Postharvest Biology and Technology 58 (2010) 142–146

Contents lists available at ScienceDirect

Postharvest Biology and Technology

journal homepage: www.elsevier.com/locate/postharvbio

The dynamics of starch and sugar utilisation in cut peony (*Paeonia lactiflora* Pall.) stems during storage and vase life

E.F. Walton[a,*], H.L. Boldingh[b], G.F. McLaren[c], M.H. Williams[a,1], R. Jackman[a]

[a] Plant & Food Research Mt Albert, Private Bag 92 169, Auckland Mail Centre, Auckland 1142, New Zealand
[b] Plant & Food Research Ruakura, Private Bag 3123, Waikato Mail Centre, Hamilton 3240, New Zealand
[c] Plant & Food Research Clyde, 990 Earnscleugh Rd, RD 1, Alexandra 9391, New Zealand

ARTICLE INFO

Article history:
Received 29 December 2009
Received in revised form 20 May 2010
Accepted 20 May 2010

Keywords:
Peony
Paeonia lactiflora
Cut flowers
Vase life
Carbohydrates
Long-term storage

ABSTRACT

The carbohydrate dynamics of cut peony (*Paeonia lactiflora* Pall. 'Sarah Bernhardt') stems were examined during vase life of fresh-cut stems, while in storage at 0 °C and during their vase life after storage. During flower opening of fresh-cut stems, the rate of starch hydrolysis in the flower buds was more rapid than in those still attached to the plant, and once the flowers had opened, the total sugar concentrations of the flowers, leaves and stems were lower than in those still attached to the plant. Quantification of the sugar content of fresh-cut stems during flower opening and those still attached to the plant, suggests that an additional 3.2 g of sugars are translocated into attached stems during flower opening, which equates to nearly 42% of an open flower. However, reserves in fresh stems were still sufficient to provide a total vase life of 14 d, only 2 d less than stems still attached to the plant. During the first 4 weeks of cool-storage, starch reserves in the flower buds were almost completely hydrolysed, contributing to similar hexose concentrations but much higher sucrose concentrations than in fresh-cut stems. Flower opening was more rapid but the subsequent vase life was only 9 d, shorter than that for fresh-cut stems. Much of that difference could be attributed to the faster opening of buds (2 d cf. 5 d), which is likely to have been the result of the starch having already been hydrolysed during storage. Together, these results indicate that cut peony stems have sufficient carbohydrate reserves to drive flower opening and still have an acceptable vase life even after 8 weeks of storage.

1. Introduction

Flower crops used commercially in the cut flower industry have to survive harvest, packing and distribution, and still have acceptable quality for the consumer. Two important characteristics of cut flowers are the ability of flower buds to open after the stems have been harvested, and for open flowers to have a reasonable vase life. Cut flowers rely on stored carbohydrate reserves for flower opening and maintenance, as their carbohydrate supply from the rest of the plant ceases at harvest, and as cut flowers are often placed in low light conditions, there is little or no net carbon gain from photosynthesis (Halevy and Mayak, 1979). Dehydration and wilting, caused by either air embolisms in the stem xylem (at the time of cutting) or bacteria entering the stem from the vase water and blocking water uptake (Van Doorn, 1997), can also affect both the ability of flower buds to open and their vase life. For ethylene-sensitive species, such as rose and *Curcuma alismatifolia* Gagnep., ethylene-induced senescence, expressed as premature petal drop or leaf yellowing, can markedly decrease vase life (Ichimura et al., 2005; Bunya-atichart et al., 2004).

Herbaceous peonies are perennial plants that have been cultivated for many centuries and are valued for their highly attractive flowers. Modern cultivars used for commercial cut flower production are mainly derived from the species *Paeonia lactiflora* Pall. (Stern, 1946). Production of peonies has expanded in New Zealand over the last 20 years, primarily for export to Northern Hemisphere markets, as the domestic market is relatively small. To maximise returns, postharvest cool-storage is used to extend the service window, with flowers entering overseas markets when there is little or no competition. Peony stems are harvested before flower opening and typically have good postharvest performance, with a vase life of around 5–7 d, depending on the cultivar (Heuser and Evensen, 1986), the stage of maturity at which they are picked, the climate in which the plants had been growing (Gast et al., 2001) and the temperature at which they open.

The primary source of carbohydrate reserves for opening and maintenance of peony flowers on the plant is starch accumulated

* Corresponding author at: University of Otago, PO Box 5543, Auckland 1141, New Zealand. Tel.: +64 9 373 9711; fax: +64 9 373 9701.
E-mail address: eric.walton@otago.ac.nz (E.F. Walton).
[1] Department of Horticulture, Aarhus University, Kristinebjergvej 10, 5792 Aarslev, Denmark.

0925-5214/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.postharvbio.2010.05.008

in the flower bud during development (Walton et al., 2007). However, the degree to which opening flowers rely on additional carbohydrates supplied by the parent plant is unclear. As no additional carbohydrates are available to cut stems after harvest, their absence may limit vase life and/or storage potential. We would like to be able to manipulate the carbon dynamics during production to maximise the postharvest performance of stored peony stems. Consequently, the aims of the current study were fourfold: (i) to compare the vase lives of freshly cut peony stems with those cool-stored for 8 weeks, (ii) to compare the carbohydrate dynamics of freshly cut stems during their vase life with those for stems attached to the plant (Walton et al., 2007), (iii) to describe the carbohydrate dynamics during cool-storage, and (iv) to compare the carbohydrate dynamics during flower opening of stored stems with those that were not stored.

2. Materials and methods

2.1. Plant source

On 13 November 2001, flowering stems were harvested from mature peony (*P. lactiflora* Pall. 'Sarah Bernhardt') plants growing at a commercial property near Clyde, Central Otago, New Zealand. Stems were selected following the industry standards for export grade flowers, i.e., buds were beginning to soften and outer petals had started to loosen and separate. Stems were then packed dry for overnight transport by refrigerated courier to Plant & Food Research Mt Albert, Auckland, New Zealand, for storage and postharvest evaluation.

2.2. Postharvest storage and evaluation

Stems that were to be stored were packed into export boxes (cardboard) containing polyliners, and placed into a coolstore at 0 °C. Polyliners were used to minimise water loss but were not sealed, allowing continued gas exchange. Stems were then stored for periods of up to 10 weeks by which time there were small but visible losses in quality (some tissue browning).

Vase life assessments were carried out on both freshly cut stems and those that had been cool-stored for 8 weeks. For vase life assessments, peony stems were re-cut to 50 cm and put into vases containing water. Vases were then placed into an evaluation room set to standard conditions (20 °C, 60% RH, 8 μmol s^{-1} m^{-2} and 12 h day/night cycle). For each vase life experiment, the course of flower opening was assessed on eight stems each day, for up to 14 d using the following rating scale:

(1) Tight bud, petal showing colour
(2) Loose bud, outer petals soft and loosening, firm inside
(3) Almost open flower, petal curved inwards
(4) Fully open flower, outer petals unfurled from inner petals
(5) Petals wilting, 50% of petals wilting, or petals starting to drop, end of flower life.

2.3. Carbohydrate analyses

Carbohydrate analysis was carried out on freshly cut stems and stems that had been stored for 8 weeks at 0, 1, 2, 3, 5, 7, and 10 d after placing them in the vase. Three replicates (each of two stems), were collected on each sampling date and each was separated into the buds/flowers, leaves and stem, weighed, a representative subsample retained, weighed and frozen in liquid nitrogen. In addition, stems were also sampled during storage, at 2, 4, 6, 8, and 10 weeks. At each date three replicates (each of two stems), were separated into buds/flowers, leaves and stems, weighed, sub-sampled and frozen as described above. Total weights of the stems were determined by summing the weights of the component parts. Samples were stored at −25 °C.

For analysis, frozen tissue was lyophilised, weighed and then ground to a fine powder. A sub-sample was extracted using 80% (v/v) ethanol and the filtrates analysed using gas-chromatography (Miller et al., 1998). Starch was estimated after the insoluble fraction was autoclaved, treated with amyloglucosidase to release glucose, and then quantified colorimetrically (Smith et al., 1992). All carbohydrate data are presented on a dry weight basis.

3. Results

3.1. Vase and storage life

On the fresh-cut (non-stored) peony stems, flower buds opened after, on average (with ±SEM), 4.9 ± 0.6 d and remained open for 9.1 ± 0.6 d (Fig. 1). In contrast, flower buds on stems that had been stored for 8 weeks opened more quickly (1.9 ± 0.4 d) and remained open for only 7.3 ± 0.3 d (Fig. 1). Consequently, the total vase life of fresh-cut flowers was 14.0 ± 0.4 d, whereas stems stored for 8 weeks only lasted for 9.1 ± 0.2 d. During the vase life studies, the fresh weights of the fresh-cut flower buds peaked at Day 5 (Fig. 2), when the flowers were fully open. There was little change in bud fresh weight during the 8 weeks of storage (mean 22.4 ± 0.43 g), but when placed in vases increased markedly (by 30%) in the 2 d it took the flowers to open (Fig. 2). After flower opening, flower fresh weights steadily declined in both fresh-cut and stored flowers.

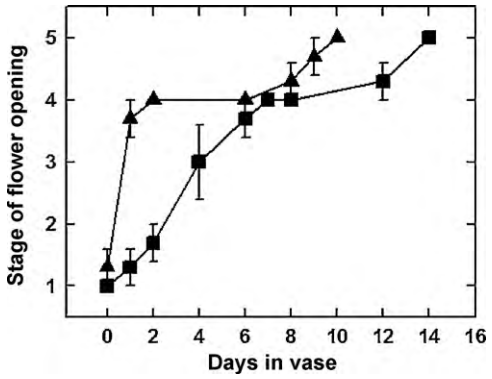

Fig. 1. Vase lives of fresh-cut peony stems (■) and after 8 weeks of storage at 0 °C (▲). Stages of flower opening: 1 = tight bud, Stage 2 = loose bud, Stage 3 = almost open, Stage 4 = fully open, and Stage 5 = petals wilting. Error bars represent ±SEM.

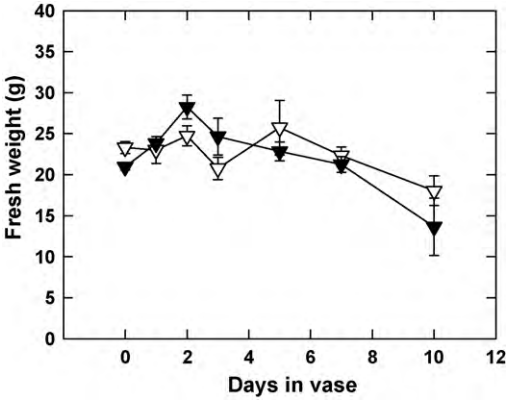

Fig. 2. Changes in fresh weights of fresh-cut (non-stored) (▽) and stored (▼) peony buds/flowers during vase life studies. Error bars represent ±SEM.

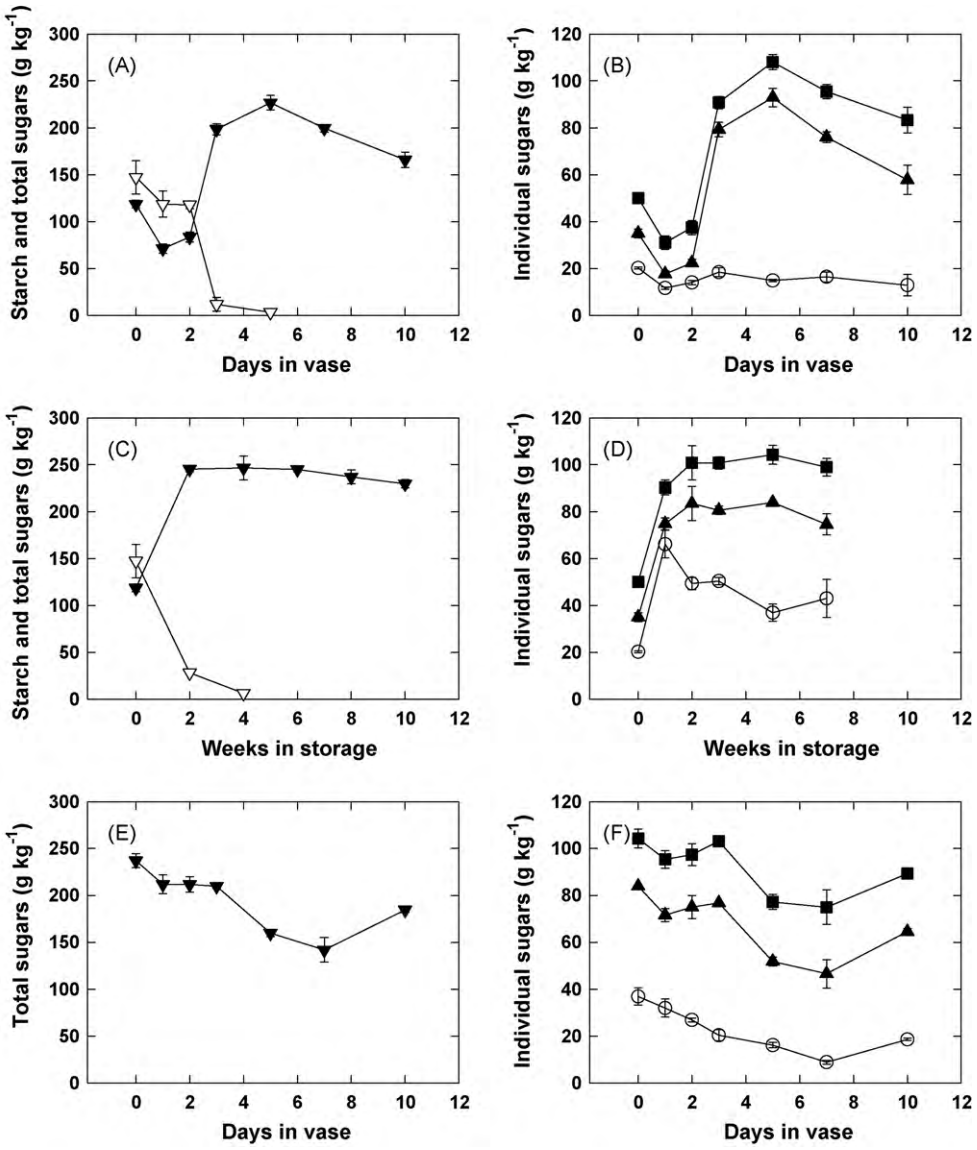

Fig. 3. Changes in the concentrations of sugars and starch in the buds/flowers of peony stems. (A) Total sugars (▼) and starch (▽) in the buds/flowers during the vase lives of fresh-cut (non-stored) stems. (B) Fructose (■), glucose (▲) and sucrose (○) in the buds/flowers during the vase lives of fresh-cut (non-stored) stems. (C) Total sugars (▼) and starch (▽) in the buds/flowers during 10 weeks of storage at 0 °C. (D) Fructose (■), glucose (▲) and sucrose (○) during 10 weeks of storage at 0 °C. (E) Total sugars (▼) during vase life after 8 weeks of storage at 0 °C. (F) Fructose (■), glucose (▲) and sucrose (○) during vase life after 8 weeks of storage at 0 °C. All data presented on a dry weight basis; error bars represent ±SEM.

3.2. Carbohydrate dynamics of fresh-cut stems

At the start of the vase life experiment on the fresh-cut stems (Day 0; 1 d after harvest), concentrations of starch and total sugars in unopened buds were approximately 150 g kg^{-1} and 120 g kg^{-1}, respectively (Fig. 3A). This indicates that approximately 27% of the bud dry weight consisted of non-structural carbohydrate. During flower opening (Days 1–5), starch concentrations declined to trace amounts, with the largest decrease occurring just prior to full bloom, as the petals started to unfurl (Stages 2 and 3 of flower opening). This decrease was accompanied by an increase in the concentrations of total sugars, which peaked when the buds had fully opened (Day 5), and then gradually decreased as the flowers senesced (Day 10).

The main sugars detected in the buds and open flowers were fructose and glucose, with much lower concentrations of sucrose (Fig. 3B). Concentrations of fructose were always higher than concentrations of glucose. After an initial drop (Days 2 and 3), fructose and glucose concentrations increased and peaked at Day 5 (Fig. 3B). The concentration of sucrose declined on Day 1, and then remained at a similar level until flowers senesced. Background levels of *myo*-inositol were detected in all tissues.

No starch was detected in the leaves or stems of the fresh-cut peony stems. The initial concentration (Day 0) of total sugars in the leaves was approximately 100 g kg^{-1}, whereas in the stems this was nearly double that, at approximately 190 g kg^{-1}. Total sugar concentrations in both the leaves and stems decreased rapidly over the first 2 d of vase life, as flower buds began to loosen and separate and by Day 6, when the flowers were fully open, the total sugars in leaves and stems were only 50% of their initial concentration. This decline was primarily due to a decrease in sucrose in leaf tissue, whereas all three major sugars (i.e. fructose, glucose and sucrose) decreased in stems.

3.3. Carbohydrate dynamics of flower stems during cool-storage

During the first 2 weeks of cool-storage, starch in the flower buds hydrolysed rapidly, with a concomitant increase in the con-

centration of total sugars (Fig. 3C), to a concentration similar to that observed in non-stored stems at flower opening. After that, the total sugar pool remained stable, declining by less than one percent during the rest of the storage period. Starch hydrolysis significantly increased fructose and glucose concentrations (Fig. 3D), similar to that during bud opening in non-stored stems. However, in contrast to fresh-cut stems, sucrose concentrations trebled by Week 2 (during starch hydrolysis) and then slowly declined until the end of the sampling period.

The total sugar concentrations in the leaves and stems of stored peony stems started at concentrations similar to fresh stems and then decreased in the first during the first 6 weeks of storage. In leaves, this decrease was primarily associated with a decline in sucrose concentration whereas decreases in total sugar concentrations of stored stems were due to decreases in all sugars.

3.4. Carbohydrate dynamics of flower stems following storage

As starch had hydrolysed during storage, total sugar concentrations in stored flower buds were at their highest at the beginning of the vase life evaluation (Day 0) (Fig. 3E), similar to those in non-stored stems at flower opening, after all the starch had been hydrolysed. The concentration of total sugars decreased gradually over the first 3 d of vase life, and then more rapidly until Day 7. Between Days 7 and 10, the concentration of total sugars rose again, during flower senescence. The pattern of fructose and glucose utilisation was similar to that of total sugars, while sucrose concentrations decreased linearly until Day 7 and then increased (Fig. 3F).

Total sugar concentrations in the leaves of stored stems showed little change during the vase life experiment (mean $59 \pm 2\,g\,kg^{-1}$). However, while the concentrations of fructose and glucose in leaves declined steadily during the vase life study, the concentration of sucrose increased, so that by Day 2, it was higher than the concentrations of other sugars (data not presented). After storage, the total sugar concentrations in the stems declined slowly, with all sugars in the stems showing a similar pattern (data not presented).

4. Discussion

4.1. Vase lives and carbohydrate dynamics of fresh-cut flower stems

The flowers on fresh-cut peony stems remained open for approximately 9 d, which was similar to that observed for stems of the same cultivar growing in the field (Walton et al., 2007), even though they were produced in different growing seasons. This is longer than the 6–7.5 d previously reported (Heuser and Evensen, 1986; Gast et al., 2001; Eason et al., 2002), and this is likely to be due to differences in growing seasons, cultivars, methods of assessment and/or growth room conditions where the vase life studies were performed. The average time to flower opening of fresh-cut stems (4.9 d) was longer than that for stems attached to the plants in the field (2 d) (Walton et al., 2007). This delay in flower opening of cut stems may be associated with the stresses induced by stem-cutting, shipping and/or maturity at harvest (Gast et al., 2001; Eason et al., 2002).

In general, patterns of carbohydrate utilisation in cut stems were similar to those of stems grown in the field (Walton et al., 2007). As flowers opened, the starch in the petal tissue was rapidly hydrolysed, with associated increases in fructose and glucose. Starch hydrolysis was more rapid in the buds of fresh-cut stems than those in the field (5 d cf. 9 d; Walton et al., 2007), and the maximum total sugar concentrations were significantly lower (approximately $225\,g\,kg^{-1}$ cf. approximately $350\,g\,kg^{-1}$; Walton et al., 2007). Total sugar concentrations in the leaves and stems of freshly cut peonies declined by approximately 50% during the vase life experiments but there was little change in these organs in the field experiment (Walton et al., 2007). In fresh-cut stems, the declines in the total sugar concentrations in leaves and stems were greatest during initial bud loosening, suggesting that they were utilised during the process of flower opening. Similar declines in leaf and stem carbohydrates were associated with flower opening in vase life studies of fresh-cut roses (Marissen and La Brijn, 1995).

Considered together, these data are consistent with additional sugars being transported into the flower, from the parent plant, as part of the normal flower opening process. An estimate of the amount required can be made by determining the difference in the sums of the sugar contents of the fresh-cut and field leaf, stem and flower portions, when the flowers are fully open. The average dry weight of an open flower was 7.7 g. As the difference in sugar concentrations was approximately $75\,g\,kg^{-1}$, this equates to approximately 0.58 g per flower. The leaf and stem dry weights from the field were on average 5.6 and 9.0 g, respectively, whereas the same values for the fresh-cut flower stems were on average 1.8 and 3.2 g, respectively. (This difference is because the fresh-cut stems were trimmed to a standard length and most of the lower leaves had been removed, as per standard commercial practice.) Consequently, the sugar contents of the leaves and stems from the field were approximately 1.12 and 1.87 g, respectively, and approximately 0.30 and 0.08 g for the fresh-cut stems, respectively. Therefore, the amount of sugar translocated into a stem during flower opening would be approximately 3.2 g, which equates to 14.3% of the dry weight of the whole stem or 42% of the dry weight of the open flower.

Given these results, one could expect that addition of sugars to the vase water could be beneficial and increase flower opening and vase life, as has been shown with other cut flower, such as roses (Kuiper et al., 1995; Ichimura et al., 1999), snapdragon (Ichimura and Hisamatsu, 1999), carnations (Paulin and Jamain, 1982) and *Grevillea* (Ligawa et al., 1997). However, adding sugar and/or floral preservatives to vase water gives variable results with peony, and is cultivar-specific (Gast, 2000). With 'Sarah Bernhardt', a 2-h pulse of a 10% solution of sucrose at room temperature ($\approx 22\,^{\circ}C$) was beneficial for stems stored for 4 weeks but not for stems stored for 8 weeks (Gast, 2000). However, given that the vase lives of cut stems in this study were similar to those of stems growing in the field (Walton et al., 2007), it would appear that availability of carbohydrate reserves was not a limiting factor for the vase life of fresh-cut peonies of the cultivar 'Sarah Bernhardt'.

4.2. Carbohydrate dynamics in peony stems during storage

Starch concentrations in the flower buds decreased rapidly during the first 2 weeks of storage and only trace amounts remained after 4 weeks. Concentrations of fructose and glucose increased during starch hydrolysis, in a similar manner to that observed during flower opening in fresh-cut stems and those attached to the plant (Walton et al., 2007). These concentrations of fructose and glucose were maintained throughout the remainder of the storage period. This can be interpreted in two ways: in the first, the normal processes of flower opening, including starch hydrolysis, continued during cool-storage, albeit at a slower rate but the lack of additional water meant that the flowers did not open. In the second, the processes associated with flower opening are slowed or suspended during storage, and that the rise in sucrose was the result of 'low temperature sweetening', an important phenomenon in the roots of many species (Wismer et al., 1995), including peony (Walton et al., 2007) where a significant proportion of starch reserves are hydrolysed in the lead-up to winter, with the onset of lower temperatures.

4.3. Carbohydrate dynamics and vase life of peony stems following storage

Peony flowers that had been stored for 8 weeks opened more quickly than those on fresh-cut stems (approximately 2 d cf. 5 d), probably because the starch in the bud had been fully hydrolysed during storage. At the beginning of the vase life period, the concentration of total sugars in stored stems was similar to the peak concentration of total sugars in fresh stems (approximately 230 g kg^{-1}), suggesting that carbohydrate supply did not limit opening of the stored stems. Instead, the shorter vase life (approximately 7.4 d cf. 9.1 d) appears to be due to starch hydrolysis occurring during the storage period. The increase in total sugars and decrease in fresh weight at the end of vase life are consistent with tissue breakdown and senescence in peony flowers (Halevy and Mayak, 1979). Similar reductions in vase life have been observed in most peony cultivars (including 'Sarah Bernhardt'), with increasing periods of cool-storage (Gast, 1997). Therefore, factors other than carbohydrate supply may determine the length of the vase life of stored 'Sarah Bernhardt' stems. However, as other peony cultivars have much shorter vase lives than 'Sarah Bernhardt', it would be useful to determine whether carbohydrate reserve status and/or the stem's ability to remobilise these reserves play a significant role in shortening the vase lives of those cultivars.

Acknowledgements

The authors thank the New Zealand Paeony Society for providing the material used in this study. This work was funded by the New Zealand Foundation for Research, Science and Technology Contract No. C02X0202.

References

Bunya-atichart, K., Ketsa, S., Van Doorn, W.G., 2004. Postharvest physiology of *Curcuma alismatifolia* flowers. Postharvest. Biol. Technol. 34, 219–226.

Eason, J., Pinkney, T., Heyes, J., Brash, D., Bycroft, B., 2002. Effect of storage temperature and harvest maturity on bud opening and vase life of *Paeonia lactiflora* cultivars. N. Z. J. Crop Hortic. Sci. 30, 61–67.

Gast, K.L.B., 1997. Fresh-cut Peonies. Kansas State University Agricultural Experiment Station and Cooperative Extension Service, Contribution No. 99-122-S.

Gast, K.L.B., 2000. Production of Postharvest Evaluations of Fresh-cut Peonies. Kansas State University Agricultural Experiment Station and Cooperative Extension Service, Contribution No. 01-210-S.

Gast, K., McLaren, J., Kampjes, R., 2001. Identification of bud maturity indicators for fresh-cut peony flowers. Acta Hortic. 543, 317–325.

Halevy, A.H., Mayak, S., 1979. Senescence and postharvest physiology of cut flowers, Part 1. Hortic. Rev. 1, 204–236.

Heuser, C.W., Evensen, K.B., 1986. Cut flower longevity of peony. J. Am. Soc. Hortic. Sci. 111, 896–899.

Ichimura, K., Hisamatsu, T., 1999. Effects of continuous treatment with sucrose on the vase life, soluble carbohydrate concentrations, and ethylene production of cut snapdragon flowers. J. Jpn. Soc. Hortic. Sci. 68, 61–66.

Ichimura, K., Kojima, K., Goto, R., 1999. Effects of temperature, 8-hydroxyquinoline sulphate and sucrose on the vase life of cut rose flowers. Postharvest. Biol. Technol. 15, 33–40.

Ichimura, K., Kisimoto, M., Norikoshi, R., Kawabata, Y., Yamada, K., 2005. Soluble carbohydrates and variation in vase life of cut rose cultivars 'Deliah' and 'Sonia'. J. Hortic. Sci. Biotechnol. 80, 280–286.

Kuiper, D., Ribot, S., van Reenen, H.S., Marissen, N., 1995. The effect of sucrose on the flower bud opening of 'Madelon' cut roses. Sci. Hortic. 60, 325–336.

Ligawa, J.K., Joce, D.C., Hetherington, S.E., 1997. Exogenously supplied sucrose improves the postharvest quality of *Grevillea* 'Sylvia' inflorescences. Aust. J. Exper. Agric. 37, 809–816.

Marissen, N., La Brijn, L., 1995. Source-sink relations in cut roses during vase life. Acta Hortic. 405, 81–88.

Miller, S.A., Smith, G.S., Boldingh, H.L., Johanssen, A., 1998. Effects of water stress on fruit quality in kiwifruit. Ann. Bot. 81, 73–81.

Paulin, A., Jamain, C., 1982. Development of flowers and changes in various during opening of cut carnations. J. Am. Soc. Hortic. Sci. 107, 258–261.

Smith, G.S., Clark, C.J., Boldingh, H.L., 1992. Seasonal accumulation of starch by components of the kiwifruit vine. Ann. Bot. 70, 19–25.

Stern, F.C., 1946. A Study of the Genus *Paeonia*. Royal Horticultural Society, London.

Van Doorn, W.G., 1997. Water relations of cut flowers. Hortic. Rev. 18, 1–85.

Walton, E.F., McLaren, G.F., Boldingh, H.L., 2007. Seasonal patterns of starch and sugar accumulation in herbaceous peony (*Paeonia lactiflora* Pall.). J. Hortic. Sci. Biotechnol. 82, 365–370.

Wismer, W.W., Marangori, A.G., Yada, R.Y., 1995. Low-temperature sweetening in roots and tubers. Hortic. Rev. 17, 203–231.