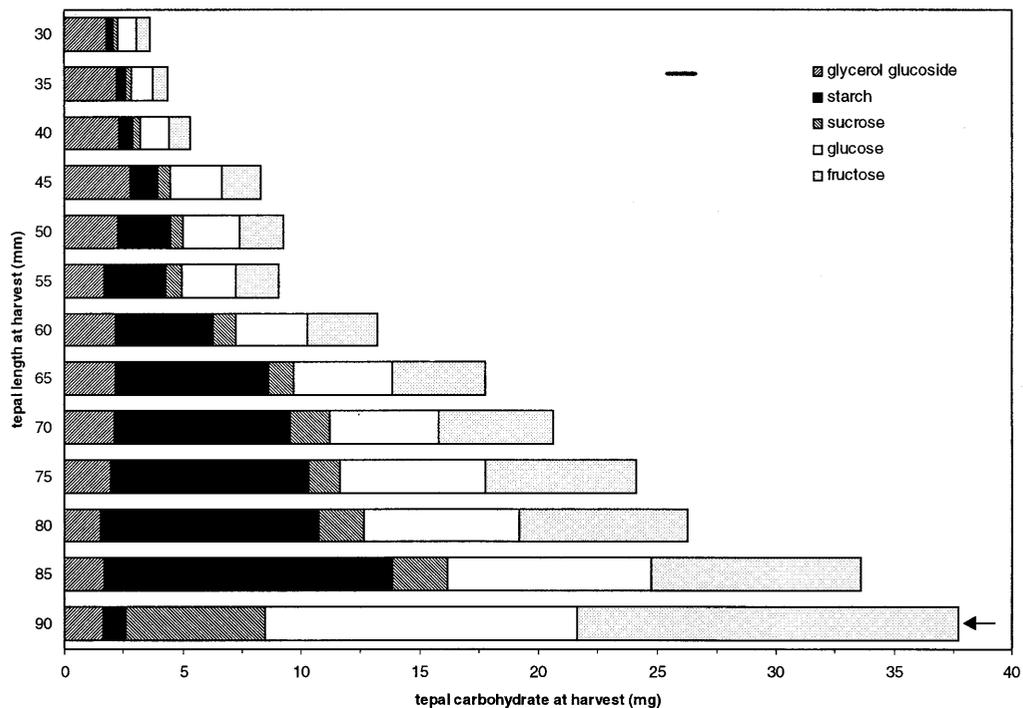


Fig. 4. Carbohydrate composition in tepals of 'Orlito' at the stages of development present at anthesis of the most mature flower bud. Developmental stages are defined by the tepal length of the flower buds (in mm) and are arranged in decreasing order, comparable with their location within the inflorescence. Arrow indicates open flower. Small bar indicates least significant differences between means (LSD) at  $P = 0.05$ ;  $n = 4$  samples per treatment combination.

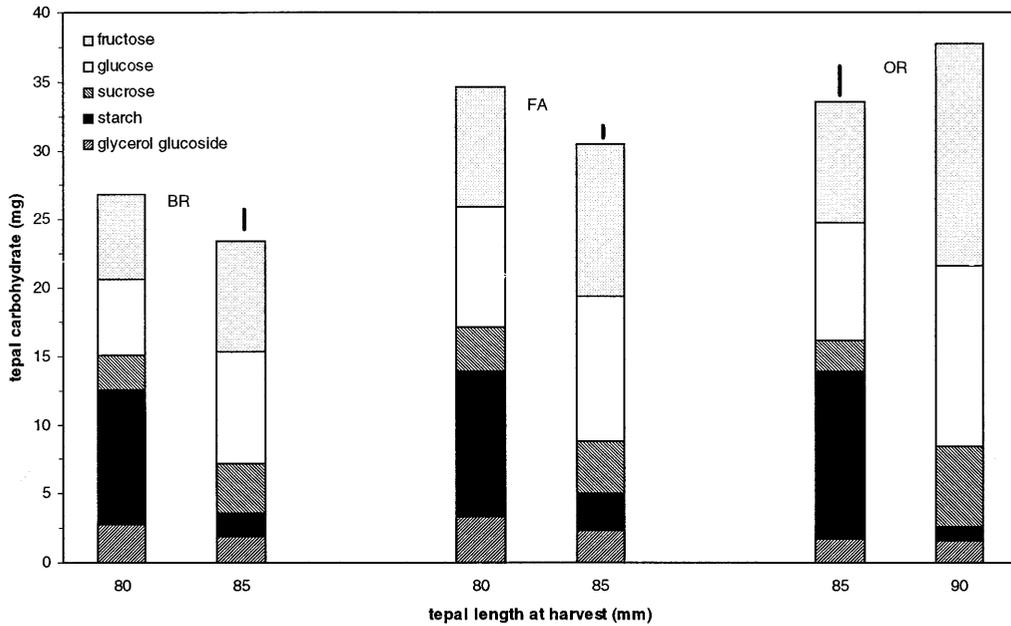


Fig. 5. Carbohydrate composition in tepals of the largest bud (left bar) and open flower (right bar) of 'Bright Beauty' (BR), 'Fashion' (FA) and 'Orlito' (OR). Small bars indicate least significant differences between means (LSD) at  $P = 0.05$ ;  $n = 4$  samples per treatment combination.

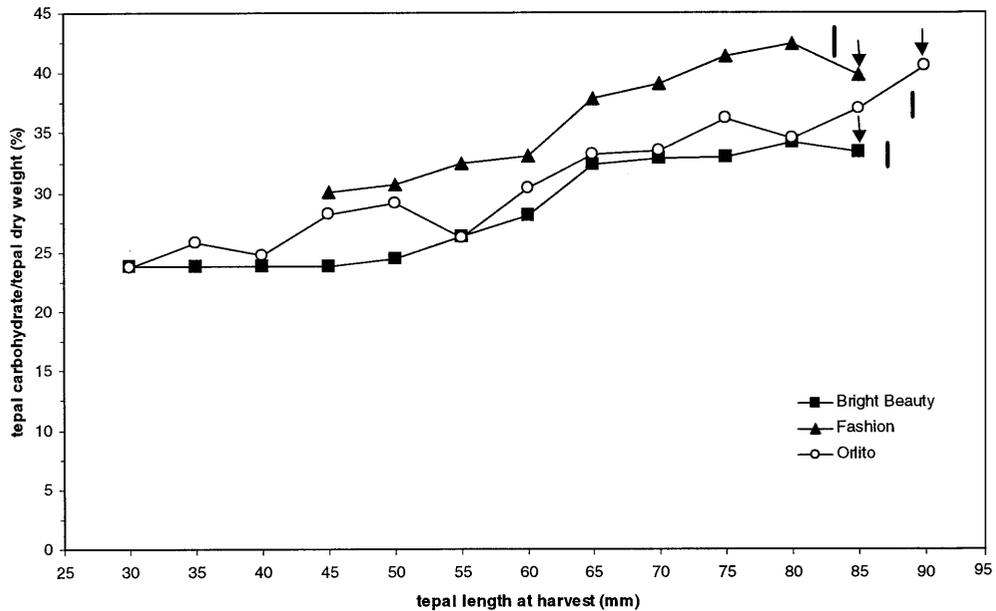


Fig. 6. Tepal carbohydrate status of lily flower buds of 'Bright Beauty' (BR), 'Fashion' (FA) and 'Orlito' (OR) at the stages of development present at the time of anthesis of the most mature flower bud. Developmental stages are defined by the tepal length of the flower buds (in mm). Arrows indicate open flowers. Bars indicate least significant differences between means (LSD) at  $P = 0.05$ ;  $n = 4$  samples per treatment combination.

anthesis, postharvest senescence of the attached lily flowers hardly changes with the position of the flower on the stem resulting in a constant longevity level within the inflorescence (Fig. 2).

Data on detached floral buds showed that preventing translocation of metabolites within the inflorescence altered the pattern of postharvest maturation (Fig. 1, e.g. 'Orlito') and senescence (Fig. 2) in nearly all the buds. Detachment increased failure of bud opening compared with attached buds from the smallest bud sizes up to a size of about 60 mm. At the same time, in the largest bud stages tepal size at anthesis (Fig. 1, e.g. 'Orlito') and longevity (Fig. 2) improved in the detached flowers as compared to the attached flowers. These results suggest that within cut lily inflorescences the developing buds up to about 60 mm in size are strong sinks throughout their

growth. The demands of those sinks are, at least partially, accounted for by translocation of metabolites from the larger flower buds (and open flower) reducing their tepal length at anthesis and/or their longevity. However, the smallest buds sizes in 'Bright Beauty' (30–40 mm) and to a lesser extent in 'Orlito' (30 mm) appeared to be weak sinks. Their growth was minimal when attached to the inflorescence and they failed to open (Table 1, class 1). Their sink strength might be insufficient to compete with the other developing buds for substrate provided by the open flower and the largest bud stages within the inflorescence. In 'Fashion' no such small buds were present at harvest (Table 1), mainly due to cultivar differences in flower bud distribution as reported before (Van der Meulen-Muisers and Van Oeveren, 1996). For buds up to 60 mm, developmental differences between attached and detached flower buds became visible about 3–4 days after harvest (Fig. 1, e.g. 'Orlito'). Within the inflorescence, translocation of substrate from the basal to the upper buds apparently starts near this point of time.

The stage of maturity of the buds is marked by the content of carbohydrate of the tepals, more mature buds containing more tepal carbohydrate (Fig. 4, e.g. 'Orlito'). Failure of bud opening in lily could be due to the lack of carbohydrate as discussed in other inflorescence-type bulbous species such as freesia (Spikman, 1989) and *Gladiolus* (Serek et al., 1994). In lily, failure of bud opening is known to increase when inflorescences are harvested in a less mature stage (Van der Meulen-Muisers and Van Oeveren, 1997). From the data presented above, it can be concluded that harvesting inflorescences at a less mature stage will considerably reduce the carbohydrate content available for redistribution from the larger to the smaller buds.

In buds of 70 mm ('Bright Beauty', 'Fashion') or 75 mm ('Orlito'), with a tepal carbohydrate content of 21–25 mg, comparable bud development and flower longevity of attached and detached floral buds was determined (Table 1 [class 4], Figs. 1 and 2). Those carbohydrate amounts cover 68 ('Fashion') to 78% ('Bright Beauty') of the total tepal carbohydrate content found in the

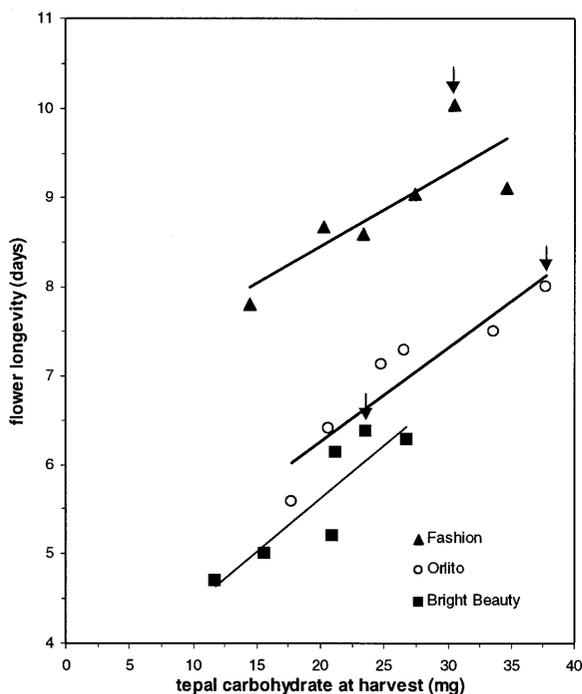


Fig. 7. Relationship between longevity of 'Bright Beauty', 'Fashion' and 'Orlito' flowers and total tepal carbohydrate content at the time of detachment of the buds. Buds were detached from the inflorescence at several stages of development, present at the time of anthesis of the most mature flower bud. Arrows indicate open flowers at harvest;  $r$  = correlation coefficient of linear regression.

largest bud stage just prior to anthesis, indicating a carbohydrate surplus in tepals of the most mature floral bud stages and in tepals of the open flower. In attached floral buds at least part of the carbohydrate surplus will likely be available for redistribution to smaller buds. As discussed above, redistribution will lead to an increase in the number of buds that will reach anthesis (Table 1, Fig. 1, e.g. 'Orlito'), comparing attached and detached floral buds. At the same time, longevity of the flowers obtained from the largest bud sizes and of the open flower at harvest will decrease in attached flowers compared to detached flowers (Fig. 2). The relatively smallest carbohydrate surplus (22%) was found in tepals of the cultivar with the shortest flower longevity ('Bright Beauty'), and the relatively largest carbohydrate surplus (32%) was found in tepals of the cultivar with the longest flower longevity ('Fashion'). This could be an important factor in the search for an explanation of the existence of cultivar differences in flower longevity.

The gradual increase of the total carbohydrate/dry weight ratio with developmental stage of the buds indicates carbohydrate filling of the tepals as they develop (Fig. 6). Near anthesis total tepal carbohydrate in percentage of dry-weight appeared to amount to 33–41%, comparable with the value that can be derived from data on *Gladiolus* flowers (Yamane et al., 1993). Anthesis after detachment of floral buds appeared to be dependent on the stage of maturity of the buds at harvest. To obtain anthesis, a bud length of about 60 mm, concomitant with 12–14 mg carbohydrate content per tepal, appeared to be critical (Table 1, Fig. 4, e.g. 'Orlito').

Reducing sugars appeared to form a large proportion of the carbohydrate pool in the tepals (Figs. 4 and 5). This supports the view that the floral buds are active metabolic centres, since the translocation sugar is probably sucrose. The nearly identical amounts of fructose and glucose within lily tepals (Figs. 4 and 5) suggest that sucrose is probably rapidly converted by invertase at its site of accumulation, a characteristic which is specific for sink organs (Avigad, 1982).

Anthesis appeared to be accompanied by hydrolysis of starch leading to an increase in the

sugar content (Fig. 5). Similar interactions between starch and sugar content have been reported during the expansion of rose petals (Evans and Reid, 1988) and *Alstroemeria* petals (Collier, 1997). Besides supplying substrate for respiratory processes, starch hydrolysis especially provides osmotic solutes for water influx and cellular expansion. The tepal fw/dw ratio, an indirect measure of the proportion of dry weight that consists of osmotically active solutes (Evans and Reid, 1988), increased at anthesis (Fig. 3). This shows that part of the tepal expansion was due to an increased water uptake.

The increase in sugar content near anthesis did not quantitatively correspond with the disappearance of starch (Fig. 5). Within 'Orlito' the total tepal carbohydrate content increased, whereas in 'Bright Beauty' and 'Fashion' it decreased at the time of starch hydrolysis. These data suggest that at anthesis both net-import and net-export of carbohydrates can take place in lily tepals, depending on the cultivar.

Tepals of developing lily buds contained, in addition to glucose, fructose, sucrose and starch, glycerol glucoside (Figs. 4 and 5). Glycerol glucosides seem to be characteristic constituents of the genus *Lilium* and their structures have been reported to vary depending on the species (Kaneda et al., 1974, 1982, 1984). The glycerol glucoside detected in our study could be lilioid C, isolated from *Lilium tigrinum* (syn. *Lilium lancifolium*) (Kaneda et al., 1982) one of the ancestors of the Asiatic hybrids. Tepal glycerol glucoside was especially a dominant component at the youngest bud stages, while its content hardly changed at the developmental stage of the floral buds. Glycerol glucoside is, therefore, not likely to play an important role in the carbohydrate metabolism of lily flowers.

Per cultivar no association was found between longevity of attached flowers and the total tepal carbohydrate content at harvest. This was likely due to postharvest redistribution of tepal carbohydrate present at harvest, leading to constant flower longevity within the inflorescence. Despite its limited range flower longevity after detachment was well correlated with total carbohydrate content of the tepals per cultivar (Fig. 7). A moderate

association ( $r = 0.62$ ) between flower longevity and tepal carbohydrate was found using the unified data of all three cultivars. Apparently besides tepal carbohydrate content also other factors account for cultivar differences in lily flower longevity.

Asiatic lily inflorescences offer an interesting model system for studies on postharvest flower development, because individual flowers provide a graded series of stages of development in an identical genetic and environmental background. Furthermore, cultivars differing in flower longevity correspond in a similar way. A dominant role of tepal carbohydrate content in bud development and flower longevity of Asiatic lilies can be proposed from the findings of the present study. Further studies on factors such as carbohydrate degradation and redistribution in lily flowers and inflorescences are needed for a better understanding of cultivar differences in the relationship between carbohydrates and longevity of Asiatic hybrid lilies.

### Acknowledgements

The authors are grateful to S.M. De Bruijn, J.R. Mouris and G.P. Terwoert for technical assistance, J. Jansen for statistical advice, and F.A. Hoekstra for constructive discussions and critical reading of the manuscript. This work was financially supported by the Urgency Programme for Research on Diseases and Breeding of Flower Bulbs.

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