ABSTRACT

LOCKE, EMMA LOUISE. Extending Cut Flower Vase Life by Optimizing Carbohydrate Status: Preharvest Conditions and Preservative Solution. (Under the direction of John M. Dole and John D. Williamson.)

Carbohydrates have numerous roles in plants, serving as photosynthetic precursors required for growth, respirable substrates, osmoregulators, and sometimes, as osmoprotectants. Additionally, carbohydrates can act as cellular signals, controlling gene expression. In experiments with cut *Helianthus*, *Lilium*, and *Rosa*, we explored the effects of endogenous and exogenous carbohydrates on vase life and ethylene sensitivity.

Cut *Rosa* produced in South America are shipped for thousands of miles, frequently stored prior to shipment, and are held dry during shipping and storage. To see if protective carbohydrates would prevent or aid recovery from dehydration stress associated with dry shipping and storage, we conducted a number of pulsing and vase solution experiments with carbohydrates not currently used as pulsing and vase solutions. In cut *Rosa* 'Freedom', treatment with protective carbohydrates such as polyols, trehalose, and raffinose as vase solutions frequently resulted in a vase life similar to that of stems treated with sucrose, which averaged 14.6 and 15.7 days. The longest vase life for stems treated with protective carbohydrates was 13.9 and 15.5 days for one Splenda® and raffinose concentration, respectively. Vase life of water treated stems for these experiments was 13.2 and 13.9 days. In a subsequent experiment, no increase in vase life above the water control was observed for Splenda® or for either component of Splenda®, maltodextrin or sucralose, while

sucrose yielded an increased vase life. The monosaccharides glucose and fructose yielded vase life as good as, or better than, vase life of stems treated with sucrose. Fructose increased vase life by as much as 4.4 days over sucrose; a commercial preservative solution increased vase life by 4.5 days over sucrose. When sucrose, glucose, and fructose were used as vase solutions, glucose and fructose contents of petals sampled on day 6 were the same in all cases, ranging from 31.83-34.96 and 67.03-69.86 $mg \cdot g^{-1}$ dry weight for glucose and fructose, respectively. In contrast, glucose and fructose contents were decreased in water-treated roses (21.52 and 44.19 $mg \cdot g^{-1}$ dry weight, respectively). In two experiments using carbohydrates as pulsing solutions prior to shipping, and in a third experiment using carbohydrates as holding solutions prior to storage, no increase in vase life above the water control was noted for any carbohydrate solution for *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', or 'Versilia', although vase life differed by cultivar. Pulsing with solutions of abscisic acid, ascorbic acid, giberellic acid, indole-acetic acid or quercetin did not yield noticeable changes in vase life in cut *Rosa* 'Charlotte' or 'Freedom'; however, these pulses may have influenced carbohydrate content.

Some reports suggest *Lilium* species are not sensitive to ethylene, while other reports indicate otherwise. A previous report indicated that 'Stargazer' had increased sensitivity to ethylene after cold storage. We hypothesized that differences in sensitivity might be due to carbohydrate status, particularly starch levels, which can change as a result of cold exposure. To test this hypothesis, we pretreated *Lilium* of different genetic backgrounds with 1-methylcyclopropene (1-MCP) or silver thiosulfate (STS) before exposing them to a two-week cold storage period and

subsequent treatment with 10 $\mu L \cdot L^{-1}$ ethylene. Storage decreased vase life of cut *Lilium* 'Princess Amalia', 'Red Alert', 'Renoir', and 'Stargazer' by 4.1, 5.5, 5.8, and 2.0 days, respectively. Storage decreased tepal starch content and leaf sucrose content, but increased tepal sucrose and fructose content. The magnitude of changes in carbohydrate content was dependent on cultivar. Vase life was positively correlated with starch in tepals and stems plus carpels, and with sucrose in leaves, but was negatively correlated with sucrose in tepals. Ethylene treatment reduced vase life in 'Red Alert' while pretreatment with either 1-MCP or STS increased vase life in both 'Red Alert' and 'Renoir'. Postharvest bud blast during vase life evaluation differed only by cultivar, ranging from 0 to 0.24 buds per stem for 'Red Alert' and 'Renoir', respectively.

Vase life of *Lilium* 'Vermeer' and 'Dazzle' was decreased by high temperature but not by low light during production. Differences between vase life of 'Vermeer' in year 1 and 'Dazzle' in years 2 and 3 between high and low production temperatures were 0.5, 3.0, and 1.2 days, respectively. However, the number of marketable stems (stems with three or more buds) was decreased by both low light and high temperature. Out of 20 stems per crate, low light decreased the number of marketable stems by 4.5 and 5.0 stems in years 2 and 3, respectively, while high temperature decreased marketable stems by 10.2 and 12.4 stems in years 2 and 3, respectively. Vase life of *Helianthus* 'Sunbright was decreased by high production temperature in year one of the study (2.6 days) and was affected by a light and temperature interaction in year 2, where vase life tended to be decreased at high temperatures and shade promoted vase life at lower temperatures but decreased vase

life at higher temperatures. The longest vase life for *Helianthus* grown during year 2 was 15.5 days for stems grown at 10 °C night temperature in 30% shade, while the shortest vase life was 10.2 days for stems grown at 20 °C in 30% shade. Neither temperature nor light affected vase life of *Helianthus* in year 3. Temperature and light affected carbohydrates sampled during years 2 and 3 in both *Lilium* and *Helianthus*, but carbohydrates had more of an effect on the vase life and quality of *Lilium* than of *Helianthus*. When buds from a *Lilium* stem were pooled for sampling, vase life did not correlate with tepal carbohydrate content, but was correlated with carbohydrates from leaves, stems, and non-tepal inflorescence tissue. In year 2, changes in vase life of *Helianthus* correlated with changes in different carbohydrates in leaf, stem, ray floret, and non-ray floret inflorescence tissues, but in year 3, vase life was only positively correlated with sucrose in ray florets.

Extending Cut Flower Vase Life by Optimizing Carbohydrate Status: Preharvest Conditions and Preservative Solution

by
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DEDICATION

I grew up in a very conservative family and social circle where divorce was considered highly unacceptable. For this reason, my only reference for stepfamilies was the fairy tale, *Cinderella*. The thought of ever having a stepfamily filled me with pure dread.

Although I had outgrown this fear by the time my mother remarried after my dad died when I was fourteen, I was still not happy about the new people that had come into my life. My stepdad sensed what I needed, and never tried to fill my dad's shoes. He was there when I needed him but his guidance was gentle. My dad planted the seed of thought in me to go to a public university, to achieve more, but that seed was watered and fertilized by my stepdad.

I dedicate this dissertation to my stepfather, Dean Babb, because I'm not sure where I'd be without him. I did not welcome him into my life, but he was the only person who saw the problems that surrounded me and was willing and able to break through them. He's sat through three of my graduations, even though pomp and circumstance is not his cup of tea. He's helped me move, even the washer and dryer for the basement laundry room. He's the one who's held each of my nieces and nephews as babies. It's impossible to put words to who he is to me. He's never been my dad, but he is my stepdad.

BIOGRAPHY

Emma Louise Locke was born August 3, 1981, in Lamar, Colorado, to Marvin D. and Peggy L. Locke and older sisters Brenda and Karen. Her great-grandparents, Ray and Grace Locke, James and Ellen Yates, and Vital and Nellie Bamber homesteaded on the plains of southeastern Colorado in 1916, 1929, and 1918, respectively. Her fourth great-grandfather, William Ballou (m. Evelyn) was a section foreman for the Santa Fe Railroad. As a descendent of people with the tenacity to settle in the region termed "The Great American Desert" by Louisiana Purchase explorer Zebulon Pike in 1806, Emma has a stubborn, independent, problem-solving, opinionated spirit that has emboldened her when obstacles have blocked her path.

Emma attended kindergarten in Glenwood Springs, and first through eighth grades at Ordway Baptist Christian School in Ordway, Colorado from 1988-1996 while living in La Junta. When she was a child, her family frequently went tent camping, hiking, driving, and fishing in the mountains. They also drove through the cañons of southeastern Colorado, sometimes on the way to see her grandparents, other times just for pleasure. She remembers seeing tree cacti (*Opuntia imbricata*), soapweed (*Yucca glauca*), roadrunners, tarantulas, coyotes, bald eagles and thousands of LGBs—little gray birds—on those trips. Her father attempted to teach her algebra when she was in third grade. Her family visited Capulin Volcano in northern New Mexico several times and her maternal

grandparents accompanied her and her parents to Carlsbad Caverns for her 13th birthday.

Emma attended Weld Central Jr./Sr. High School in Keenesburg from 1996-2000 and Colorado State University in Fort Collins from 2000-2006 (B.S. 2004; M.S. 2006). She was advised by Steven Newman and Yaling Qian. Her early research was directed by Cecil Stushnoff and Ann McSay.

Emma began her work at North Carolina State University in August, 2006, under the direction of John M. Dole and John D. Williamson.

Emma lost her father in September, 1995; grandmother, Mary Ellen Locke, in August, 1996; grandfather, Grover Thomas Bamber, in October, 1999; and grandmother, Lois Evelyn Bamber, in November, 1999. She gained brother-in-law Danny Hayes in June, 1992; a stepfather, Dean Babb; three stepsiblings, Deanna, Jay (m. Heidi), and Curt; and three nephews, Cody, Cole, and Clay, in August, 1996. Her family was embiggened with a brother-in-law and nephew, Darrell and Joseph, in September, 1997 and six more nephews and nieces: Logan (2001), Berklie (2002), Josh (2004), Amelia (2006), Colin (2008), and Abigail (2009). Sister-in-law Amanda married Curt in July, 2005, and niece-in-law Amanda married Joseph in July, 2009.

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vent to over, well, everything, and when I needed someone to freak out over the things my dogs have decided make good food.

Michelle McElhannon, you are so selfless and always willing to give people the benefit of the doubt. You have come through for me when no one else has come through. No one else could have a broken hand, go in the hospital for a week, and still be smiling. I have faith you will come through this process shining.

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LITERATURE REVIEW

Introduction

A long postharvest life ensures that the customers – wholesalers, retailers and final consumers – will be satisfied and will return to purchase more flowers. Furthermore, consumers might be willing to pay a higher price for flowers perceived as superior. However, cut flower vase life is difficult to predict, varying by season (Van Gorsel, 1993), and by production source (Slootweg, 2005), suggesting that environmental factors, which change with time of year and from grower to grower, are responsible for discrepancies in vase life.

Four major factors during both production and postharvest that influence vase life are water relations, carbohydrate status, ethylene, and pathogens (Darras et al., 2004; Schroeder and Stimart, 2005; Slootweg, 2005). Soluble sugars not only provide substrates for respiration but also act as osmotic adjusters and may suppress ethylene biosynthesis and lower ethylene sensitivity (Pun and Ichimura, 2003). Therefore, carbohydrate status likely affects at least two of the four major factors contributing to vase life.

Preharvest conditions may affect vase life

Many studies have shown that supplying exogenous soluble sugars, sucrose in particular, tends to increase cut flower vase life (Shimamura et al., 1997; Liao et al., 2000), although effects are species specific (Han, 2003). Halevy and Mayak (1979) and Slootweg (2005) have speculated that preharvest environmental factors that alter

endogenous carbohydrate status also alter vase life. Despite support for this hypothesis from early research, preharvest effects on vase life are not well documented. Conflicting reports exist and new tools have been developed to understand biochemical mechanisms. Light, temperature, mineral nutrition, and water status have been studied previously (Halevy and Mayak, 1979). High light levels led to longer vase life in *Dianthus* and *Dendranthemum,* and supplementing flowers grown at low light levels with exogenous sugars during bud opening reduced the difference in vase life of cut stems grown at low light versus high light, further supporting the hypothesis that light affects vase life through carbohydrates (Halevy and Mayak, 1979).

In contrast to high light, high temperatures during production tend to reduce vase life (Halevy and Mayak, 1979), likely by increasing respiration rates and preventing accumulation of carbohydrate reserves. However, temperature effects are not well defined. Some reports indicate that increasing temperatures reduced vase life only at temperatures above approximately 25°C (Halevy and Mayak, 1979). Possible interactions between temperature and other factors complicate understanding temperature effects on vase life. For example, under low temperatures, carbohydrate reserves may increase, and pigments may also increase with low temperatures (Halevy and Mayak, 1979; Chalker-Scott, 1999), causing plants to use carbohydrate reserves for pigment biosynthesis. Flavonoid biosynthesis is increased by glucose, fructose, and sucrose (Weiss, 2000) and requires acetyl-CoA as a precursor (Koes et al., 1994). Although the resulting depletion of carbohydrate reserves likely decreases

vase life, anthocyanins are often induced by osmotic stress, which some have speculated help maintain water balance (Chalker-Scott, 1999).

There are also interactions among environmental factors in the production greenhouse or field. During the winter when light levels are low, the temperature is also low, retarding loss of carbohydrates. Conversely, in the summer, the loss of carbohydrates from increased respiration may be partially or completely offset by the higher light levels. During late summer and early fall, as light levels decrease but temperatures remain high, vase life of some species also declined. This may be due to decreasing carbohydrate reserves, as photosynthetic rates decline but respiration rates remain high. In recent work with field-grown *Zinnia*, vase life decreased from 15 days during the summer (July and August) to 7 days during the fall (September and early October) (J.M. Dole, unpublished data). This decrease in vase life occurred even with flowers held in floral preservatives containing sugars demonstrating that although sucrose-containing solutions alleviated endogenous carbohydrate shortages in previous studies, factors likely exist that complicate these findings (Halevy and Mayak, 1979). For example, optimum vase life of *Zinnia* was obtained using only water during the summer but using floral holding preservatives during the fall (J.M. Dole, unpublished data).

As noted earlier, soluble sugars increase cut flower postharvest vase life by providing energy for respiration and by decreasing osmotic values for increased water uptake (Halevy and Mayak, 1979; Van der Meulen-Muisers et al., 2001; Pun and Ichimura, 2003). In Asiatic *Lilium*, a carbohydrate surplus correlated with increasing

longevity (Van der Meulen-Muisers et al., 2001). Climate factors such as high CO_2 and higher light led to increased carbohydrate reserves. In turn, these climate factors correlated with longer vase life in *Freesia* (Slootweg, 2005). Furthermore, the climate during the last two weeks prior to harvest was the most important to vase life in *Freesia* (Slootweg, 2005).

Supporting the hypothesis that soluble sugars increase vase life, glucose, fructose, sucrose, and methyl glucoside were higher in petals of the long-lived *Rosa* cultivar 'Delilah' than in the short-lived cultivar 'Sonia' while *myo*-inositol and xylose concentrations were the same (Ichimura et al., 2005). Starch concentrations were higher in the petals of the short-lived cultivar and in the leaves in the long-lived cultivar (Ichimura et al., 2005). Interestingly, the long-lived cultivar 'Delilah' was more sensitive to ethylene (Ichimura et al., 2005). Furthermore, reduced quality in *Delphinium* occurs when sepal sucrose reserves become a source for the pistil, leading to reduced sepal turgor (Kikuchi et al., 2003).

Carbohydrates in vase solutions

While there is little research on endogenous carbohydrates in cut flowers and how they are affected by environment, many have researched vase solution components. For instance, the addition of sucrose to vase solutions lengthened vase life of 'Sonia' *Rosa* more than the germistat 8-hydroxyquinoline sulphate (HQS), demonstrating that for this cultivar, an available carbohydrate pool is more important to vase life than xylem hydraulic conductance (Ichimura et al., 2003). In these

studies, sucrose treatments led to higher levels of glucose, fructose, sucrose, and methyl glucoside than in cut flowers treated with distilled water or HQS, suggesting that sucrose undergoes further metabolism leading to a greater ability to retain water as the monosaccharides glucose and fructose produce a lower osmotic potential than the disaccharide sucrose. In contrast, sucrose in the vase solution of 'Stargazer' *Lilium* did not increase vase life, but sucrose did increase opening of secondary buds and increase anthocyanin content (Han, 2003).

Sucrose in floral preservative solutions can cause leaf crisping in winter-grown roses. Decreasing sucrose concentrations or adding abscisic acid (ABA) to the vase solution reduced leaf crisping (Markhart and Harper, 1995). As such, supplying other carbohydrates in the vase solution and lowering the sucrose concentration also might prevent leaf crisping. However, as Halevy and Mayak (1979) point out, non-metabolic sugars cannot enter the respiration cycle to promote vase life as energy reserves.

Protective carbohydrates

Despite the importance of sucrose as a carbon source for respiration and as an osmolyte, other sugars and sugar alcohols (or polyols), including raffinose, trehalose, mannitol, and sorbitol, have the added function of protecting plants from stress (Loescher, 1987; Bohnert et al., 1995; Pilon-Smits et al., 1998; Chiang et al., 2005; Locke and Stushnoff, 2006). The polyols mannitol and sorbitol have two important functions: acting as both osmotic adjusters and protective compounds (Loescher,

1987). Therefore, we believe these sugars and polyols could be beneficial when added to vase solutions or used as pulse treatments following harvest.

The disaccharide trehalose improves drought tolerance in transgenic tobacco (Pilon-Smits et al., 1998). Trehalose accumulated to about 0.20 mg g^{-1} dry weight, much lower than concentrations normally required for osmotic adjustment, suggesting trehalose acts as an osmoprotectant (Pilon-Smits et al., 1998; Bohnert et al., 1995; Locke and Stushnoff, 2006). Although trehalose concentrations were low in the trehalose-accumulating transgenic plants, glucose, fructose, sucrose, and starch concentrations were high (Pilon-Smits et al., 1998). As a vase solution component, trehalose was more effective than glucose, maltose, or sucrose in preventing senescence of cut gladiolus spikes, likely because fresh/dry weight ratio increased in florets held in trehalose over the control (distilled water) (Otsubo and Iwaya-Inoue, 2000). Ranwala and Miller (2009) found that trehalose increased vase life above water in cut *Tulipa*, although not as much as sucrose, and phytotoxicity was observed in trehalose-treated stems. Trehalose resulted in carbohydrate concentrations in tepals similar to concentrations of stems treated with water when leaves were left on the stem. However, when leaves were removed, trehalose treatment resulted in tepal carbohydrate concentrations similar to concencentrations of stems treated with sucrose (Ranwala and Miller, 2009).

Ichimura et al. (1999, 2000) reported that mannitol in vase solutions delayed sepal abscission in *Delphinium*, but inhibited flower opening in *Rosa* ‘Sonia’. In both cases, mannitol appeared on the petal surfaces after treatment. However, treatment

concentrations ranged from 20 to 120 $g \cdot L^{-1}$ for *Delphinium* and the concentration was 40 $g \cdot L^{-1}$ for *Rosa*. Using mannitol at such concentrations in vase solutions would be cost prohibitive at current prices. Since mannitol functions as an osmoprotectant at nanomolar concentrations (Bohnert et al., 1995; Chiang et al., 2005), a mannitol pretreatment or a very low mannitol concentration in the vase solution might increase vase life.

Sorbitol accumulation correlates with frost hardiness in several plants (Loescher, 1987). Sorbitol is also associated with boron (B) translocation in *Oryza*, due to the formation of proposed B-sugar-alcohol complexes (Bellaloui et al., 2003). This leads to the hypothesis that stress protection functions of sorbitol might be related to its ion-binding capability. Many species of the Rosaceae use sorbitol as a metabolite (Loescher, 1987). Thus, for *Rosa*, sorbitol in vase solutions could function as both an osmoprotectant and a source of energy, as the enzymes needed for sorbitol metabolism are likely present in *Rosa*. Using exogenous sorbitol for metabolism is more cost-effective than using mannitol, as the price for an equivalent weight of sorbitol is roughly 15% that of mannitol.

Ethylene sensitivity relating to carbohydrate status

Ethylene promotes senescence in many cut flower species. Work by Zhou et al. (1998) suggests that there is a connection between carbohydrate status and the ethylene pathway. They showed that application of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) induces wild type *Arabidopsis* to

exhibit the phenotype of a non-treated glucose-insensitive mutant (Zhou et al., 1998). Additionally, an *Arabidopsis* ethylene insensitive mutant had increased sensitivity to glucose compared to the wild type and this sensitivity was eliminated by crossing the ethylene insensitive mutant with the glucose insensitive mutant (Zhou et al., 1998).

Ethylene sensitivity is of great concern to growers of floriculture crops. Ethylene exposure has numerous symptoms; the most problematic for cut flower growers are abscission of leaves, flowers, and buds; bud abortion; and premature floral senescence (Dole and Wilkins, 1999; Elgar et al., 1999). Ethylene sensitivity varies widely by crop. Lilies have been characterized as sensitive (Dole and Wilkins, 1999), although there is apparently varying sensitivity based on genetic background (Elgar et al., 1999; Ranwala and Miller, 2005). Asiatic lilies, for instance, are reported to be more sensitive than Oriental lilies (Elgar et al., 1999). However, after cold storage, bud opening in Oriental lily 'Stargazer' was reduced in flowers treated with ethylene (Han and Miller, 2003). Questions regarding ethylene sensitivity are important because cut lilies are a high value floriculture crop. In 2008, the wholesale value of cut lilies produced in the U.S. by growers with over $100,000 of total floriculture sales was estimated at $72 million (NASS, 2009), the highest wholesale value of any domestic U.S. cut flower crop.

Ethylene sensitivity in lily is not well understood, despite several studies on the subject (Elgar et al., 1999; Han and Miller, 2003; Dole et al., 2005). Treatment with the anti-ethylene agents silver thiosulfate (STS) and 1-methylcyclopropene (1-MCP) increased vase life of Asiatic lily 'Polyanna' (Dole et al., 2005). In another

study, STS and 1-MCP increased vase life of Asiatic lily 'Cordelia' in summer-grown stems but not in winter-grown stems (Elgar et al., 1999). Treatment with STS or 1-MCP did not affect the vase life of Asiatic lily 'Elite' or *Lilium longiflorum* 'Lorena'. The same study found that exogenous ethylene decreased vase life of Asiatic lily hybrids 'Cordelia', 'Apeldoorn', 'Goldena', and 'Mona' as well as Oriental lily 'Casablanca' and *Lilium longiflorum* 'Lorena'. However, ethylene did not decrease vase life of Asiatic hybrids 'Romano', 'Grand Paradiso', and 'Nova Cento'; Oriental hybrids 'Cassandra' and 'Stargazer'; or *Lilium longiflorum* 'Gelria' and 'Princess Gracia' (Elgar et al., 1999).

A carbohydrate surplus was associated with increased longevity in Asiatic lily (Van der Meulen-Muisers et al., 2001), which had previously been attributed to increased substrate for respiration. However, studies with vegetative cuttings indicated that higher levels of endogenous carbohydrates reduce sensitivity to ethylene, but do not reduce ethylene production (Rapaka and Faust, 2007; Rapaka et al., 2007a; 2007b). Therefore, in cut flowers, increased endogenous carbohydrates may not only increase vase life by increasing respirable substrate, but might also decrease ethylene sensitivity. The difference in response to treatment with STS and 1-MCP, where treatments increased vase life in summer but not in winter, in Asiatic lily 'Cordelia' (Elgar et al., 1999) also points to a possible link between carbohydrate status and ethylene sensitivity. Higher summer temperatures might decrease endogenous carbohydrates, thus increasing ethylene sensitivity and thereby decreasing effectiveness of anti-ethylene agents.

In cuttings of *Portulaca grandiflora* and *Lantana camara* used for vegetative propagation, ethylene sensitivity decreased while starch levels continued to increase after levels of the soluble carbohydrates sucrose, fructose, and glucose had peaked and steadied, indicating that either starch or total carbohydrates may be linked to ethylene sensitivity (Rapaka et al., 2007a; 2007b). Glucose, fructose, and sucrose were higher in petals of the long-lived rose cultivar 'Delilah' than in the short-lived cultivar 'Sonia', while starch concentrations were higher in the petals of the short-lived cultivar and in the leaves of the long-lived cultivar (Ichimura et al., 2005). Interestingly, the long-lived cultivar was more sensitive to ethylene (Ichimura et al., 2005). In many species, *Solanum tuberosum* (potato) being the most characterized, cold storage of tubers results in the hydrolysis of starch to soluble sugars (Chen et al., 2008). We speculate that cold storage increases sensitivity to ethylene, as was seen in Oriental lily 'Stargazer' (Han and Miller, 2003), by increasing the relative levels of soluble sugars to starch.

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Vase life and postharvest characteristics of cut *Rosa* are affected by exogenous carbohydrate source

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Additional index words. Cut flower, polyol, sugar alcohol, blueing

Abstract. Cut *Rosa* produced in South America are frequently stored prior to shipment and are held dry during shipping and storage. We conducted a number of pulsing and vase solution experiments to see if protective carbohydrates and other chemicals could prevent or aid recovery from dehydration stress. For cut *Rosa* 'Freedom', vase solutions containing protective carbohydrates, such as polyols, or trehalose, and raffinose, frequently resulted in a vase life similar to that of stems treated with sucrose, averaging 14.6 to 15.7 days. The best vase life for stems treated with protective carbohydrates was 13.9 and 15.5 days for one Splenda® and one raffinose concentration, respectively. Vase life of water treated stems for these experiments was 13.2 and 13.9 days. In a subsequent experiment, no increase in vase life above the water control was observed for Splenda® or for either component of Splenda®, maltodextrin or sucralose, while sucrose yielded an increased vase life. The monosaccharides glucose and fructose yielded vase life as good as, or better than, vase life of stems treated with sucrose. Fructose increased vase life by as much as 4.4 days over sucrose; a commercial preservative solution increased vase life by 4.5 days over sucrose. When sucrose, glucose, and fructose were used as vase solutions, glucose and fructose contents of petals sampled on day 6 were the same in all cases,

ranging from 31.83 to 34.96 and 67.03 to 69.86 $mg \cdot g^{-1}$ dry weight for glucose and fructose, respectively. In contrast, glucose and fructose contents were decreased in water-treated roses (21.52 and 44.19 $mg \cdot g^{-1}$ dry weight, respectively). In two experiments using carbohydrates as pulsing solutions prior to shipping, and in a third experiment using carbohydrates as holding solutions prior to storage, no increase in vase life above the water control was noted for any carbohydrate solution for *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', or 'Versilia', although vase life did differ by cultivar. Pulsing with solutions of abscisic acid, ascorbic acid, giberellic acid, indole-acetic acid, or quercetin did not yield significant changes in vase life in cut *Rosa* 'Charlotte' or 'Freedom'; however, phytochemical pulses may have influenced carbohydrate content.

Traditionally, vase solutions have used sucrose as a carbohydrate source. Numerous studies have noted increased vase life when sucrose was used in vase solutions for cut *Rosa* (rose) (Borochov et al., 1976; Ichimura et al., 2003; Liao et al., 2000). The addition of sucrose to vase solutions lengthened vase life of 'Sonia' *Rosa* more than the germistat 8-hydroxyquinoline sulphate (HQS), demonstrating that for this cultivar, an available carbohydrate pool is more important to vase life than xylem hydraulic conductance (Ichimura et al., 2003). In these studies, sucrose treatments led to higher levels of glucose, fructose, sucrose, and methyl glucoside in petals than did treatment with distilled water or HQS. This suggests that sucrose undergoes further metabolism leads to a greater ability to retain water as the monosaccharides glucose and fructose together decrease osmotic potential more than the disaccharide sucrose (Ichimura et al., 2003). In contrast, sucrose in the vase solution of *Lilium* 'Stargazer' did not lead to increased vase life (where the end of vase life was senescence of all buds and flowers on a stem), but did increase opening of secondary buds and increase anthocyanin content (Han, 2003).

Sucrose in floral preservative solutions can cause leaf crisping in winter-grown roses, but lower sucrose concentrations or abscisic acid (ABA) in the solution negated leaf crisping (Markhart and Harper, 1995). However, non-metabolic carbohydrates cannot enter the respiration cycle and promote vase life as energy reserves (Halevy and Mayak, 1979).

Despite the importance of sucrose as a carbon source for respiration and as an osmolyte, other sugars and sugar alcohols (or polyols), including raffinose, trehalose,

mannitol, and sorbitol, have the added function of protecting plants from stress (Loescher, 1987; Bohnert et al., 1995; Pilon-Smits et al., 1998; Chiang et al., 2005; Locke and Stushnoff, 2006). The polyols mannitol and sorbitol have two important functions: acting as both osmotic adjusters and protective compounds (Loescher, 1987).

Ichimura et al. (1999, 2000) reported that mannitol in vase solutions delayed sepal abscission in *Delphinium*, but inhibited flower opening in *Rosa* 'Sonia'. Furthermore, mannitol appeared on the petal surfaces of both species after treatment. However, for *Delphinium*, treatment concentrations ranged from 20 to120 $g \cdot L^{-1}$, and for *Rosa*, the treatment concentration was 40 $g \cdot L^{-1}$. Using mannitol in vase solutions at these concentrations would be cost prohibitive at current prices. Since mannitol functions as an osmoprotectant at nanomolar concentrations (Bohnert et al., 1995; Chiang et al., 2005), a mannitol pretreatment or a very low mannitol concentration in the vase solution might increase vase life.

In addition to its proposed function as an osmoprotectant, sorbitol accumulation is associated with frost hardiness (Loescher, 1987). Sorbitol is also associated with boron (B) translocation in *Oryza*, due to the formation of proposed B-sugar-alcohol complexes (Bellaloui et al., 2003). Thus additional stress protection functions of sorbitol might be related to ion-binding capability. In many Rosaceae species, sorbitol, rather than sucrose, is the major translocated carbohydrate (Loescher, 1987). As such, sorbitol in vase solutions for *Rosa* could function as both an osmoprotectant and a source of energy, as the enzymes needed for sorbitol

metabolism are likely present in *Rosa*. Using exogenous sorbitol for metabolism is more cost-effective than using mannitol, as the current price for an equivalent weight of sorbitol is roughly 15% the price of mannitol.

The disaccharide trehalose improved drought stress tolerance in transgenic tobacco (Pilon-Smits et al., 1998). Trehalose accumulated at about 0.20 mg g^{-1} dry weight; a much lower concentration than normally required for osmotic adjustment; thus, trehalose seems to act as an osmoprotectant (Pilon-Smits et al., 1998, Bohnert et al., 1995, Locke and Stushnoff, 2006). Although trehalose concentrations were low in trehalose-accumulating transgenic plants, glucose, fructose, sucrose, and starch were highly concentrated (Pilon-Smits et al., 1998). As a component of vase solution, trehalose was more effective than glucose, maltose, or sucrose in preventing senescence of cut gladiolus spikes. The fresh/dry weight ratio increased in florets held in trehalose over the distilled water (DI) control, indicating that flowers treated with trehalose had an increased ability to either take up or retain water (Otsubo and Iwaya-Inoue, 2000). Ranwala and Miller (2009) found that trehalose increased vase life above water in cut *Tulipa*, although not as much as sucrose, and phytotoxicity was observed in trehalose-treated stems, where progressive blackening occurred on distal leaf regions and progressed to basal regions. Trehalose resulted in carbohydrate concentrations in the tepals similar to concentrations in stems treated with water when leaves were left on the stem, but when leaves were removed, trehalose treatment resulted in tepal carbohydrate concentrations similar to concentrations in stems treated with sucrose (Ranwala and Miller, 2009).

Yamada et al. (2007) and Kumar et al. (2008) demonstrated that invertase activities decrease during vase life, and that this tendency is specific to cut rather than intact roses. Oren-Shamir et al. (2001) found that blueing correlated to increasing cell sap pH. Both might be due to oxidative damage of the tonoplast, resulting in increased vacuolar pH, which could inactivate invertase and cause the absorbance shift in anthocyanins supposed to be the cause of blueing in petals of red roses. We hypothesized that treatment with hormones shown to promote invertase activity, hormones which oppose wounding responses, or antioxidants that would delay oxidative damage to the tonoplast might increase conversion of sucrose to glucose and fructose by invertase and thus delay blueing in cut roses.

A series of experiments was conducted to 1) determine if carbohydrates previously described as osmoprotectants might increase vase life when added to vase solutions, 2) determine suitable rates for application of osmoprotectant carbohydrates, 3) determine if osmoprotectant carbohydrates might prevent stress associated with shipping if applied as a pulsing solution at the production source, 4) determine if osmoprotectant carbohydrates might protect against stress associated with dry storage, 5) determine if the monosaccharide sugars fructose and glucose are more effective than the disaccharide sucrose at increasing vase life, and 6) determine if blueing can be prevented by application of plant hormones or antioxidants after cutting, and if this application might promote sustained carbohydrate metabolism, possibly by protecting membrane integrity.

Materials and Methods

General procedures. Stems were received via air transportation from a commercial supplier in Colombia and recut to 45 cm after receipt and prior to the start of vase life studies. Vase life was assessed under 20 μmol·m-2s^{-1} light supplied by fluorescent lamps for 12 hours per day and held at 40 to 60% relative humidity. Vases were filled with 300 ml of vase solution and were refilled as necessary. Kathon™ CG was added to all carbohydrate solutions at a rate of 7 ppm to prevent microbial growth. Roses were monitored daily. Vase life was defined as the number of days until roses reached an unacceptable as appearance due to petal blackening, discoloration, blueing, or wilting, or when the head of the flower bent to an acute angle with the stem. At termination, each of these conditions was rated from 0 to 10 (see Appendix 1). Leaf drop, stem blackening, and stem rot typical of botrytis infection were noted when present. To assess vase life, we used three stems per vase and five vases per treatment or treatment combination. Each vase served as a replicate, thus vases were treated as random effects for analysis. Data were analyzed using PROC MIXED in SAS, using the Kenward-Roger denominator degrees of freedom method. Means were separated using Tukey's LSD. PROC CORR was used to determine relationships between vase life and the termination criteria for each experiment.

Experiment 1. Cut *Rosa* 'Freedom' were placed in treatment vase solutions including mannitol (10 g·L^{-1}, 1 g·L^{-1}, 100 mg·L^{-1}, and 10 mg·L^{-1}), sorbitol (10 g·L^{-1}, 1 g·L^{-1}, 100 mg·L^{-1}, and 10 mg·L^{-1}), trehalose (200 mg·L^{-1}, 20 mg·L^{-1}, and 2 mg·L^{-1}),

raffinose (10 g·L^{-1}, 1 g·L^{-1}, and 100 mg·L^{-1}), Splenda® (5 g·L^{-1}, 500 mg·L^{-1}, and 50 mg·L^{-1}), galactinol (10 mg·L^{-1} and 2 mg·L^{-1}), and pinitol (500 mg·L^{-1}, 50 mg·L^{-1}, and 5 mg·L^{-1}). Both deionized water (DI) and sucrose at 10 g·L^{-1} with and without Kathon™ CG at 7 ppm were used as controls (four controls total).

Vase life was terminated when severe petal blackening, discoloration, or wilting affected three or more petals or when the head of the flower bent to an acute angle with the stem. At termination, any of these criteria affecting the cut flower stem were noted as were petal blueing, leaf drop, stem blackening, and stem rot caused by botrytis. Data were analyzed using PROC GLM in SAS (Cary, NC).

Experiment 2. Cut *Rosa* 'Freedom' were place in treatment vase solutions including fructose (50 g·L^{-1}, 10 g·L^{-1}, and 1 g·L^{-1}), mannitol (25 mg·L^{-1}, 10 mg·L^{-1}, and 5 mg·L^{-1}), mannose (10 g·L^{-1}, 1 g·L^{-1}, and 100 mg·L^{-1}), raffinose (15 g·L^{-1}, 10 g·L^{-1}, and 5 g·L^{-1}), sorbitol (5 g·L^{-1}, 1 g·L^{-1}, and 500 mg·L^{-1}), Splenda® (100 mg·L^{-1}, 50 mg·L^{-1}, and 25 mg·L^{-1}), and trehalose (500 mg·L^{-1}, 200 mg·L^{-1}, and 100 mg·L^{-1}). Sucrose with 7 ppm Kathon™ CG and DI water with and without Kathon™ CG at 7 ppm were used as controls (three controls total). Data were analyzed with PROC GLM in SAS (Cary, NC). Means were separated by Tukey's procedure.

Experiment 3. Cut *Rosa* 'Freedom' were place in treatment vase solutions including fructose at five concentrations (50 g·L^{-1}, 35 g·L^{-1}, 20 g·L^{-1}, 10 g·L^{-1}, and 5 g·L^{-1}) combined with sucrose at two concentrations (10 g·L^{-1} and 5 g·L^{-1}), fructose only at 50 g·L^{-1} and 10 g·L^{-1}, and sucrose only at 10 g·L^{-1} and 5 g·L^{-1}. DI water with and without Kathon™ CG at 7 ppm, and two commercial preservative solutions

mixed according to package directions [Chrysal Consumer (Chrysal USA, Miami, FL) and Floralife Consumer (Floralife, Inc., Walterboro, SC)] were used as controls (four controls total).

Data were analyzed with PROC GLM in SAS (Cary, NC). Means were separated by Tukey's procedure.

Experiment 4. Cut *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' stems were treated with pulsing solutions for 18 hours at the grower source in Colombia then shipped to Raleigh, NC, via air transportation. Pulsing solutions were fructose (10 $g \cdot L^{-1}$ and 50 $g \cdot L^{-1}$), mannitol (10 $mg \cdot L^{-1}$ and 50 $mg \cdot L^{-1}$), raffinose (15 $g \cdot L^{-1}$ and 75 $g \cdot L^{-1}$), sorbitol (25 $g \cdot L^{-1}$), Splenda® (25 $mg \cdot L^{-1}$ and 125 $mg \cdot L^{-1}$), and trehalose (500 $mg \cdot L^{-1}$). Tap water and sucrose (10 $g \cdot L^{-1}$ and 50 $g \cdot L^{-1}$) were used as controls. EC and pH of treatment solutions are presented in Table 1. Upon receipt in Raleigh, NC, stems were recut placed in DI water with three stems per vase and four vases per treatment. Vases were filled with 400 ml of DI water and refilled as necessary.

*Experiment 5***.** Cut *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' were recut to 50 cm after arrival in Raleigh, NC, and sorted into treatment groups. After recutting, stems were placed in carbohydrate solutions at 1 °C overnight, then were stored dry in shipping boxes for two weeks at 1 °C. Carbohydrate solutions were fructose (10 and 50 $g \cdot L^{-1}$), mannitol (10 and 50 $mg \cdot L^{-1}$), raffinose (15 and 75 $g \cdot L^{-1}$), sorbitol (25 $g \cdot L^{-1}$), Splenda® (25 and 125 $mg \cdot L^{-1}$), sucrose (10 and 50 $g \cdot L^{-1}$), trehalose (500 $mg \cdot L^{-1}$), and water (control). After storage all stems were recut to 45

cm and placed in 300 ml DI water for vase life evaluation. Three 'Freedom' stems from each treatment were weighed prior to treatment on day -14. After recutting on day 0, the stems and stem ends were reweighed, and stems were placed in DI water. Stems were weighed again 4 hours after recutting on day 0 and again on day 3.

Experiment 6. Cut *Rosa* 'Freedom' stems were placed in 500 mL treatment vase solutions: Splenda® (5 $g \cdot L^{-1}$, 100 $mg \cdot L^{-1}$, and 25 $mg \cdot L^{-1}$), maltodextrin (5 $g \cdot L^{-1}$, 100 $mg \cdot L^{-1}$, and 25 $mg \cdot L^{-1}$), and sucralose (60 $mg \cdot L^{-1}$, 1.2 $mg \cdot L^{-1}$, and 0.3 $mg \cdot L^{-1}$). Sucrose and DI water were used as controls. Data were analyzed with PROC GLM in SAS (Cary, NC). Means were separated by Tukey's procedure.

Experiment 7. Cut *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' were pulsed overnight at a commercial supplier in Colombia with mannitol (10 $mg \cdot L^{-1}$ and 50 $mg \cdot L^{-1}$), raffinose (25 $g \cdot L^{-1}$), sucrose (10 $g \cdot L^{-1}$), and tap water. All carbohydrates were dissolved in tap water and the solutions had pH and EC values as described in Table 1. After treatment, roses were shipped via air transportation to Raleigh, NC. Upon arrival, stems were placed in 400 ml DI water for vase life evaluation. Five replicate vases holding two stems each were used for each treatment.

Experiment 8. Cut *Rosa* 'Freedom' and 'Charlotte' were pulsed overnight in Colombia with six pulsing treatments: 100 μM abscisic acid (ABA), 6 mM ascorbic acid (AsA), 10 $mg \cdot L^{-1}$ giberellic acid (GA4+7), and 5 μM 1H-indole-3-acetic acid (IAA). ABA, AsA, and IAA, were dissolved into 20 ml 0.1 M potassium hydroxide then diluted into 4 L of pulsing solution. Tap water and 0.0005 M potassium hydroxide were used as control pulsing solutions. pH and EC of each pulsing

solution is presented in Table 1. After treatment, roses were shipped via air transportation to Raleigh, NC. Upon arrival, stems were placed in vase solution treatments (10 $g \cdot L^{-1}$ sucrose or DI water) for vase life evaluation. Three stems were used for each treatment combination. Each stem was used as a statistical replicate.

Experiment 9. Cut *Rosa* 'Freedom' were placed in jars filled with 400 ml of treatment solution. Vase solution treatments were fructose (5 $g \cdot L^{-1}$, 10 $g \cdot L^{-1}$, 25 $g \cdot L^{-1}$, and 50 $g \cdot L^{-1}$) and glucose (5 $g \cdot L^{-1}$, 10 $g \cdot L^{-1}$, 25 $g \cdot L^{-1}$, and 50 $g \cdot L^{-1}$). Sucrose (10 $g \cdot L^{-1}$) was used as a control. Water uptake was measured on day 4. Additional blueing and appearance ratings were taken on days 7 and 10.

Experiment 10. Cut *Rosa* 'Freedom' and 'Charlotte' stems were placed in 400 ml of treatment solutions. Treatments included 10 $g \cdot L^{-1}$ fructose, glucose, or sucrose, Premium Rose Flower Food (Floralife, Inc., Walterboro, SC), RoseProTM by Chrysal (Chrysal USA, Miami, FL), and DI water (as a control). Water uptake was measured on day 4.

Experiment 11. Cut *Rosa* 'Freedom' was pulsed overnight in Colombia with one of six pulsing treatments: 100 μM abscisic acid (ABA), 6 mM ascorbic acid (AsA), 10 $mg \cdot L^{-1}$ giberellic acid (GA4+7), 5 μM 1H-indole-3-acetic acid (IAA), and 3.4 $mg \cdot L^{-1}$ quercetin. IAA and quercetin were dissolved in 2 ml 80% ethanol then diluted into 2 L of pulsing solution. Tap water and 0.08% ethanol were used as control pulsing solutions. After treatment, roses were shipped via air transportation to Raleigh, NC. Upon arrival, stems were placed in vase solution treatments (10 $g \cdot L^{-1}$ fructose, glucose, sucrose, or DI water) for vase life evaluation. Three additional

stems for each treatment combination were sacrificed on day 1 and day 6 of vase life for analysis of electrolyte leakage and/or carbohydrate content.

Electrolyte leakage was tested after Valenzuela-Vázquez et al. (2007). A representative sample of petals from inner, middle and outer whorls was weighed, immersed in distilled, DI water and water was tested with an EC meter after 24 hours. Tubes containing petals and water were frozen at -20 °C and EC was measured a second time. EC of fresh tissue was divided by EC of frozen tissue to calculate relative leakage ratio (RLR).

Petal tissue was weighed, flash frozen, freeze dried, and pulverized. Carbohydrates were extracted as follows: approximately 100 mg was extracted in 3 ml ethanol and 1 ml 20 $mg \cdot ml^{-1}$ mannitol as an internal standard. Samples were vortexed to suspend dried tissue, placed in sonicating water bath for 5 min. and heated in an 80 °C water bath for 5 min. before being centrifuged at 3000xg for 5 min at 4 °C. The supernatant was removed to a new tube. The pellet was resupended in 3 ml ethanol, vortexed, sonicated, heated in an 80 °C water bath, centrifuged, and the supernatant removed twice more. Total supernatant for each sample was 10 ml (9 ml ethanol + 1 ml internal standard). Aliquots (500 μL) of the supernatant were dried in a rotary evaporator then stored at -20 °C until reconstitution and analysis. Samples were reconstituted in 500 μL distilled/DI water, centrifuged to remove remaining particulate matter, and analyzed by HPLC (LaChrom Elite, Hitachi, Pleasanton, CA) equipped with a refractive index detector using an isocratic gradient of distilled/DI water with a flow rate of 0.4 $ml \cdot min^{-1}$. A calcium column (BP-100 Ca++, Benson

Polymeric, Reno, NV) was used for separation. A standard curve containing sucrose, glucose, fructose, mannitol, and sorbitol (each at 10, 5, 2, 1, and 0 $g \cdot L^{-1}$) was used for peak quanitification. Calculations were based on peak height and the mannitol internal standard was used to normalize peak heights.

Residual starch from soluble carbohydrate extractions was quantified after Ranwala and Miller (2008 and 2009). The pellet left after soluble carbohydrate extraction was boiled for 30 min in 4 ml 100 mM Na-acetate buffer adjusted to pH 4.5 with 1 N acetic acid and subsequently cooled to room temperature. One ml amyloglucosidase solution (50 $units \cdot ml^{-1}$ in Na-acetate buffer, pH 4.5) was added to digest each sample and incubated at 50-55 °C for 2 days. After digestion, samples were centrifuged at 3000xg. One hundred microliters (100 µl) of the cleared supernatant was removed to a new tube and 5 ml of cold phosphate buffer containing with 5 $units \cdot ml^{-1}$ glucose oxidase, 1 $unit \cdot ml^{-1}$ horseradish peroxidase, and 40 $\mu g \cdot ml^{-1}$ *o*-dianisidine were added. Samples were incubated at 30 °C for 30 min before absorbance was read in a spectrophotometer (Lambda Bio20, Perkin Elmer, Waltham, MA) at 450 nm. Glucose concentration was calculated using a glucose standard curve. Due to evaporation of liquid during the digestion process, a concentration factor was calculated based on the approximated remaining volume of liquid after digestion for each sample and used to adjust final starch calculations. Amyloglucosidase blanks and potato starch digests were used as controls. All enzymes used for starch digestion were obtained from Sigma (St. Louis, MO). In addition to the statistical procedures used in all experiments, PROC CORR was used

to compare mean carbohydrate contents to mean vase life and postharvest characteristics for each treatment.

Experiment 12. Cut *Rosa* 'Freedom' stems were stored for two days at 4°C before vase life evaluation. Vase solutions were formulated with fructose (10 $g \cdot L^{-1}$), sucrose (10 $g \cdot L^{-1}$) or DI as a primary carbohydrate source and with mannitol (5 and 10 $mg \cdot L^{-1}$), mannose (5 $g \cdot L^{-1}$), raffinose (5 and 10 $g \cdot L^{-1}$), sorbitol (1 and 5 $g \cdot L^{-1}$), Splenda® (25 $mg \cdot L^{-1}$), trehalose (200 $mg \cdot L^{-1}$), or DI as protective carbohydrate sources. Jars were filled with 500 ml vase solution. Water uptake was measured on day 4 of vase life.

Results

Experiment 1. At least one tested concentration of mannitol, raffinose, sorbitol, Splenda®, and trehalose had similar vase life to the Sucrose + Kathon™ CG control (Table 2). The following treatments had a vase life less than that of DI water: mannitol 10 $g \cdot L^{-1}$, raffinose 100 $mg \cdot L^{-1}$, Splenda® 5 $g \cdot L^{-1}$, sucrose, and trehalose 20 $mg \cdot L^{-1}$. Mannitol at 10 $g \cdot L^{-1}$ caused marginal necrosis and chlorosis of leaves.

As expected, a dosage effect was seen with mannitol and Splenda®, where low to intermediate concentrations resulted in longer vase life than higher concentrations likely because higher concentrations had phytotoxic effects. Most notably, stems treated with 50 $mg \cdot L^{-1}$ Splenda® had a vase life 2.5 days shorter than the 5 $g \cdot L^{-1}$ concentration (Table 2).

Petal discoloration was less prevalent in the sucrose controls (Table 2), except for the treatments 5 g·L^{-1} Splenda®, 10 g·L^{-1} raffinose, and 10 g·L^{-1} mannitol, which were not significantly different from 10 g·L^{-1} sucrose + Kathon™ CG.

Petal wilting was seen in 53% of 10 g·L^{-1} sucrose + Kathon™ CG stems (Table 2). Compared to the 10 g·L^{-1} sucrose + Kathon™ CG control, 10 g·L^{-1} raffinose had increased petal wilting (93%), while the following treatments showed decreased wilting: 10 mg·L^{-1} sorbitol (20%), DI water + Kathon™ CG (13%), 500 mg·L^{-1} pinitol (13%), 50 mg·L^{-1} pinitol (7%), and 10 mg·L^{-1} galactinol (7%).

Bent neck was most severe in 10 g·L^{-1} sucrose without Kathon™ CG (87%) and in 5 g·L^{-1} Splenda® (60%) (Table 2). The remaining treatments showed significantly less bent neck and were similar to the sucrose + Kathon™ CG control.

At termination, petal blueing was visible on 100% of stems treated in the 10 g·L^{-1} sucrose + Kathon™ CG control (Table 2). Treatments showing less blueing than this control were 100 mg·L^{-1} mannitol (80%), 5 g·L^{-1} Splenda® (67%), and 10 g·L^{-1} sucrose without Kathon™ CG (60%).

Stems treated with the highest concentrations of trehalose and mannitol had the most leaf drop (Table 2). No leaf drop was seen in the Sucrose + Kathon™ CG control or in stems treated with 10 g·L^{-1} raffinose and in only 7% of stems treated with 10 g·L^{-1} sorbitol or the sucrose without Kathon™ CG control (Table 2). Four treatments, raffinose (10 g·L^{-1}); sorbitol (10 g·L^{-1}); sorbitol (1 g·L^{-1}); and pinitol (5 mg·L^{-1}), were not significantly different from the sucrose + Kathon™ CG control for either length of vase life or percentage of stems exhibiting leaf drop.

There were no treatment differences in petal blackening (P=0.1878), stem blackening (P=0.6073), or neck rot (P=0.0527) caused by botrytis.

Experiment 2. Vase life ranged from 11.3 days for roses treated with 25 mg·L^{-1} mannitol to 20.1 days for roses treated with 50 g·L^{-1} fructose (Table 3). At least one concentration of each carbohydrate tested resulted in a vase life similar to that of the sucrose + Kathon^{TM} CG control (Table 3). Petal discoloration was reduced in stems treated with 25 mg·L^{-1} mannitol and 500 mg·L^{-1} trehalose; however, these treatments also had low vase life (Table 3). Vase life and petal discoloration were correlated for this experiment (Table 4). Petal wilting was lowest in stems treated with 10 g·L^{-1} mannose; vase life for this treatment was not different from the sucrose control (Table 3). Bent neck was higher in stems treated with 25 mg·L^{-1} mannitol than in all other treatments (Table 3). The mannitol (25 mg·L^{-1}) treatment also had low petal blueing, but again, vase life was short; fructose (50 g·L^{-1}) had less petal blueing than the sucrose control and also a vase life 4.4 days longer than the sucrose control. Increased petal blackening was seen in fructose at 10 and 50 g·L^{-1}; at least one concentration of all other sugars except sorbitol resulted in reduced petal blackening compared to the sucrose control, often with vase life similar to the sucrose control. Fructose (10 g·L^{-1}), mannose (1 g·L^{-1}), raffinose (10 g·L^{-1}), and Splenda® (25 mg·L^{-1}) increased flower opening compared to the sucrose control. High levels of phytotoxicity, as exhibited by chlorosis, crisping, and/or leaf drop rather than in vase life, were seen in treatments of mannose (1 and 10 g·L^{-1}), raffinose (10 and 15 g·L^{-1}), sorbitol (1 and 5 g·L^{-1}), and trehalose (200 mg·L^{-1}) (Table 3). Stem blackening was

seen in DI water, 1 $g \cdot L^{-1}$ fructose, 5 $mg \cdot L^{-1}$ mannitol, 100 $mg \cdot L^{-1}$ mannose, 500 $mg \cdot L^{-1}$ and 1 $g \cdot L^{-1}$ sorbitol, all concentrations of Splenda®, and 100 and 200 $mg \cdot L^{-1}$ trehalose.

Experiment 3. Vase solution had a significant effect on vase life. Vase life ranged from 9.3 days for stems treated with 10 $g \cdot L^{-1}$ sucrose plus 50 $g \cdot L^{-1}$fructose to 18.9 days for stems treated with fructose alone (10 $g \cdot L^{-1}$). A dosage effect was observed in these roses, with a decrease in vase life being associated with total carbohydrate concentrations at or above 30 $g \cdot L^{-1}$ (Table 5).

Vase solution treatments also significantly affected each of the termination criteria. Of note, high levels of petal discoloration were associated with the water control and with several other treatments (Table 5). Interestingly, petal blackening did not seem to be linked with total carbohydrate concentration as sucrose at either 5 or 10 $g \cdot L^{-1}$ plus fructose at 50 $g \cdot L^{-1}$ were among the treatments that resulted in low levels of petal blackening, although this condition may not have had sufficient time to develop in these treatments as they had the shortest vase lives (Table 5). Petal wilting was lower in flowers treated with DI water plus Kathon™ CG than in flowers treated with DI water without Kathon™ CG or than in stems treated with 35 $g \cdot L^{-1}$ fructose in combination with sucrose at 5 or 10 $g \cdot L^{-1}$ (Table 5). DI water without Kathon™ CG and sucrose (10$g \cdot L^{-1}$) plus fructose (50 $g \cdot L^{-1}$) increased bent neck compared to the sucrose control (Table 5). Petal blueing was lower in stems treated with 50 $g \cdot L^{-1}$ fructose in combination with sucrose at 5 or 10 $g \cdot L^{-1}$ than in the control; however these two fructose/sucrose treatments also had the lowest vase lives (Table 5).

Flowers treated with Chrysal professional were the most open. Stem blackening, leaf drop, and rot were highest in the DI water and DI water plus Kathon^{TM} CG controls compared to all other treatments (Table 5), indicating that all carbohydrate treatments may have allowed stems to recover from shipping stress.

Experiment 4. There was a significant treatment by variety interaction for vase life, bent neck incidence, stem blackening, and leaf drop in cut *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' pulsed in Colombia with different carbohydrate solutions prior to shipping (Table 6). Because of the high number of significant differences for vase life, we chose to analyze vase life and termination criteria individually for each cultivar. Since the cultivars are each economically important, it is valuable to know the best treatments for each. There were no significant differences for vase life or any of the termination criteria for 'Freedom' or 'Polo' (Table 6).

As shown in Table 6, pulsing with sucrose at 50 g·L^{-1} resulted in the best vase life for 'Judy' at 13.3 days while mannitol at 10 mg·L^{-1} resulted in the lowest (8.8 days). Appearance at termination rated from 0 to 10 (0 best; 10 poor) was better for stems pulsed with sorbitol (25 g·L^{-1}) than for those pulsed with sucrose (10 g·L^{-1}). Percentage of stems showing leaf drop, a potential indicator of phytotoxicity, was highest in stems treated with sucrose (10 g·L^{-1}) and lowest in stems treated with fructose (50 g·L^{-1}), raffinose (15 g·L^{-1}), and sucrose (50 g·L^{-1}).

Treatment significantly affected stage of opening for ‘Verdi’ (Table 6). Splenda® (25 mg·L^{-1}) was associated with a higher stage of opening than sorbitol (25 g·L^{-1}) or sucrose (10 g·L^{-1}).

Pulsing treatments did not affect vase life in ‘Versilia’; however, several treatments (fructose at 50 g·L^{-1}, sorbitol at 25 g·L^{-1}, Splenda® at 25 mg·L^{-1}, and sucrose at 10 and 50 g·L^{-1}) were associated with lower incidence of bent neck than with mannitol (10 mg·L^{-1}) and the water control (Table 6). Raffinose at 15 g·L^{-1} increased petal blackening compared to the control.

Appearance, petal discoloration, petal wilting, petal blueing, petal blackening, stage, and incidence of neck rot caused by botryis were affected by a cultivar main effect but not by an interaction between pulsing treatment and cultivar (Table 7). Vase life was greatest in ‘Versilia’, followed by ‘Freedom’ and ‘Verdi’, then ‘Polo’, with ‘Judy’ having the shortest vase life (Table 7). Appearance in ‘Judy’ was poorest at termination; this cultivar also had a high rating for petal discoloration, while little discoloration was seen in ‘Polo’ and ‘Versilia’ (Table 7). Petal wilting was greatest in ‘Verdi’, with no differences among the other cultivars (Table 7). ‘Polo’ had high levels of bent neck, which is not surprising, as this cultivar has a very large flower; ‘Verdi’ and ‘Versilia’ had low levels of bent neck (Table 7). Petal blueing was only seen in ‘Freedom’, the red cultivar, and, to a lesser extent, ‘Verdi’, which has pink edges (Table 7). Petal blackening was highest in ‘Freedom’ and lowest in ‘Polo’; ‘Judy’ had less petal blackening than ‘Verdi’ (Table 7). ‘Polo’ and ‘Verdi’ open to the greatest extent, followed by ‘Freedom’ then ‘Judy’, then ‘Versilia’ (Table 7).

Stem blackening was seen most in ‘Versilia’, while very little was seen in ‘Judy’, ‘Polo’, and ‘Verdi’ (Table 7). Leaf drop was seen in ‘Verdi’ and ‘Versilia’ at high levels, while ‘Judy’ had higher levels of leaf drop than ‘Polo’. Neck rot was seen most in ‘Versilia’, although it was not significantly different than in ‘Verdi’. ‘Freedom’ and ‘Polo’ had the lowest levels of leaf drop, though not different than ‘Judy’ (Table 7). Petal discoloration was affected by a pulsing treatment main effect, where discoloration increased in stems pulsed with raffinose at 75 $g \cdot L^{-1}$ (rating of 4.4 on 0-10 scale) more than in those pulsed with 50 $mg \cdot L^{-1}$ mannitol (rating of 2.5 on 0-10 scale).

Experiment 5. Roses treated with water had more petal discoloration than those treated with 10 $g \cdot L^{-1}$ sucrose (mean ratings for water and sucrose were 3.0 and 1.9, respectively); there was not a significant treatment by variety interaction for vase life or any other postharvest characteristic. There was a significant cultivar effect for all dependent variables, indicating that each cultivar senesced in a different manner with regard to termination criteria, and with different timing. For the cultivar main effect, vase life ranged from 6.8 days for Judy to 17.6 days for Versilia (Table 8). ‘Judy’ and ‘Polo’ had an improved appearance over the other cultivars at termination (Table 8). Petal discoloration was seen least in ‘Judy’ and ‘Polo’ and most in ‘Freedom’ and ‘Versilia’ (Table 8). Petal wilting was decreased in ‘Polo’ (Table 8). Bent neck was seen most in ‘Judy’ and ‘Polo’ and least in ‘Verdi’ and ‘Versilia’ (Table 8). Petal blueing was seen only in ‘Freedom’ (Table 8). Petal blackening was seen least in ‘Polo’; ‘Freedom’ had more petal blackening than ‘Verdi’ (Table 8).

Stage of opening ranked from most open to least open as follows: 'Polo', 'Verdi', 'Judy', 'Freedom', 'Versilia' (Table 8). Stem blackening was greatest in 'Freedom' and least in 'Verdi' and 'Versilia' (Table 8). The highest percentages of leaf drop were seen in 'Freedom', 'Verdi', and 'Versilia' (Table 8).

Holding solution affected weight of cut 'Freedom' stems after removal from storage but did not affect their ability to rehydrate following storage. Two treatments, Splenda® and trehalose, had a significant increase in fresh weight; after treatment, both were 106% of their weight prior to treatment, while treatment with sorbitol decreased fresh weight, which was 96% of the weight prior to treatment. There were no significant differences for weights at four hours after recutting on day 0 or on day 3 when they were expressed as a percentage of the weight on day 0 (Table 9). This indicates that although certain holding solutions might have allowed increased imbibition of water during treatment and/or an ability to retain water during storage, they did not allow increased rehydration following storage.

Experiment 6. Vase life was longer for the sucrose vase solution control than for any other treatment, amongst which there were no differences in vase life (Table 9). Because Splenda® at 50 mg·L^{-1} previously (Experiment 1) extended vaselife of cut rose stems, we expected that the component of Splenda® causing the treatment effects should have the same effect as Splenda® alone. However, Splenda® at the highest treatment concentration used here instead increased petal wilting, its only difference from the sucrose control and the highest sucralose concentration (Table 9). The sucrose control had the least stem blackening, followed by maltodextrin at 100

mg·L^{-1}, which was not significantly different from Splenda® at the highest concentration. All other treatments had very high levels of stem blackening (Table 9). Leaf drop was high in all treatments and the water control was not significantly different than the sucrose control (Table 9).

Experiment 7. Vase life was only different by cultivar in stems pulsed with carbohydrate solutions prior to shipping. 'Versilia' had the longest vase life, while 'Judy' had the shortest (Table 10). Petal discoloration, petal wilting, bent neck, petal blueing, petal blackening, neck rot, and petal flop were also different only by cultivar (Table 10). The interaction of pulsing solution with cultivar showed that appearance was improved in 'Polo' treated with mannitol at 10 mg·L^{-1} and water than in many of the treatments in other cultivars (Table 11). Mannitol (10 mg·L^{-1}) treatment in 'Judy' resulted in flowers that were more open than 'Judy' treated with sucrose and water, while there were no differences in opening for the other cultivars (Table 11). Stem blackening was affected by treatment in 'Freedom', 'Verdi', and 'Versilia', while there was no stem blackening for any treatment in 'Judy' and 'Polo' (Table 11). Similarly, leaf drop was affected by treatment in 'Freedom', 'Polo', 'Verdi', but not in 'Versilia', or in 'Judy' (Table 11). Petal shatter was only affected in'Judy', 'Polo', and 'Verdi', and amongst these, 'Polo' treated with raffinose had decreased petal shatter compared to 'Polo' treated with mannitol (50 mg·L^{-1}) and sucrose (Table 11).

Experiment 8. To explore the possibility that plant hormones and antioxidants protect the tonoplast and/or at least one invertase (probably vacuolar acid invertase), we pulsed cut *Rosa* 'Charlotte' and 'Freedom' with plant hormones prior to shipment,

then, after receipt, used either sucrose or water as vase solutions. The potassium hydroxide pulsing control decreased vase life compared to abscisic acid (Table 12). Pulsing with indole-acetic acid resulted in less petal discoloration than pulsing with water (Table 12). Postharvest use of sucrose vase solution increased vase life, and decreased bent neck, petal blueing, stem blackening, and leaf drop, but increased petal discoloration and petal blackening (Table 12). There was no difference between the vase life of 'Charlotte' and 'Freedom'; however, 'Charlotte' decreased petal discoloration, petal blueing, stem blackening, and leaf drop compared to 'Freedom' (Table 12).

Weights taken four hours and three days after placement in vase solutions were affected by cultivar by pulsing solution and cultivar by vase solution interactions. When compared to weights taken after recutting and before placement in vase solution treatments, water increased weight gain in 'Charlotte' compared to sucrose (105% of initial weight compared to 103%, respectively), while there was no difference between sucrose and water treatments after four hours in 'Freedom'. After three days, 'Freedom' pulsed with ABA retained water better than stems pulsed with AsA, GA, IAA, or KOH (percent of initial weights were 107, 100, 100, 99, and 100, respectively); while there were no differences between pulsing treatments for 'Charlotte' at three days.

Experiment 9. Vase life of stems treated with fructose, glucose, and sucrose vase solutions ranged from 13.1 days (glucose 5 $g \cdot L^{-1}$) to 16.5 days (glucose 50 $g \cdot L^{-1}$). Appearance was poor for stems treated with glucose (5 $g \cdot L^{-1}$) (Table 13).

Fructose (50 g·L^{-1}) decreased petal discoloration compared to glucose at 5, 10, and 50 g·L^{-1} (Table 13). Glucose (5 g·L^{-1}) increased petal wilting compared to fructose (25 g·L^{-1}), and glucose (10 and 25 g·L^{-1}); this same treatment increased bent neck compared to fructose (25 and 50 g·L^{-1}) and glucose (25 and 50 g·L^{-1}) (Table 13). The 5 g·L^{-1} glucose treatment also increased petal blueing compared to fructose (10, 25, and 50 g·L^{-1}) and glucose (25 and 50 g·L^{-1}) (Table 13). Fructose (5 g·L^{-1}) increased stem blackening compared to all other treatments except fructose at 10 g·L^{-1} (Table 13). There were no significant differences in blueing and appearance at days 7 and 10.

Experiment 10. Floralife® Premium Rose Flower Food (Floralife) increased vase life in 'Freedom' compared to RosePro™ by Chrysal (Chrysal), sucrose and water, but was not different from fructose or glucose (Table 14). Possiel (2008) indicated that commercial preservative solution performance is highly dependent on variety. Fructose and glucose also increased vase life compared to sucrose and water. Increased wilting was associated with use of water as a vase solution compared to Floralife and fructose (Table 14). Water treated stems also had increased bent neck compared to Floralife, fructose, and glucose (Table 14). The Floralife treatment decreased bent neck compared to all other vase solutions (Table 14). Chrysal had decreased petal blackening compared to glucose (Table 14). Stage of opening was highest in Floralife and Chrysal and lowest in stems treated with sucrose and water (Table 14). Floralife increased water uptake compared to fructose, sucrose, or water (Table 14).

In this experiment, ‘Freedom’ had a longer vase life than ‘Charlotte’ and also showed decreased petal wilting (Table 14). Compared to ‘Freedom’, ‘Charlotte’ had decreased petal discoloration, petal blueing, and petal blackening (Table 14). There was a significant treatment by cultivar interaction for petal blueing where treatment did not affect petal blueing in ‘Charlotte’, but blueing was decreased in stems treated with Floralife, fructose, and glucose compared to water in ‘Freedom’ (Table 14). For ‘Freedom’, blueing was also decreased in fructose treated stems compared to sucrose (data not presented). ‘Charlotte’ had higher levels of blueing than ‘Freedom’ for all treatments except water (data not presented). There was also a treatment by cultivar interaction for leaf drop, where none of the treatments resulted in leaf drop in ‘Charlotte’, but treatment with Chrysal and water resulted in 33% and 20% leaf drop, respectively, in ‘Freedom’ (Table 14).

Experiment 11. To determine if a pulsing solution caused sucrose to affect vase life in a similar manner to glucose and fructose, we separated vase solution means within pulsing solution to deal with the significant interaction. Vase lives of roses treated with ABA, AsA, GA, and quercetin were affected by vase solution, with either fructose or glucose resulting in a vase life greater than that of water for each of these pulsing solutions (Table 16). Sucrose did not significantly decrease vase life compared to glucose or fructose for any of the pulsing solutions (Table 16). Petal wilting, petal blueing, stem blackening, and leaf drop were all greater for stems treated with water compared to sucrose, glucose, and fructose treatments (Table 15).

Bent neck was increased in water and sucrose treated stems compared to fructose and glucose treated stems (Table 15).

Vase life of 'Freedom' was affected by a pulse solution by vase solution interaction. We chose to separate means by vase solution within pulse solution as we were concerned with how the pulsing treatments affected metabolism of the carbohydrates in the vase solutions. Generally, treatment with carbohydrates extended vase life longer than treatment with water. There were no differences between treatment with sucrose and treatment with either glucose or fructose for any pulsing solution (Table 16).

Appearance, petal discoloration, and stage of opening were also affected by a pulse solution by vase solution interaction. Water resulted in a poor appearance compared to all other vase solutions for ethanol-pulsed stems; petal discoloration was also increased in the water treated stems compared to glucose treated stems within this group. Glucose treated flowers were more open (stage) than those treated with sucrose in ethanol-pulsed stems while glucose treated flowers were more open than water treated flowers among stems pulsed with giberellic acid (Table 16).

Vase solution had a main effect on weights taken on day 3 where fructose, glucose, and sucrose allowed greater water uptake and retention than did water, with percent of initial weight equaling 116, 115, 113, and 107, respectively, for fructose, glucose, sucrose, and water. Pulsing solution did not have an effect on percent weight on day 3 or at hour 4 on day 0, where percent of initial weight averaged 107.

Petal starch was affected by sampling date only, averaging 1.21 mg per gram dry weight on day 1 and 0.95 mg per gram dry weight on day 6. A pulsing solution by sampling day interaction affected petal sucrose, but means were not separable and the interaction is not presented. Means ranged from 3.97 to 10.71 mg per gram dry weight on day 1 and from 4.58 to 8.14 mg per gram dry weight on day 6 (data not shown). Glucose and fructose in petals were both affected by a pulsing solution main effect and a vase solution by sampling date interaction (Table 17). A tap water pulse resulted in higher levels of petal glucose than did the IAA pulse and higher levels of petal fructose than all pulsing treatments except ascorbic acid (Table 17). Fructose and sucrose as vase solutions resulted in higher levels of glucose in petals on day 6 than did water as a vase solution while all three carbohydrates (fructose, glucose, and sucrose) as vase solutions resulted in higher fructose on day 6 than did water as a vase solution (Table 17). Additionally, glucose decreased in petals of the water treated stems from day 1 to day 6 and fructose in petals was higher on day 6 than on day 1 for stems treated with fructose, glucose, and sucrose (separations not shown, but data presented in Table 17). Sorbitol was undetectable in numerous samples, which were treated as missing data values. The missing data did not allow sufficient denominator degrees of freedom to analyze interactions affecting sorbitol levels. Sorbitol was not affected by pulsing solution, vase solution, or sampling date, and averaged 3.41 $mg \cdot g^{-1}$ dry weight. Samples for electrolyte leakage were taken on day 1 of vase life only. Relative leakage ratio affected by a pulsing solution by vase solution interaction where relative leakage of petals on stems pulsed with ABA and held in a

fructose vase solution was higher than those pulsed with ABA and held in sucrose as a vase solution (Table 18). Stems pulsed with ABA and held in fructose as a vase solution also had higher relative leakage than stems pulsed with ascorbic acid or water when fructose was used as a vase solution (mean separation not shown).

We used Pearson correlations to find relationships between treatment means of vase life, relative leakage ratio, and carbohydrates sampled on days 1 and 6. Vase life was positively correlated with levels of petal glucose and fructose on day 6 (r=0.56, p=0.002) and (r=0.59, p=0.0009), respectively. Starch sampled on days 1 and 6 and relative leakage ratio had no significant correlations. Sucrose sampled on day 1 was positively correlated with glucose and sorbitol sampled on day 1 (r=0.59, p=0.001) and (r=0.45, p=0.0202), respectively. In addition to the sucrose correlation, glucose sampled on day 1 was also positively correlated to fructose (r=0.59, p=0.0009) and sorbitol (r=0.52, 0.0068) sampled on day 1, but was negatively correlated to sucrose sampled on day 6 (r=-0.47, p=0.0107). As previously mentioned, glucose and fructose sampled day 6 were positively correlated to vase life and were also positively correlated with each other (r=0.89, p<0.0001). Sorbitol sampled on day 6 had no significant correlations.

Experiment 12. The type of primary carbohydrate in a vase solution had a main effect on petal wilting where fructose decreased wilting compared to water (Table 19). Petal blackening was increased in fructose and sucrose treated stems compared to water treated stems (Table 19).

Primary carbohydrate by protective carbohydrate interactions affected vase life, appearance, petal discoloration, bent neck, stem blackening, and leaf drop in stems treated with combinations of fructose, sucrose, or water plus mannitol (5 or 10 $mg \cdot L^{-1}$), mannose (5 $g \cdot L^{-1}$), raffinose (5 or 10 $g \cdot L^{-1}$), sorbitol (1 or 5 $g \cdot L^{-1}$), Splenda® (25 $mg \cdot L^{-1}$), trehalose (200 $mg \cdot L^{-1}$), or water. We chose to separate means by protective carbohydrate within primary carbohydrate as we hypothesized that adding a protective carbohydrate to a primary carbohydrate would increase vase life above that of the primary carbohydrate alone. For stems treated with fructose as a primary carbohydrate, vase solutions containing mannitol (5 $mg \cdot L^{-1}$) and trehalose (200 $mg \cdot L^{-1}$) had a longer vase life than stems treated with raffinose (5 $g \cdot L^{-1}$) (Table 20). For stems treated with water in combination with protective carbohydrates, stems treated with raffinose (5 $g \cdot L^{-1}$) had a longer vase life than those treated with mannose (5 $g \cdot L^{-1}$), sorbitol (5 $g \cdot L^{-1}$), or with only water (Table 20).

For stems treated with water plus protective carbohydrates, stems treated with trehalose had greater petal discoloration than did stems treated with mannose. Stems treated with water in combination with raffinose (5 $g \cdot L^{-1}$) had decreased bent neck compared to those treated with water only (Table 20). High levels of stem blackening were present in many of the stems treated with water in combination with protective carbohydrates but not in stems treated with sucrose or fructose as primary carbohydrates (Table 20). Among stems treated with water plus protective carbohydrates, low levels of stem blackening were observed in stems treated with mannose, raffinose at both concentrations, and in those treated with sorbitol; all other

treatments within this group had at least 60% of stems showing stem blackening (Table 20).

Stems treated with mannose in combination with sucrose had high levels of leaf drop, indicative of phytotoxicity, when compared to all other sucrose treatments (Table 20). Among water treatments, stems treated with raffinose at both concentrations and sorbitol had low levels of leaf drop; all other water treatments had high levels of leaf drop (Table 20).

Discussion

Vase solutions. Across experiments, sucrose vase solutions increased vase life compared to water, confirming results of Ichimura et al. (2003) and others. This indicates that the prevalent thought that either additional respirable carbohydrate or decreased water potential for increased water uptake increases vase life is likely correct. In our experiments, vase life of treatments using fructose or glucose as vase solutions was at least as long as or longer than sucrose (Tables 3, 5, 13, 14, 16, and 20). Vase life increases associated with use of fructose or glucose may be due to increased substrate for respiration when loss of sucrose synthase and invertase activities decreases sucrose conversion to a respirable carbohydrate (Yamada et al., 2007; Kumar et al., 2008); however, weight for weight, the hexoses have twice the molarity and therefore twice the osmoregulatory potential of sucrose. Our results, however, do not show differences in glucose and fructose levels between stems

treated with sucrose and stems treated with glucose or fructose. Potential funtions of these carbohydrates are discussed further.

We did not see an increase in vase life above sucrose for any of the protective carbohydrates tested as vase solutions. However, many of the other postharvest characteristics varied by carbohydrate source. For instance, in Experiment 2, treatment with mannose at 10 $g \cdot L^{-1}$ resulted in an acceptable vase life (14.1 days compared to 15.1 for the sucrose control) and stems showed reduced levels of petal wilting (3.3 compared to 6.3 for the control) and bent neck (0.1 compared to 1.87). It may be possible to design carbohydrate solutions that would increase vase life by focusing on each individual termination criterion. Although a protective carbohydrate might not by itself support water uptake if the concentration is too low or enter metabolism to increase vase life above sucrose, we hypothesized that when added to a respirable primary carbohydrate (fructose, glucose, or sucrose), the beneficial effects of each might be additive and increase vase life. In Experiment 12, however, we did not find significant differences between combinations of protective and primary carbohydrates and primary carbohydrates alone, but do not rule out our original hypothesis as several of the combinations did have mean vase lives that were higher than fructose or sucrose alone, but were not significant (Table 20).

In Experiment 1, we noticed a white substance, possibly mannitol, accumulated on leaf margins of roses treated with 10 $g \cdot L^{-1}$ mannitol. Ichimura et al. (1999, 2000) observed that cut stems of *Delphinium* and *Rosa* 'Sonia' treated with mannitol vase solutions accumulated a white substance on petals and confirmed the

substance was mannitol. In Experiment 1, we saw a dosage effect for several carbohydrates, where high concentrations result in a lower vase life than low to intermediate concentrations. However, we did not see a dosage effect with sorbitol, as we expected since sorbitol is a primary metabolite in Rosaceae (Loescher, 1987). Surprisingly, as raffinose is not a major metabolite in roses, we also did not see a dosage effect for raffinose. Although raffinose is a major metabolic carbohydrate only in the cucurbits, it promotes seed dessication tolerance in many diverse plant species (Peterbauer and Richter, 2001). Furthermore, when α-galactosidase, the enzyme responsible for breakdown of raffinose, was down-regulated in *Petunia*, raffinose accumulated in vegetative tissues and was associated with increased tolerance to osmotic stresses (Locke and Stushnoff, 2006; Pennycooke et al., 2003). Thus, enzymes involved in the metabolism of raffinose are likely widely distributed throughout the plant kingdom, and raffinose may have been metabolized in rose when applied as a vase solution.

In Experiment 1, we found that Splenda® at 50 $mg \cdot L^{-1}$ was among the better vase solutions for extending vase life of cut rose stems when compared to water. In Experiment 2, we tested Splenda® at 25, 50, or 100 $mg \cdot L^{-1}$, with respective vase lives of 14.9, 14.0 and 14.6 days, which were not significantly different from any control. Splenda® is approximately 98.8% maltodextrin + 1.2% sucralose. The purpose of Experiment 6 was to determine if the positive effects of Splenda® on vase life of cut flowers were due to maltodextrin, sucralose, or the combination of both. However, vase life showed no difference between any Splenda®, sucralose, or maltodextrin

treatment. Only stems treated with sucrose had an increased vase life compared to water. It might be that Splenda® is only effective as a vase solution when roses have been grown or shipped in a specific manner.

Pulsing solutions. As pulsing solutions, carbohydrates had an effect on the vase life of 'Judy' in experiment 4. Use of sucrose (50 $g \cdot L^{-1}$) as a pulsing solution increased vase life above fructose (50 $g \cdot L^{-1}$) and mannitol (10 $mg \cdot L^{-1}$), while use of sorbitol (25 $g \cdot L^{-1}$) increased vase life above mannitol (10 $mg \cdot L^{-1}$); however, there was not a significant difference from the water control (Table 6). Although only seen in one cultivar, carbohydrates normally transported, stored, and metabolized in roses may be beneficial when applied immediately after cutting, before the changes in enzyme activities described above have had a chance to take effect.

Depending on cultivar, we saw increases in leaf drop associated with different carbohydrate pulsing solutions in experiments 4 and 7; however, in experiments 7 and 12 we saw that water-only pulse treatments also led to increases in leaf drop. We speculate that a carbohydrate status that is either too high or too low causes leaf drop, resulting from phytotoxicity and nutrient remobilization, respectively. In *Eustoma*, pulsing with sucrose is associated with increased leaf drop, while the addition of 10 µM ABA to the pulsing solution allows vase life to remain as high as in sucrose-pulsed flowers and also keeps foliage quality high (Shimizu-Yumoto and Ichimura, 2009). When *Eustoma* was pulsed with solutions containing ^{13}C labeled sucrose, less labeled sucrose was found in leaves of stems pulsed with ABA and sucrose than in stems pulsed with sucrose alone (Shimizu-Yumoto et al., 2010), indicating that

phytotoxic effects of carbohydrates on leaves may be due to concentrations that are too high. Similarly, Markhart and Harper (1995) found that the addition of ABA to sucrose vase solutions prevented leaf-crisping in winter-grown roses; these researchers speculated that environmental conditions of high CO_2 and low light in the winter cause high transpiration during postharvest life, encouraging excessive uptake of carbohydrate solutions.

Postharvest characteristics. Petal discoloration did not seem to be associated with any specific treatments between experiments, although evidence linking petal discoloration to specific treatments within individual experiments was strong. This may be due to seasonal and handling variation in the roses received and also may be due to differences between visual symptoms termed discoloration. Discoloration was used to describe either petal browning of entire petals developing from the distal region associated with botrytis infection (Friedman et al., 2010; Zenaida Viloria, personal communication) or isolated brown spotting of petals not associated with botrytis infection. Furthermore, discoloration had strong positive correlations with vase life in red varieties for most experiments (Table 4); therefore, treatments having a long vase life would likely show increased petal discoloration, which would not be indicative of treatment causing petal discoloration. Isolated brown spotting was termed "loss of pigment" by Regan (2008), who also found a relationship between long vase life and this postharvest characteristic.

Similarly, petal wilting varied by vase solution but differed from experiment to experiment and often had a moderate positive correlation to vase life (Table 4).

The two carbohydrates we dropped after the first experiment because they were cost prohibitive, galactinol and pinitol, reduced petal wilting for at least one concentration (Table 2). In several experiments, reduced petal wilting was obtained with a 10 $g \cdot L^{-1}$ concentration of one of the carbohydrates, although the carbohydrate differed by experiment (Tables 3 and 13), while water sometimes resulted in increased petal wilting (Tables 9, 14, 15, and 19). Notably, however, water plus Kathon™ CG was among the treatments with a low percentage of wilted flowers in experiments 1 and 3 (Tables 2 and 5). High levels of carbohydrates likely decrease osmotic potential and, therefore, increase water status of petals, reducing wilting.

Incidence of bent neck tended to be highest, though not severe, in the water-only control, possibly indicating the need for an antimicrobial or indicating that addition of carbohydrates may improve water status in receptacle and stem tissue. Bent neck often showed strong negative correlation to vase life (Table 4); thus, stems exhibiting bent neck were among the first stems to be terminated. Consequently, bent neck should be targeted for prevention with postharvest treatments and treatments showing high rates of bent neck should be avoided.

In many experiments, petal blueing was positively correlated with vase life (Table 4). Consequently, treatments that had decreased petal blueing are commercially useful if they also resulted in a long vase life. For instance, in experiment 1, the 5 $g \cdot L^{-1}$ Splenda® and 10 $g \cdot L^{-1}$ sucrose treatments decreased blueing but were among the first treatments to be terminated (Table 2); therefore, of the treatments which decreased blueing in experiment 1, 100 $mg \cdot L^{-1}$ mannitol is the most

promising treatment for prevention of blueing. In experiment 9, the only experiment which showed a significant negative correlation between vase life and blueing, hexose sugars were used as treatments. Fructose (50 $g \cdot L^{-1}$); and fructose (25 $g \cdot L^{-1}$), glucose (25 $g \cdot L^{-1}$), and glucose (50 $g \cdot L^{-1}$) from experiments 2 and 7, respectively, were treatments with both low levels of blueing and long vase lives (Tables 3 and 15). Although hexose sugars did not always decrease blueing on the rating scale (APPENDIX 1), we observed that hexose sugars caused petals to become a more fuschia or salmon color rather than purple (data not shown).

Petal blackening was also positively correlated with vase life (Table 21); however, in this case, we believe that sucrose and hexose treatments resulted in a long vase life, which subsequently allowed high levels of those carbohydrates to be absorbed and cause phytotoxicity. Markhart and Harper (1995) found that sucrose tended to increase leaf crisping in winter-grown roses, indicating that primary carbohydrates can result in phytotoxicity. We observed that petal blackening on flowers with a long vase life tended to occur on entire petals around the outer whorl. Despite our belief that sucrose and hexoses caused petal blackening, we recommend hexoses as carbohydrate sources as they lengthen vase life.

When stem blackening was correlated with leaf chlorosis/drop for each cultivar within each experiment, both conditions were present 18 out of 25 times. Of the eighteen, fourteen correlations between the two conditions were significant at $p < 0.05$, twelve were significant at $p < 0.001$ and Pearson correlations for the significant correlations were between 0.1765 to 0.8803. Neither stem blackening nor leaf

chlorosis/drop were consistently positively or negatively correlated with vase life. We did not terminate stems for stem blackening or leaf chlorosis/drop, but the conditions were noted when present. Leaf chlorosis and leaf drop were associated with phytotoxicity but were also seen in roses treated with water but not with carbohydrates, indicating that leaf chlorosis and leaf drop may also result as carbohydrates become depleted in the leaves during remobilization to the flower.

Neck rot was associated with particular treatments for experiment 3 only and was likely caused by botrytis (Zenaida Viloria, personal communication). Since botrytis infection occurs prior to receipt, we would not expect postharvest treatments to affect incidence of neck rot unless the treatment affects the rate of symptom manifestation. Significant correlations of neck rot to vase life were negative (Table 21), indicating that botrytis infected flowers were among the first to be terminated.

Cultivar variation. In experiments 4, 5, and 7 using the cultivars 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia', we consistently saw that 'Versilia' had the longest vase life while 'Judy' and 'Polo' had short vase lives. 'Freedom' and 'Verdi' tended to have intermediate vase lives. 'Judy' and 'Polo' also had the highest incidence of bent neck for all three experiments. We believe that at least part of the discrepancy in vase life between these cultivars is due to the relative size of the flowers to the neck. Although we did not measure flower size, 'Judy' and 'Polo' have large flowers, and for the three experiments, 'Polo' was the cultivar that opened to the greatest extent. The small neck of these stems is insufficient to support the weight of the flower once it begins to open. In contrast, 'Versilia' opened very little,

even though the vase life was long in all three experiments. Although the coloration and progression was somewhat different, and therefore not considered petal discoloration, 'Judy' developed a deeper color in the center of the flower, rather than the outside as we saw with botrytis infection in 'Freedom', and tissues affected by this coloration were soft; thus 'Judy' may be susceptible to a postharvest disorder or pathogenic infection.

Functions of carbohydrates during vase life. Ethylene sensitivity in roses is cultivar dependent (Possiel, 2008). 'Freedom', which was used for most of the studies presented herein, has been characterized as sensitive to ethylene, showing an increase in vase life when treated with STS, and having a decrease in vase life when treated with ethylene compared to commercial preservative solutions (Possiel, 2008). Exogenous carbohydrate treatment decreases ethylene sensitivity in sensitive species, actually seeming to block ethylene signaling (Attri et al., 2008; Ichimura et al., 2000; van Doorn and Woltering, 2008); so alternatively to carbohydrates acting as respirable substrates or as osmolytes, carbohydrates may extend vase life in cut *Rosa* 'Freedom' by decreasing ethylene sensitivity. However, carbohydrates may extend vase life in cut flowers by a combination of all three mechanisms, which are not necessarily independent of each other. For instance, an ample supply of carbohydrates for respiration may delay the onset of senescence through ethylene signaling, as the plant would not sense that nutrient supply in other organs is depleted. With regard to carbohydrates acting as osmolytes, decreased water loss has been reported with the application of carbohydrates (Possiel, 2008). This indicates that

ABA signaling may also be affected by carbohydrate application, and ABA and ethylene signaling are most probably interconnected (Zhang et al., 2009).

Yamada et al. (2007) demonstrated that insoluble acid invertase, soluble acid invertase, and soluble neutral invertase activities decreased during opening in cut *Rosa* 'Febesa', regardless of sucrose or water treatment, but that invertase activities increased during opening when roses are not cut. Although invertase activity was decreased in cut roses, sucrose-treated cut roses had increased levels of sucrose, glucose, and fructose compared to water-treated cut roses (Yamada et al., 2007), indicating that the ability to metabolize sucrose is preserved, at least to some degree, in cut roses, similar to findings of Ichimura et al. (2003). This is not likely due to compensatory sucrose synthase activity as Kumar et al. (2008) found reducing carbohydrates increased in *Rosa* 'First Red' throughout bud development and senescence, but noted decreased activity in sucrose synthase and all three isoforms of invertase as vase life progressed. This neither proves nor disproves the argument that increased vase life in sucrose-treated roses is not due to increased respirable substrate, but simply to an increased ability to take up water. Although metabolism does continue, allowing respiration, sucrose hydrolysis to glucose and fructose results in decreased osmotic potential, as pointed out above.

Although well characterized in *Rosa*, invertase activity is not consistently increased or decreased in comparisons of different genera (van Doorn and Woltering, 2008). As in rose, invertase activity was decreased in *Delphinium* (Kikuchi et al., 2003). Mapeli et al. (2009) found that invertase activity in an orchid, *Epidendrum*

ibaguense, increased during senescence; however, concentrations of glucose and fructose remained low, while sucrose remained high, indicating that invertase activity may be regulated by some mechanism that is undetectable in *in vitro* assays. Various mechanisms of invertase regulation, including sequestration in precursor protease vesicles (PPV), are reviewed by Huang et al. (2007). A mechanism of rapid synthesis and degradation of invertase might explain the conundrum that invertase and sucrose synthase activities in cut *Rosa* are low in *in vitro* assays (Kumar et al., 2008; Yamada et al., 2007) while measurements of sucrose, glucose, and fructose indicate that exogenous sucrose is hydrolyzed to glucose and fructose.

Blueing during senescence. As mentioned above, invertase and sucrose synthase activities have been previously shown to decrease during vase life in cut roses (Yamada et al., 2007; Kumar et al., 2008). We speculated that petal blueing may be caused by an increase in vacuolar pH resulting from tonoplast membrane leakage and that this pH change also results in the inactivation of vacuolar acid invertase (Oren-Shamir et al., 2001). Sood et al. (2006) demonstrated that antioxidant scavenging systems are downregulated while lipoxygenase and invertase activities and membrane permeability increase as non-cut roses mature. Van Doorn and Woltering (2008) assert that it is unknown whether increases in free radicals and membrane leakage are a symptom of or a programmed event during senescence. We further speculated that certain phytochemicals, applied as pulsing solutions, would increase invertase activity by negatively affecting the wounding response or would protect the tonoplast and thus prevent blueing and loss of invertase activity. In

experiment 8, we found that ABA increased vase life above the KOH control, but there were no differences for blueing in this experiment. In experiment 11, we found that, compared to water, blueing was decreased in stems treated with fructose, glucose, or sucrose as vase solutions. We had supposed that, if a phytochemical pulse would maintain invertase activity, the vase life of stems in a vase solution of sucrose would be similar to the vase life of stems treated with glucose or fructose; however, we did not have significan differences between vase life of stems treated with sucrose and with glucose or fructose in experiment 11, which was unexpected given previous longer vase lives achieved with glucose or fructose, and the potential cause may be the condition of the flowers on arrival, as discussed below. Although some of our results for other experiments, such as experiment 2, are different, we believe the lack of difference in carbohydrate contents for this experiment is due to the fact that invertase activity is maintained in senescing rose petals, at least to some degree.

Although we did not measure vacuolar pH or invertase activity, our results for experiment 11 indicate that fructose concentration increases during vase life when carbohydrates are supplied during vase life, regardless of the carbohydrate source, which is important in light of our correlation showing that increased vase life is associated with high levels of glucose and fructose sampled on day 6 of vase life. Even though studies show that invertase activity decreases in cut roses, others have also found that reducing carbohydrate contents increases as cut *Rosa* flowers mature (Ichimura et al., 2003; Kumar et al., 2007; Yamada et al., 2007), although Kumar et al. (2007) found these increases even in the absence of exogenous carbohydrate

application. Our results do not agree with those of Kumar et al. (2007), as glucose and fructose sampled on day six were higher in stems treated with glucose, fructose, or sucrose than in stems treated with water. There was not a significant interaction between sampling date and pulsing solution for either glucose or fructose concentrations; however, when averaged over sampling dates, tap water as a pulsing solution resulted in the highest concentrations of glucose and fructose (Table 17), indicating that the phytochemical pulses we hypothesized would either prevent tonoplast leakage or prevent inactivation of invertase may have instead promoted tonoplast leakage or invertase inactivation. However, we did not see a notable increase in relative leakage ratio above water for any of the pulsing treatments. As mentioned previously, while *in vitro* assays show the loss of invertase and sucrose synthase activities, sucrose hydrolysis to glucose and fructose clearly continues; thus, invertase or sucrose synthase activity must be maintained *in planta* by some mechanism undetectable in *in vitro* assays.

This work focused on a number of treatments, including carbohydrates and other phytochemicals, with the goal of extending postharvest vase life in cut roses. We found promising results with glucose and fructose; however, we saw variation with their efficacy compared to sucrose. Production season, storage, or shipping conditions may play a role in their effectiveness. When price per stem or customer satisfaction is of utmost importance, we recommend minimizing storage time and the use of a vase solution that includes glucose and/or fructose, which may be more costly than sucrose, as we saw that carbohydrate treatments on 'Freedom' were most

effective at increasing vase life when the vase life of the water-treated control was at least 12 days, and thus stems were of good quality. Future work in postharvest treatment of cut roses should focus on prevention of botrytis infection, bent neck, and discovery of the cause of blueing.

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Table 1. pH and electrical conductivity (EC) of carbohydrate solutions used for pulsing in Experiments 4, 7, and 8.

Pulsing treatment	Concentration	pH	EC ($ds \cdot m^{-1}$)
	Experiment 4		
Fructose	10 $g \cdot L^{-1}$	6.6	0.39
	50 $g \cdot L^{-1}$	6.8	0.34
Mannitol	10 $mg \cdot L^{-1}$	7.1	0.40
	50 $mg \cdot L^{-1}$	6.8	0.39
Raffinose	15 $g \cdot L^{-1}$	2.3	0.38
	75 $g \cdot L^{-1}$	6.7	0.34
Sorbitol	25 $g \cdot L^{-1}$	7.0	0.36
Sucrose	10 $g \cdot L^{-1}$	7.2	0.39
	50 $g \cdot L^{-1}$	7.2	0.35
Splenda	25 $mg \cdot L^{-1}$	7.0	0.39
	125 $mg \cdot L^{-1}$	6.9	0.39
Trehalose	500 $mg \cdot L^{-1}$	7.2	0.39
Tap water		7.0	0.39
	Experiment 7		
Mannitol	50 $mg \cdot L^{-1}$	7.4	0.24
Mannitol	10 $mg \cdot L^{-1}$	7.5	0.24
Raffinose	25 $g \cdot L^{-1}$	7.7	0.25
Sucrose	10 $g \cdot L^{-1}$	8.0	0.25
Tap Water		7.7	0.25
	Experiment 8		
Abscisic Acid	10 µM	8.7	0.27
Ascorbic Acid	6mM	4.1	0.27
Giberellic Acid ($_{4+7}$)	10 $mg \cdot L^{-1}$	7.2	0.24
Indole Acetic Acid	5 µM	8.5	0.26
Potassium Hydroxide	5 mM	8.3	0.26
Tap Water		7.1	0.25

Table 2. Effect of various carbohydrates as vase solutions on postharvest characteristics of cut *Rosa* 'Freedom' for Experiment 1. Stems were treated with galactinol, mannitol, pinitol, raffinose, sorbitol, Splenda®, and trehalose at the concentrations listed. Dionized (DI) water and sucrose (10 $g \cdot L^{-1}$) with and without Kathon™ CG were controls. Vase life was the number of days until unacceptable level of senescence was reached. Petal discoloration, wilting, bent neck, petal blueing, and leaf drop are expressed as percentage of stems showing the symptom. Stage was rated from 0-3; 0=tight, 1=medium, 2=open, 3=blown. Means are an average of 15 stems.

Treatment (carbohydrate)	Vase life (days)	Petal discoloration (%)	Petal wilting (%)	Bent neck (%)	Petal blueing (%)	Stage (0-3)	Leaf drop (%)
Controls							
DI H_2O	13.2 abcd^{Z}*	73.3 abc**	53.3 abc^{NS}	0 c*	100.0 a^{NS}	1.27 abc	53.3 abc***
DI H_2O + Kathon	12.6 abcd***	93.3 ab***	13.3 bc*	0 c*	93.3 ab^{NS}	1.33 abc	26.7 abc^{NS}
Sucrose	11.9 bcd***	13.3 d^{NS}	66.7 abc^{NS}	86.7 a***	60.0 c***	0.80 bc**	6.7 bc^{NS}
Sucrose + Kathon	14.6 a^{NS}	33.3 cd^{NS}	53.3 abc^{NS}	13.3 c^{NS}	100.0 a^{NS}	1.47 abc	0 c^{NS}
Galactinol							
2 $mg \cdot L^{-1}$	13.2 abcd*	93.3 ab***	66.7 abc^{NS}	0 c*	100.0 a^{NS}	1.53 abc	26.7 abc^{NS}
10 $mg \cdot L^{-1}$	12.6 abcd***	86.7 ab***	6.7 c**	0 c*	100.0 a^{NS}	1.27 abc	26.7 abc^{NS}
Mannitol							
10 $mg \cdot L^{-1}$	13.7 ab^{NS}	86.7 ab***	46.7 abc^{NS}	0 c*	100.0 a^{NS}	1.33 abc	33.3 abc*
100 $mg \cdot L^{-1}$	13.2 abcd*	93.3 ab***	73.3 ab^{NS}	0 c*	80.0 abc*	1.13 abc	46.7 abc**
1 $g \cdot L^{-1}$	13.5 abc^{NS}	80.0 abc***	33.3 abc^{NS}	6.7 c^{NS}	93.3 ab^{NS}	1.60 ab	73.3 a***
10 $g \cdot L^{-1}$	11.6 cd***	60.0 abcd^{NS}	40.0 abc^{NS}	6.7 c^{NS}	100.0 a^{NS}	1.13 abc	73.3 a***
Pinitol							
5 $mg \cdot L^{-1}$	13.3 abc*	100.0 a***	40.0 abc^{NS}	0 c*	93.3 ab^{NS}	1.67 a	26.7 abc^{NS}

Table 2 Continued.

50 mg·L^{-1}	12.7	abcd*	86.7	ab***	6.7	c**	0	c*	100.0	a^{NS}	1.53	abc	46.7	abc**
500 mg·L^{-1}	12.3	bcd***	73.3	abc**	13.3	bc*	0	c*	100.0	a^{NS}	1.07	abc	13.3	bc^{NS}
Raffinose														
100 mg·L^{-1}	12.0	bcd***	80.0	abc***	40.0	abc^{NS}	6.7	c^{NS}	93.3	ab^{NS}	1.27	abc	46.7	abc**
1 g·L^{-1}	12.4	bcd***	86.7	ab***	40.0	abc^{NS}	0	c*	93.3	ab^{NS}	1.33	abc	13.3	bc^{NS}
10 g·L^{-1}	13.7	ab^{NS}	53.3	abcd^{NS}	93.3	a*	6.7	c^{NS}	93.3	ab^{NS}	1.20	abc	0	c^{NS}
Sorbitol														
10 mg·L^{-1}	12.8	abcd*	93.3	ab***	20.0	bc*	0	c*	100.0	a^{NS}	1.53	abc	60.0	ab***
100 mg·L^{-1}	12.8	abcd*	93.3	ab***	26.7	bc^{NS}	0	c*	100.0	a^{NS}	1.20	abc	40.0	abc*
1 g·L^{-1}	13.6	abc^{NS}	93.3	ab***	60.0	abc^{NS}	0	c*	93.3	ab^{NS}	1.53	abc	13.3	bc^{NS}
10 g·L^{-1}	13.7	ab^{NS}	73.3	abc**	66.7	abc^{NS}	0	c*	100.0	a^{NS}	1.07	abc	6.7	bc^{NS}
Splenda														
50 mg·L^{-1}	13.9	ab^{NS}	93.3	ab***	73.3	ab^{NS}	0	c*	100.0	a^{NS}	1.47	abc	40.0	abc*
500 mg·L^{-1}	13.1	abcd*	80.0	abc***	53.3	abc^{NS}	0	c*	100.0	a^{NS}	1.53	abc	13.3	bc^{NS}
5 g·L^{-1}	11.2	d***	46.7	bcd^{NS}	73.3	ab^{NS}	60.0	b***	66.7	bc***	0.73	c***	13.3	bc^{NS}
Trehalose														
2 mg·L^{-1}	13.0	abcd**	86.7	ab***	33.3	abc^{NS}	0	c*	100.0	a^{NS}	1.67	a	33.3	abc*
20 mg·L^{-1}	11.6	cd***	80.0	abc***	53.3	abc^{NS}	6.7	c^{NS}	93.3	ab^{NS}	0.93	abc*	40.0	abc*
200 mg·L^{-1}	13.6	abc^{NS}	80.0	abc***	60.0	abc^{NS}	0	c*	100.0	a^{NS}	1.27	abc	73.3	a***
Significance	***		***		***		***		***		**		***	

^{NS},*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively, for experiment or compared to Sucrose + Kathon™ CG control.

^{Z}Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 3. Effect of various carbohydrates on postharvest characteristics of cut *Rosa* 'Freedom' evaluated in Experiment 2. Stems were treated with galactinol, mannitol, pinitol, raffinose, sorbitol, Splenda®, and trehalose at the concentrations listed. Dionized (DI) water and sucrose (10 $g \cdot L^{-1}$) with and without Kathon™ CG were used as controls. Vase life was determined as the number of days until unacceptable level of senescence is reached. Petal discoloration, wilting, bent neck, petal blueing, and petal blackening were rated from 0 (condition not present) to 10 (condition severe). Stage was rated from 0-3; 0=tight, 1=medium, 2=open, 3=blown. Phytotoxicity (phyto) and stem blackening are expressed as the percentage of stems with the condition present at termination. Means are an average of 15 stems.

Treatment	Vase life (days)	Petal discoloration (0-10)	Petal wilting (0-10)	Bent neck (0-10)	Petal blueing (0-10)	Petal blackening (0-10)	Stage (0-3)	Phyto. (%)	Stem blackening (%)
Controls									
DI H_2O	13.9 bc^{Z}*	5.27 abc^{NS}	6.33 ab^{NS}	2.00 bc^{NS}	7.20 a^{NS}	2.60 c**	1.07 ab^{NS}	0 c^{NS}	26.7 a*
DI H_2O + Kathon	13.9 bcd*	7.73 a^{NS}	5.73 ab^{NS}	0.47 c*	6.33 ab^{NS}	3.60 bc^{NS}	1.53 ab*	13.3 c^{NS}	20.0 a^{NS}
Sucrose + Kathon	15.7 b^{NS}	6.40 ab^{NS}	6.33 ab^{NS}	1.87 bc^{NS}	6.60 ab^{NS}	4.07 bc^{NS}	0.93 b^{NS}	0 c^{NS}	0 a^{NS}
Fructose									
1 $g \cdot L^{-1}$	14.4 bc^{NS}	5.93 ab^{NS}	7.27 a^{NS}	1.33 bc^{NS}	7.00 a^{NS}	3.40 c^{NS}	1.13 ab^{NS}	0 c^{NS}	26.7 a*
10 $g \cdot L^{-1}$	18.9 a***	7.47 a^{NS}	5.27 ab^{NS}	1.53 bc^{NS}	6.13 ab^{NS}	5.40 ab**	1.87 a***	6.7 c^{NS}	0 a^{NS}
50 $g \cdot L^{-1}$	20.1 a***	7.40 a^{NS}	5.07 ab^{NS}	0.00 c**	5.00 bc**	6.27 a***	1.27 ab^{NS}	20.0 c^{NS}	0 a^{NS}
Mannitol									
5 $mg \cdot L^{-1}$	13.7 bcd**	5.67 abc^{NS}	6.47 ab^{NS}	1.80 bc^{NS}	6.47 ab^{NS}	3.13 c^{NS}	1.27 ab^{NS}	0 c^{NS}	40.0 a**
10 $mg \cdot L^{-1}$	14.7 bc^{NS}	8.07 a*	6.27 ab^{NS}	0.33 c*	6.40 ab^{NS}	2.93 c*	1.40 ab^{NS}	20.0 c^{NS}	20.0 a^{NS}
25 $mg \cdot L^{-1}$	11.3 d***	3.73 bc***	7.47 a^{NS}	6.00 a***	3.73 c***	2.67 c**	0.87 b^{NS}	6.7 c^{NS}	20.0 a^{NS}

Table 3 Continued.

Mannose										
100 mg·L^{-1}	13.9 bc*	5.80 abc^{NS}	6.67 a^{NS}	1.07 bc^{NS}	6.07 ab^{NS}	3.07 c^{NS}	1.33 ab^{NS}	6.7 c^{NS}	33.3 a*
1 g·L^{-1}	14.5 bc^{NS}	7.47 a^{NS}	5.67 ab^{NS}	0.47 c*	6.67 ab^{NS}	3.07 c^{NS}	1.47 ab*	33.3 bc**	6.7 a^{NS}
10 g·L^{-1}	14.1 bc*	7.27 a^{NS}	3.27 b***	0.07 c**	6.07 ab^{NS}	2.67 c**	1.33 ab^{NS}	93.3 a***	0 a^{NS}
Raffinose										
5 g·L^{-1}	15.1 bc^{NS}	7.00 a^{NS}	5.93 ab^{NS}	0.87 bc^{NS}	6.53 ab^{NS}	2.93 c*	1.27 ab^{NS}	6.7 c^{NS}	0 a^{NS}
10 g·L^{-1}	15.2 bc^{NS}	6.80 a^{NS}	7.33 a^{NS}	1.87 bc^{NS}	6.60 ab^{NS}	3.27 c^{NS}	1.47 ab*	93.3 a***	0 a^{NS}
15 g·L^{-1}	15.5 b^{NS}	5.53 abc^{NS}	7.67 a^{NS}	1.93 bc^{NS}	7.13 a^{NS}	3.47 c^{NS}	1.33 ab^{NS}	93.3 a***	0 a^{NS}
Sorbitol										
500 mg·L^{-1}	14.0 bc*	7.13 a^{NS}	5.60 ab^{NS}	0.20 c*	6.73 ab^{NS}	3.40 c^{NS}	1.13 ab^{NS}	0 c^{NS}	26.7 a*
1 g·L^{-1}	14.7 bc^{NS}	7.80 a^{NS}	6.33 ab^{NS}	0.53 c*	7.27 a^{NS}	3.67 bc^{NS}	1.40 ab^{NS}	26.7 bc*	40.0 a**
5 g·L^{-1}	14.8 bc^{NS}	7.00 a^{NS}	6.53 ab^{NS}	0.47 c*	6.93 a^{NS}	3.33 c^{NS}	1.33 ab^{NS}	66.7 ab***	6.7 a^{NS}
Splenda										
25 mg·L^{-1}	14.9 bc^{NS}	6.53 ab^{NS}	7.00 a^{NS}	0.73 c^{NS}	6.80 ab^{NS}	2.67 c**	1.60 ab**	6.7 c^{NS}	33.3 a*
50 mg·L^{-1}	14.0 bc*	5.40 abc^{NS}	6.07 ab^{NS}	0.80 c^{NS}	6.53 ab^{NS}	3.73 bc^{NS}	0.87 b^{NS}	0 c^{NS}	46.7 a***
100 mg·L^{-1}	14.6 bc^{NS}	7.40 a^{NS}	6.40 ab^{NS}	0.93 bc^{NS}	7.07 a^{NS}	3.73 bc^{NS}	1.27 ab^{NS}	6.7 c^{NS}	40.0 a**
Trehalose										
100 mg·L^{-1}	14.7 bc^{NS}	8.07 a*	7.67 a^{NS}	0.87 bc^{NS}	6.80 ab^{NS}	3.07 c^{NS}	1.20 ab^{NS}	20.0 c^{NS}	33.3 a*
200 mg·L^{-1}	14.2 bc*	6.00 ab^{NS}	5.40 ab^{NS}	0.47 c*	6.67 ab^{NS}	4.00 bc^{NS}	1.47 ab*	40.0 bc***	26.7 a*
500 mg·L^{-1}	12.8 cd***	3.00 c***	7.53 a^{NS}	3.20 b*	5.73 ab^{NS}	2.80 c*	0.93 b^{NS}	0 c^{NS}	13.3 a^{NS}
Significance	***	***	***	***	***	***	*	***	***

^{NS},*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively, for experiment or compared to Sucrose + Kathon™ CG control.

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 4. Pearson correlation and probability of significance for petal discoloration (PD), petal wilting (WP), bent neck, and petal blueing (PB) correlated to vase life in cut *Rosa* for all experiments presented here.

Experiment and cultivar	PD		WP		Bent neck		PB	
	r	p	*r*	p	*r*	p	*r*	p
1	0.1555	0.0021	0.1800	0.0004	-0.2579	<0.0001	0.1962	<0.0001
2	0.3704	<0.0001	0.0869	0.0996	-0.3688	<0.0001	0.2018	0.0001
3	0.4953	<0.0001	0.0703	0.2495	-0.5175	<0.0001	0.5971	<0.0001
4 Freedom	-0.3164	<0.0001	0.6174	<0.0001	-0.1183	0.1466	0.1317	0.1057
4 Judy	-0.0470	0.5600	0.4112	<0.0001	-0.2257	0.0046	ND[Z]	
4 Polo	-0.3852	<0.0001	0.5432	<0.0001	-0.0043	0.9578	ND	
4 Verdi	-0.7077	<0.0001	0.2183	0.1104	0.1831	0.0221	ND	
4 Versilia	0.1074	0.1834	-0.3571	<0.0001	-0.2524	0.0015	ND	
5 Freedom	0.3832	<0.0001	0.3447	<0.0001	-0.2583	0.0005	0.5748	<0.0001
5 Judy	0.5333	<0.0001	0.2684	0.0001	-0.2750	<0.0001	ND	
5 Polo	-0.0380	0.5985	0.4529	<0.0001	0.0555	0.4436	ND	
5 Verdi	0.2060	0.0039	0.0362	0.6155	0.1452	0.0499	ND	
5 Versilia	0.2802	<0.0001	0.2298	0.0012	-0.0103	0.8878	ND	
6	0.1025	0.1901	0.0843	0.2819	-0.2845	0.0003	0.1722	0.0270
7 Freedom	0.2950	0.0003	0.5896	<0.0001	0.0944	0.5145	0.0209	0.8855
7 Judy	0.7030	<0.0001	0.3756	0.0078	-0.0357	0.8074	ND	
7 Polo	0.2503	0.0796	0.5924	<0.0001	-0.3356	0.0172	ND	
7 Verdi	0.0314	0.8284	0.0307	0.8325	-0.1045	0.4702	ND	
7 Versilia	0.2807	0.0507	-0.2666	0.0640	-0.5784	<0.0001	ND	
8 Charlotte	0.5085	0.0015	0.4825	0.0029	-0.4487	0.0061	0.3827	0.0213
8 Freedom	0.2623	0.1222	0.1633	0.3413	-0.1230	0.4749	-0.1105	0.5213
9	0.3752	<0.0001	-0.2042	0.0175	-0.3309	<0.0001	-0.1880	0.0290
10 Charlotte	0.0612	0.5665	0.2142	0.0426	-0.5299	<0.0001	0.5386	<0.0001
10 Freedom	0.3731	0.0003	-0.2138	0.0431	-0.4389	<0.0001	0.1718	0.1055
11	0.1240	0.0110	-0.1580	0.0012	-0.4367	<0.0001	-0.0477	0.3304
12	0.2627	<0.0001	0.1875	<0.0001	-0.3730	<0.0001	0.2199	<0.0001

[Z]ND: postharvest characteristic not detected in cultivar

Table 5. Effects of sucrose and/or fructose as vase solutions on postharvest characteristics of cut *Rosa* 'Freedom' in Experiment 3. Vase life was determined as the number of days until unacceptable level of senescence is reached. Carbohydrates were dissolved in dionized water (DI). The senescence criteria petal discoloration (discolor.), petal wilting, bent neck, petal blueing, and petal blackening (black.) were rated on a scale of 0-10 (criterion not present, criterion severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and rot caused by botrytis were noted at vase life termination if present and are a percentage of stems exhibiting condition. Means are an average of 15 stems subsampled by vase (three stems per vase).

Treatment	Vase life (days)	Petal discolor. (0-10)	Petal wilting (0-10)	Bent neck (0-10)	Petal blueing (0-10)	Petal black. (0-10)	Stage (0-3)	Stem black. (%)	Leaf drop (%)	Rot (%)
Controls										
DI + Kathon	14.3 bcdef[Z]*	6.87 a	6.00 b**	1.20 bc	5.47 ab	2.13 bc	1.93 bcde	86.7 a***	66.7 a***	40.0 a***
DI	12.4 efg***	4.30 abc	8.67 a	3.87 a***	5.40 ab	2.67 abc	1.80 bcde	53.3 b***	53.3 a***	33.3 a***
Sucrose 10 g·L^{-1}	17.3 abc	5.40 ab	7.80 ab	0.67 c	5.67 ab	3.13 abc	1.93 bcde	0 c	0 b	6.7 b
Chrysal	18.1 ab	6.67 a	7.13 ab	0.13 c	5.20 ab	4.07 abc	2.80 a***	13.3 c	0 b	0 b
Floralife	15.1 abcdef	5.13 ab	7.60 ab	1.00 bc	5.40 ab	2.93 abc	2.07 abcd	13.3 c	0 b	0 b
Sucrose 0 g·L^{-1} +										
Fructose 10 g·L^{-1}	18.9 a	6.07 a	7.30 ab	0.20 c	5.67 ab	4.33 ab	2.40 ab*	0 c	0 b	0 b
Fructose 50 g·L^{-1}	14.1 bcdef**	1.33 de***	7.40 ab	0.33 c	5.13 ab	4.13 abc	1.67 bcde	0 c	0 b	0 b
Sucrose 5 g·L^{-1} +										
----	15.2 abcdef	4.93 abc	7.07 ab	1.87 abc	6.60 a	3.67 abc	2.13 abcd	20.0 c*	6.7 b	6.7 b
Fructose 5 g·L^{-1}	17.1 abc	2.87 bcde**	6.53 ab*	1.33 bc	5.87 ab	4.60 a*	2.27 abc	0 c	0 b	0 b
Fructose 10 g·L^{-1}	14.4 bcdef*	2.67 bcde**	6.87 ab	1.53 abc	5.93 ab	3.53 abc	1.87 bcde	6.7 c	6.7 b	0 b

Table 5 Continued.

Fructose 20 g·L^{-1}	15.7	abcde	4.27	abcd	8.20	ab	0.47	c	6.47	a	4.00	abc	1.60	bcde	0	c	0 b	0 b
Fructose 35 g·L^{-1}	11.6	fg***	0.40	e***	8.47	a	1.73	abc	4.47	abc	2.87	abc	1.13	e***	0	c	0 b	0 b
Fructose 50 g·L^{-1}	9.5	g***	0.20	e***	8.13	ab	2.00	abc	3.73	bc**	1.93	c	1.33	de**	0	c	0 b	0 b
Sucrose 10 g·L^{-1} +																		
Fructose 5 g·L^{-1}	16.5	abcd	2.07	cde***	7.87	ab	1.27	bc	5.73	ab	3.73	abc	1.93	bcde	0	c	0 b	0 b
Fructose 10 g·L^{-1}	13.1	defg***	0.60	e***	6.60	ab	1.27	bc	5.47	ab	3.87	abc	1.47	cde*	0	c	0 b	0 b
Fructose 20 g·L^{-1}	13.9	cdef**	1.33	de***	7.87	ab	0.53	c	6.40	a	3.47	abc	1.40	de*	0	c	6.7 b	0 b
Fructose 35 g·L^{-1}	12.0	efg***	0.00	e***	8.67	a	1.47	abc	4.87	abc	2.93	abc	1.20	e**	0	c	0 b	0 b
Fructose 50 g·L^{-1}	9.3	g***	0.13	e***	7.47	ab	3.40	ab***	2.47	c***	1.87	c	1.33	de**	0	c	0 b	0 b
Significance	***		***		**		**		***		**		***		***		***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively, for experiment or compared to Sucrose + Kathon™ CG control.

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 6. Effects of pulsing treatments on postharvest characteristics of *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' evaluated in Experiment 4. Vase life was determined as the number of days until unacceptable level of senescence is reached. The senescence criteria overall appearance (AP), petal discoloration (PD), petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, best; 10, poor) at vase life termination. Stage of opening was measured as 1=tight, 2=medium, 3=open, and 4=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means are an average of 15 stems subsampled by vase. Within each cultivar, means were separated according to Tukey's procedure ($P \leq 0.05$).

Treatment	Vase life (Days)	AP (0-10)	PD (0-10)	WP (0-10)	Bent neck (0-10)	PB (0-10)	Petal black. (0-10)	Stage (1-4)	Stem black. (%)	Leaf drop (%)	Neck rot (%)
					'Freedom'						
Fructose 10 g·L^{-1}	13.7	1.8	4.4	7.6	6.5	8.6	4.0	2.2	8.3	25.0	0
Fructose 50 g·L^{-1}	13.8	1.3	4.0	7.3	5.8	8.1	3.2	1.9	0	0	0
Mannitol 10 mg·L^{-1}	14.6	1.7	4.3	7.8	5.1	7.2	3.9	2.1	19.7	63.4	11.1
Mannitol 50 mg·L^{-1}	13.8	2.3	2.8	7.1	6.9	6.6	4.6	2.0	0	8.3	0
Raffinose 15 g·L^{-1}	14.9	1.5	3.0	8.6	3.8	6.7	4.8	1.9	0	46.4	0
Raffinose 75 g·L^{-1}	13.2	2.8	3.6	6.6	5.8	7.3	4.1	1.7	0	8.3	0
Sorbitol 25 g·L^{-1}	12.0	2.8	4.0	7.1	6.3	7.7	3.5	1.6	8.3	25.0	8.3
Splenda 25 mg·L^{-1}	13.1	2.2	2.8	8.0	6.3	6.8	3.1	1.8	25.0	25.0	0
Splenda 125 mg·L^{-1}	14.1	2.0	4.1	7.3	7.2	7.6	3.3	2.1	16.7	16.7	0
Sucrose 10 g·L^{-1}	13.3	2.0	3.4	6.9	6.9	6.9	3.6	1.8	8.3	41.7	16.7
Sucrose 50 g·L^{-1}	13.1	1.4	0.8	7.8	7.0	5.4	3.1	1.8	41.7	41.7	25.0

Table 6 Continued.

Trehalose 500 mg·L^{-1}	14.5		1.8		1.9	7.9	8.9	6.5	2.8	1.5	0	9.6		9.0
Water (control)	13.7		2.8		4.0	7.3	5.5	6.8	4.1	1.8	33.3	41.7		0
Treatment	NS		NS		NS	NS	NS	NS	NS	NS	NS	NS		NS
							‘Judy’							
Fructose 10 g·L^{-1}	11.4	abc[Z]	3.9	ab	5.8	8.1	6.7		1.8	1.7		25.0	bc	0
Fructose 50 g·L^{-1}	9.0	bc	6.3	ab	4.0	6.5	6.7		0.5	2.0		8.3	c	0
Mannitol 10 mg·L^{-1}	8.8	c	5.7	ab	5.0	6.5	7.8		0.3	1.6		25.0	bc	0
Mannitol 50 mg·L^{-1}	12.4	abc	4.4	ab	4.8	7.7	2.7		2.3	1.3		75.0	ab	8.3
Raffinose 15 g·L^{-1}	11.9	abc	5.7	ab	6.3	9.0	5.1		2.3	1.7		8.3	c	8.3
Raffinose 75 g·L^{-1}	11.3	abc	5.7	ab	6.5	7.6	4.8		1.6	1.5		41.7	abc	8.3
Sorbitol 25 g·L^{-1}	12.8	ab	2.7	b	4.2	7.7	4.6		2.3	1.3		33.3	abc	8.3
Splenda 25 mg·L^{-1}	11.2	abc	4.0	ab	5.4	8.5	4.9		1.3	1.6		50.0	abc	25.0
Splenda 125 mg·L^{-1}	10.1	abc	5.2	ab	5.9	6.9	5.8		0.3	2.1		33.3	abc	16.7
Sucrose 10 g·L^{-1}	10.8	abc	6.5	a	6.4	8.3	3.9		1.5	1.8		91.7	a	16.7
Sucrose 50 g·L^{-1}	13.3	a	3.9	ab	3.8	8.3	4.7		2.7	1.2		8.3	c	16.7
Trehalose 500 mg·L^{-1}	11.0	abc	4.8	ab	6.1	8.1	5.6		1.8	1.5		16.7	bc	0
Water (control)	10.8	abc	4.8	ab	5.6	7.0	4.2		1.2	1.8		33.3	abc	16.7
Treatment	**		*		NS	NS	NS		*	NS		***		NS
							‘Polo’							
Fructose 10 g·L^{-1}	10.8		3.6		1.4	7.3	7.5		0.5	2.7		25.0		0
Fructose 50 g·L^{-1}	13.8		4.8		1.5	6.0	6.4		0.1	0.3		33.3		0
Mannitol 10 mg·L^{-1}	14.1		2.5		2.0	8.3	9.1		0.8	3.3		27.4		9.1
Mannitol 50 mg·L^{-1}	10.7		4.4		1.7	5.9	8.3		0.4	2.6		8.3		8.3
Raffinose 15 g·L^{-1}	14.8		3.2		0.7	6.0	9.0		0.2	2.8		16.7		0

Table 6 Continued.

Raffinose 75 g·L^{-1}	11.3	3.4	2.8	6.5	9.1		0.9	2.8		36.5	9.1
Sorbitol 25 g·L^{-1}	12.8	4.2	2.3	8.4	9.2		0.5	2.8		8.3	0
Splenda 25 mg·L^{-1}	13.0	4.2	3.3	8.3	8.9		0.4	3.0		8.3	8.3
Splenda 125 mg·L^{-1}	13.5	2.5	2.0	8.7	10.0		0.5	3.0		16.7	0
Sucrose 10 g·L^{-1}	12.3	4.3	1.9	7.7	9.3		0.8	2.9		25.0	0
Sucrose 50 g·L^{-1}	12.5	4.0	2.5	7.7	10.0		0.5	2.7		16.7	8.3
Trehalose 500 mg·L^{-1}	10.3	3.7	1.9	6.7	10.0		0.3	2.7		16.7	8.3
Water (control)	9.2	4.1	1.8	5.8	8.3		0.1	2.5		0	0
Treatment	*	NS	NS	NS	NS		NS	NS		NS	NS
						‘Verdi’					
Fructose 10 g·L^{-1}	13.3	4.3	2.9	7.7	1.4	3.7	2.8	2.6	ab	16.7	91.7	25.0
Fructose 50 g·L^{-1}	13.1	4.6	3.7	9.3	0.1	4.5	1.1	2.8	ab	0	100.0	8.3
Mannitol 10 mg·L^{-1}	13.6	4.1	2.9	8.9	2.2	4.1	3.1	2.6	ab	0	91.7	25.0
Mannitol 50 mg·L^{-1}	15.6	3.4	2.3	9.2	0.6	2.5	2.8	2.9	ab	0	66.7	8.3
Raffinose 15 g·L^{-1}	13.0	4.8	3.7	8.2	1.5	3.5	2.2	3.0	ab	0	50.0	8.3
Raffinose 75 g·L^{-1}	11.7	5.0	6.4	8.7	2.2	6.2	3.0	2.7	ab	0	91.7	50.0
Sorbitol 25 g·L^{-1}	14.9	3.9	3.6	8.2	2.5	3.4	3.0	2.3	b	8.3	83.3	8.3
Splenda 25 mg·L^{-1}	12.8	3.4	1.4	8.8	3.1	4.4	1.6	3.3	a	0	83.3	33.3
Splenda 125 mg·L^{-1}	16.1	4.8	4.2	8.8	3.3	1.7	3.0	2.4	ab	0	58.3	0
Sucrose 10 g·L^{-1}	14.4	3.3	3.4	8.9	4.3	3.5	2.0	2.3	b	8.3	83.3	8.3
Sucrose 50 g·L^{-1}	13.7	3.8	3.3	9.8	1.3	5.1	2.0	2.7	ab	0	83.3	16.7
Trehalose 500 mg·L^{-1}	13.5	4.2	3.8	9.2	2.2	4.3	2.3	2.5	ab	0	100.0	16.7
Water (control)	12.3	4.5	3.5	8.9	2.5	4.3	2.0	2.4	ab	0	100.0	8.3
Treatment	NS	NS	NS	NS	NS	NS	NS	*		NS	NS	NS

Table 6 Continued.

	'Versilia'									
Fructose 10 g·L^{-1}	17.0	4.1	1.3	7.6	4.8 ab	1.4 ab	1.0	16.7	100.0	8.3
Fructose 50 g·L^{-1}	17.6	4.8	2.9	8.4	1.2 b	2.5 ab	1.0	16.7	100.0	33.3
Mannitol 10 mg·L^{-1}	17.2	3.6	1.0	8.7	6.3 a	1.6 ab	1.1	25.0	83.3	25.0
Mannitol 50 mg·L^{-1}	16.6	3.3	1.2	8.2	3.1 ab	1.3 ab	1.0	16.7	81.7	16.7
Raffinose 15 g·L^{-1}	19.6	3.4	2.8	8.3	2.6 ab	2.9 a	1.0	41.7	100.0	33.3
Raffinose 75 g·L^{-1}	19.8	3.3	2.5	8.1	3.4 ab	2.4 ab	1.0	50.0	100.0	58.3
Sorbitol 25 g·L^{-1}	18.4	3.3	2.0	7.3	1.9 b	1.5 ab	1.2	16.7	83.3	33.3
Splenda 25 mg·L^{-1}	20.5	4.1	4.5	6.5	0.4 b	2.3 ab	1.2	18.2	100.0	27.9
Splenda 125 mg·L^{-1}	18.7	3.2	2.1	7.5	2.7 ab	2.3 ab	1.1	8.3	100.0	8.3
Sucrose 10 g·L^{-1}	20.9	2.6	4.3	7.9	1.8 b	2.3 ab	1.2	25.0	58.3	8.3
Sucrose 50 g·L^{-1}	17.7	3.3	3.0	8.3	1.3 b	2.6 ab	1.0	8.3	83.3	33.3
Trehalose 500 mg·L^{-1}	18.7	3.1	1.9	8.0	2.4 ab	2.0 ab	1.1	8.3	75.0	16.7
Water (control)	17.6	3.8	1.3	7.9	6.6 a	0.8 b	1.1	25.0	91.7	16.7
Treatment	NS	NS	*	NS	***	*	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 7. Effects of pulsing treatments on postharvest characteristics of *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' evaluated in Experiment 4. Vase life was determined as the number of days until unacceptable level of senescence is reached. The senescence criteria overall appearance (AP), petal discoloration (PD), petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, best; 10, poor) at vase life termination. Stage of opening was measured as 1=tight, 2=medium, 3=open, and 4=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means are an average of 15 stems subsampled by vase. Within each cultivar, means were separated according to Tukey's procedure ($P \leq 0.05$).

Treatment	Vase life (Days)	AP (0-10)	PD (0-10)	WP (0-10)	Bent neck (0-10)	PB (0-10)	Petal black. (0-10)	Stage (1-4)	Stem black. (%)	Leaf drop (%)	Neck rot (%)
Freedom	13.7 b[Z]	2.0 c	3.3 b	7.5 b	6.3 b	7.1 a	3.7 a	1.9 b	12.3 b	27.1 bc	5.3 c
Judy	11.1 d	4.9 a	5.4 a	7.7 b	5.2 b	0 c	1.5 c	1.6 c	0 c	34.6 b	9.6 bc
Polo	12.2 c	3.8 b	2.0 c	7.2 b	8.9 a	0 c	0.5 d	2.8 a	0 c	18.4 c	3.9 c
Verdi	13.7 b	4.2 b	3.5 b	8.8 a	2.1 c	3.9 b	2.4 b	2.6 a	2.6 c	83.3 a	16.7 ab
Versilia	18.5 a	3.5 b	2.4 c	7.9 b	3.0 c	0 c	2.0 bc	1.1 d	21.3 a	89.7 a	24.6 a
Effect											
Cultivar	***	***	***	***	***	***	***	***	***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 8. Cultivar main effects of overnight holding solutions on vase life of cut *Rosa* 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' prior to being stored dry at 1 °C for two weeks, as described for Experiment 5. Vase life was determined as the number of days until an unacceptable level of senescence was reached. The senescence criteria overall appearance (AP), petal discoloration (PD), Petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means are an average of 15 stems subsampled by 5 vases (3 stems per vase). Means for the main effects treatment and variety were separated according to Tukey's procedure ($P \leq 0.05$).

	Vase life (Days)	AP (1-10)	PD (1-10)	WP (1-10)	Bent neck (1-10)	PB (1-10)	Petal black. (1-10)	Stage (0-3)	Stem black. (%)	Leaf drop (%)	Neck rot (%)
Freedom	8.8 c[Z]	8.3 a	3.7 a	7.4 a	2.6 b	5.9 a	2.6 a	0.8 d	63.1 a	81.0 a	34.4 a
Judy	6.8 d	7.7 b	1.1 c	6.9 ab	3.5 a	0 b	2.2 ab	1.1 c	1.0 c	42.1 c	2.6 c
Polo	9.1 c	7.6 b	1.1 c	5.0 c	3.6 a	0 b	1.2 c	2.8 a	0 c	56.9 b	21.5 b
Verdi	11.4 b	8.2 a	2.4 b	7.0 ab	1.7 c	0 b	1.9 b	1.6 b	31.8 b	86.2 a	26.2 ab
Versilia	17.6 a	8.3 a	3.6 a	6.7 b	1.6 c	0 b	2.2 ab	0.2 e	41.0 b	86.2 a	9.2 c
Variety	***	***	***	***	***	***	***	***	***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 9. Effect of maltodextrin, Splenda®, and sucralose on vase life of cut *Rosa* 'Freedom' described for Experiment 6. Vase life was determined as the number of days until the level of senescence became unacceptable. The senescence parameters overall appearance (AP), petal discoloration (PD), Petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means are an average of 15 stems subsampled by 5 vases (3 stems per vase). Means for the main effects treatment and variety were separated according to Tukey's procedure ($P \leq 0.05$).

Treatment	Vase life (days)	AP (1-10)	WP (1-10)	Bent neck (1-10)	Stem black. (%)	Leaf drop (%)
Maltodextrin 25 mg·L^{-1}	11.4 b[Z]	8.3 ab	7.5 ab	1.9	93.3 a	80.0 a
Maltodextrin 100 mg·L^{-1}	10.1 b	8.7 ab	8.0 ab	2.5	53.3 b	93.3 a
Maltodextrin 5 g·L^{-1}	11.4 b	8.9 a	7.9 ab	4.2	93.3 a	100.0 a
Splenda 25 mg·L^{-1}	11.1 b	8.9 a	7.7 ab	1.6	100.0 a	86.7 a
Splenda 100 mg·L^{-1}	11.7 b	8.6 ab	8.0 ab	1.2	93.3 a	73.3 a
Splenda 5 g·L^{-1}	11.4 b	9.1 a	8.5 a	3.5	73.3 ab	100.0 a
Sucralose 0.3 mg·L^{-1}	11.5 b	8.0 ab	7.4 ab	2.1	93.3 a	80.0 a
Sucralose 1.2 mg·L^{-1}	11.7 b	8.8 a	7.7 ab	1.7	93.3 a	66.7 a
Sucralose 60 mg·L^{-1}	11.1 b	8.5 ab	6.7 b	1.2	93.3 a	86.7 a
Sucrose 10 g·L^{-1}	14.6 a	7.3 b	6.9 b	1.7	0 c	6.7 b
Deionized water	11.1 b	9.1 a	8.5 a	3.7	100 a	86.7 a
Significance	***	**	***	**	***	***

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 10. Cultivar main effects of the pulsing solutions mannitol at 10 and 50 mg·L^{-1}, raffinose at 25 g·L^{-1}, sucrose at 10 g·L^{-1}, and water and for the *Rosa* cultivars 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' as evaluated in Experiment 7. Vase life was determined as the number of days until the level of senescence became unacceptable. The senescence parameters overall appearance (AP), petal discoloration (PD), Petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means were separated according to Tukey's procedure ($P \leq 0.05$).

Effect	Vase Life (days)	AP (0-10)	PD (0-10)	WP (0-10)	Bent Neck (0-10)	PB (0-10)	Petal Black. (0-10)	Stage (0-3)	Stem Black. (%)	Leaf Drop (%)	Neck Rot (%)	Petal Shatter (%)	Petal Flop (%)
Freedom	11.2 c[z]	8.7 a	3.5 a	7.9 a	2.7 b	7.7 a	2.9 a	0.8 c	56.0 a	46.0 ab	0.0	0.0 c	0.0 c
Judy	9.0 d	7.7 b	1.2 c	6.9 ab	4.9 a	0.0 b	1.3 b	1.6 b	0.0 c	0.0 c	0.0	16.0 b	0.0 c
Polo	11.3 c	6.5 c	0.0 d	3.9 c	4.8 a	0.0 b	0.8 b	2.6 a	0.0 c	10.0 c	0.0	40.0 a	0.0 c
Verdi	13.2 b	8.4 ab	2.3 b	7.6 ab	1.7 c	0.0 b	1.4 b	1.9 b	26.0 b	42.0 b	0.0	4.0 bc	28.0 b
Versilia	16.9 a	7.8 b	2.4 b	6.8 b	1.0 c	0.0 b	1.1 b	0.5 c	30.0 b	64.0 a	6.0	0.0 c	50.0 a
Effect													
Cultivar	***	***	***	***	***	***	***	***	***	***	*	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

[z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 11. Simple effects effects of the pulsing solutions mannitol at 10 and 50 mg·L^{-1}, raffinose at 25 g·L^{-1}, sucrose at 10 g·L^{-1}, and water and for the *Rosa* cultivars 'Freedom', 'Judy', 'Polo', 'Verdi', and 'Versilia' as evaluated in Experiment 7. Vase life was determined as the number of days until the level of senescence became unacceptable. The senescence parameters overall appearance (AP), petal discoloration (PD), Petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means were separated according to Tukey's procedure ($P \leq 0.05$).

Cultivar	Treatment	AP (0-10)	Stage (0-3)	Stem black. (%)	Leaf drop (%)	Petal shatter (%)
Freedom	Mannitol 10 mg/L	8.8 a[z]	1.1 defg	100 a	80 a	0 c
	Mannitol 50 mg/L	8.6 a	1.0 defg	70 ab	40 abc	0 c
	Raffinose 25 g/L	8.8 a	0.7 efg	0 e	0 c	0 c
	Sucrose 10 g/L	8.3 ab	0.5 fg	50 abc	60 abc	0 c
	Water	8.8 a	0.7 efg	60 ab	50 abc	0 c
Judy	Mannitol 10 mg/L	8.1 ab	2.5 ab	0 e	0 c	40 abc
	Mannitol 50 mg/L	7.6 abcd	1.7 abcde	0 e	0 c	30 bc
	Raffinose 25 g/L	6.2 bcd	1.4 bcdef	0 e	0 c	0 c
	Sucrose 10 g/L	8.1 ab	1.1 defg	0 e	0 c	0 c
	Water	8.4 ab	1.3 cdefg	0 e	0 c	10 bc
Polo	Mannitol 10 mg/L	5.6 d	2.7 a	0 e	10 bc	40 abc
	Mannitol 50 mg/L	6.7 abcd	2.8 a	0 e	20 abc	80 a
	Raffinose 25 g/L	7.3 abcd	2.6 a	0 e	0 c	0 c
	Sucrose 10 g/L	7.2 abcd	2.8 a	0 e	20 ab	50 ab
	Water	5.7 cd	1.9 abcd	0 e	0 c	30 bc
Verdi	Mannitol 10 mg/L	8.1 ab	2.3 abc	20 cde	40 abc	10 bc
	Mannitol 50 mg/L	8.3 ab	1.8 abcde	40 bcd	40 abc	0 c
	Raffinose 25 g/L	8.5 a	1.9 abcd	0 d	0 c	0 c
	Sucrose 10 g/L	8.4 ab	2.3 abc	20 cde	60 abc	10 bc

Table 11 Continued.

	Water	8.6	a	1.3	cdefg	50	abc	70	ab	0	c
Versilia	Mannitol 10 mg/L	7.9	abc	0.7	efg	30	bcde	60	abc	0	c
	Mannitol 50 mg/L	8.4	ab	0.2	g	50	abc	70	ab	0	c
	Raffinose 25 g/L	7.4	abcd	0.2	g	10	de	30	abc	0	c
	Sucrose 10 g/L	7.6	abcd	1.0	defg	20	cde	80	a	0	c
	Water	7.9	abc	0.5	fg	40	bcd	80	a	0	c
Significance											
Treatment (T)		NS		***		***		***		***	
Cultivar (C)		***		***		***		***		***	
T*C		*		*		***		*		***	

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 12. Main effects of pulsing cut *Rosa* 'Charlotte' and 'Freedom' with abscisic acid (ABA), ascorbic acid (AsA), giberellic acid (GA), indole-3-acetic acid (IAA), potassium hydroxide (KOH), and tap water before shipping and subsequent treatment with sucrose (10 $g \cdot L^{-1}$) and deionized water as vase solutions as described for Experiment 8. Vase life was determined as the number of days until the level of senescence became unacceptable. The senescence parameters overall appearance (AP), petal discoloration (PD), Petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means were separated according to Tukey's procedure ($P \leq 0.05$).

Effect	Vase life (days)	PD (0-10)	WP (0-10)	Bent neck (0-10)	PB (0-10)	Petal black. (0-10)	Stage (0-3)	Stem black. (%)	Leaf drop (%)
Pulse									
ABA	13.4 a[z]	1.9 ab	7.5	2.5	7.3	2.6	0.8	8.3	0
AsA	12.2 ab	2.3 ab	7.8	2.8	7.6	2.8	0.8	16.7	16.7
GA	11.4 ab	1.5 ab	6.6	3.2	6.8	2.4	0.9	8.3	8.3
IAA	11.8 ab	0.9 b	7.8	2.3	7.8	2.5	0.8	0	0
KOH	10.8 b	1.9 ab	5.9	3.2	6.4	2.5	0.8	0	0
Water	11.9 ab	2.8 a	7.9	3.1	6.9	3.3	0.8	8.3	8.3
Vase Solution									
Sucrose	12.8 a	2.3 a	7.0	2.4 b	6.8 b	3.1 a	0.7	0 b	0 b
Water	11.0 b	1.4 b	7.4	3.2 a	7.5 a	2.3 b	0.9	13.9 a	11.1 a
Cultivar									
Charlotte	12.0	1.1 b	7.4	2.8	6.8 b	2.6	0.9	0 b	0 b

Table 12 Continued.

Freedom	11.8	2.7 a	7.1	2.8	7.4 a	2.8	0.7	13.9 a	11.1 a
				Effect					
Pulse (P)	*	*	*	NS	NS	NS	NS	NS	NS
Vase (V)	***	*	NS	*	*	**	NS	*	*
P*V	NS	NS	NS	**	NS	NS	NS	NS	NS
Cultivar (C)	NS	***	NS	NS	*	NS	NS	*	*
P*C	NS	NS	NS	NS	NS	NS	NS	NS	NS
V*C	NS	NS	NS	NS	NS	NS	NS	*	*
P*V*C	NS	NS	NS	NS	NS	NS	*	NS	NS

NS,*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 13. Effect of fructose and glucose at 5, 10, 25 or 50 g·L^{-1} and sucrose at 10 g·L^{-1} on vase life of cut *Rosa* 'Freedom' for Experiment 9. Vase life was determined as the number of days until the level of senescence became unacceptable. The senescence parameters overall appearance (AP), petal discoloration (PD), Petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Stem blackening (black.), leaf drop, and neck rot caused by botrytis were noted at vase life termination if present. Means were separated according to Tukey's procedure ($P \leq 0.05$).

Treatment	AP (0-10)	PD (0-10)	WP (0-10)	Bent neck (0-10)	PB (0-10)	Stem black. (%)
Fructose 5 g·L^{-1}	8.5 ab[Z]	3.9 ab	7.5 ab	1.0 ab	6.9 ab	20.0 a
Fructose 10 g·L^{-1}	8.2 ab	4.2 ab	6.3 abc	0.5 abc	6.3 bc	6.7 ab
Fructose 25 g·L^{-1}	7.6 b	4.0 ab	6.2 bc	0.3 bc	6.0 c	0 b
Fructose 50 g·L^{-1}	8.1 b	2.8 b	7.1 abc	0.1 c	6.1 bc	0 b
Glucose 5 g·L^{-1}	9.2 a	4.5 a	7.8 a	1.2 a	7.3 a	0 b
Glucose 10 g·L^{-1}	8.4 ab	4.5 a	5.9 c	0.4 abc	6.7 abc	0 b
Glucose 25 g·L^{-1}	7.9 b	4.4 ab	5.5 c	0.0 c	6.2 bc	0 b
Glucose 50 g·L^{-1}	8.6 ab	4.6 a	6.7 abc	0.1 c	5.9 c	0 b
Sucrose 10 g·L^{-1}	8.1 b	4.1 ab	6.7 abc	0.5 abc	6.5 abc	0 b
Significance	***	*	***	***	***	*

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 14. Effect of vase solutions on vase life and postharvest termination criteria of cut *Rosa* 'Charlotte' and 'Freedom' treated with RosePro™ by Chrysal (Chrysal), Floralife® Premium Rose Flower Food (Floralife), fructose (10 $g \cdot L^{-1}$), glucose (10 $g \cdot L^{-1}$), sucrose (10 $g \cdot L^{-1}$), and water. Experiment 10. Vase life was determined as the number of days until the level of senescence became unacceptable. The senescence parameters petal discoloration (PD), petal wilting (WP), bent neck, petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage of opening was measured as 0=tight, 1=medium, 2=open, and 3=blown. Leaf drop was noted at vase life termination if present. Water uptake was measured on day 4 of vase life evaluation. Means were separated according to Tukey's procedure ($P \leq 0.05$).

Effect	Vase life (days)	PD (0-10)	WP (0-10)	Bent neck (0-10)	PB (0-10)	Petal black. (0-10)	Stage (0-3)	Leaf drop (%)	Uptake (ml)
				Treatment					
Chrysal	12.7 bc[Z]	1.9	7.2 ab	0.7 abc	6.2	1.7 b	1.9 ab	16.7	151.0 ab
Floralife	15.9 a	2.0	6.6 b	0.1 d	6.7	2.3 ab	2.2 a	0	174.0 a
Fructose	14.1 ab	1.8	6.5 b	0.2 c	6.8	2.3 ab	1.6 bc	0	145.0 b
Glucose	13.8 ab	1.7	6.9 ab	0.3 b	6.7	2.6 a	1.6 bc	0	150.0 ab
Sucrose	12.2 c	1.5	7.1 ab	0.9 ab	6.3	2 ab	1.2 c	0	140.5 b
Water	11.4 c	2.0	7.5 a	1.2 a	6.9	2.1 ab	1.2 c	10	134.5 b

Table 14 Continued.

Cultivar									
Charlotte	12.4 b	0.3 b	7.9 a	0.6	5.9 b	1.7 b	1.6	0	145.0
Freedom	14.3 a	3.3 a	6.0 b	0.5	7.4 a	2.6 a	1.7	8.9	153.3
Effect									
Treatment	***	NS	**	***	NS	*	***	*	***
Cultivar	***	***	***	NS	***	***	NS	*	NS
Treatment*Cultivar	NS	NS	***	NS	NS	NS	NS	*	NS

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 15. Main effects of pulsing treatments ABA, AsA, Ethanol, GA, IAA, Quercetin, and water and vase solutions fructose, sucrose, and water on termination criteria of cut *Rosa* 'Freedom' for Experiment 11. The senescence parameters petal wilting (WP), bent neck, and petal blueing (PB) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stem blackening, leaf drop, and neck rot were noted at vase life termination if present and are a percent of stems affected. Means were separated according to Tukey's procedure ($P \leq 0.05$).

Effect	WP (0-10)	Bent Neck (0-10)	PB (0-10)	Stem Black. (%)	Leaf Drop (%)	Neck Rot (%)
			Vase Solution			
Fructose	5.7 b[Z]	1.3 b	6.3 b	1.0 b	7.6 b	1.9
Glucose	5.8 b	1.0 b	6.3 b	0.0 b	6.7 b	1.9
Sucrose	6.0 b	2.1 a	6.4 b	1.9 b	5.7 b	2.9
Water	7.0 a	2.6 a	6.8 a	32.7 a	53.1 a	8.7
Effect						
Pulse	NS	NS	NS	NS	NS	NS
Vase Solution	***	***	***	***	***	*
Pulse* Vase Solution	NS	NS	NS	NS	NS	NS

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 16. Pulse by vase solution interactions for stems treated with ABA, AsA, Ethanol, GA, IAA, quercetin, or water as pulse solutions followed by fructose glucose, sucrose, or water as vase solutions as described for Experiment 11. The senescence parameters petal discoloration (PD), and overall appearance (AP) were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stage was rated from 0-3 (0, tight; 3, blown). Means for each treatment combination are presented by and separated within pulse solution.

Pulse solution	Vase solution	Vase life (days)	AP (0-10)	PD (0-10)	Stage (0-3)
Abscisic Acid	Fructose	11.8 ab[z]	6.7	4.3	1.2
	Glucose	12.7 a	6.8	4.1	1.5
	Sucrose	11.1 ab	6.6	4.0	1.1
	Water	10.1 b	6.7	3.1	0.8
Ascorbic Acid	Fructose	12.8 a	6.7	4.1	1.3
	Glucose	11.9 a	6.3	3.9	0.7
	Sucrose	11.7 a	6.3	4.0	1.0
	Water	9.9 b	6.4	3.5	0.8
Ethanol	Fructose	12.0	6.4 b	4.5 ab	1.3 ab
	Glucose	12.2	6.5 b	3.4 b	1.7 a
	Sucrose	11.1	7.0 b	3.7 ab	0.7 b
	Water	11.0	8.5 a	5.2 a	0.9 ab
Giberellic Acid	Fructose	12.3 a	6.9	4.3	1.0 ab
	Glucose	12.8 a	6.3	3.9	1.7 a
	Sucrose	11.9 ab	7.1	4.3	1.3 ab
	Water	10.3 b	7.6	4.1	0.6 b
Indole acetic acid	Fructose	11.7	6.8	4.3	1.0
	Glucose	11.1	6.1	3.3	1.1
	Sucrose	11.4	6.9	3.6	0.8
	Water	10.7	7.1	3.9	0.5

Table 16 Continued.

Quercetin	Fructose	12.3 a	6.5	4.5	1.5
	Glucose	11.7 ab	7.1	4.6	0.9
	Sucrose	11.7 ab	6.7	3.9	1.3
	Water	10.2 b	7.6	4.1	0.7
Tap water	Fructose	11.6	6.7	4.6	1.3
	Glucose	12.1	6.6	4.1	1.2
	Sucrose	12.1	6.5	3.8	1.4
	Water	10.5	6.6	3.8	0.6
Effect					
Pulse		NS	**	NS	NS
Vase Solution		***	***	*	***
Pulse* Vase Solution		**	***	*	*

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 17. Carbohydrate content of stems pulsed with phytochemicals prior to shipping then treated with carbohydrates as vase solutions after shipping as described for Experiment 11. Samples were taken on days 1 and 6 of vase life evaluation.

Solution(s)		Glucose (mg/gdw)		Fructose (mg/gdw)	
			Pulse solution		
Abscisic acid		30.85	ab[Z]	56.52	b
Ascorbic acid		35.42	ab	57.92	ab
Ethanol		28.28	ab	52.25	b
Giberellic acid	29.74		ab	54.94	b
Indole acetic acid		26.24	b	49.91	b
Quercetin		28.77	ab	55.52	b
Tap water		37.75	a	66.67	a
Vase solution*Day					
1	Fructose	30.09		49.87	
	Glucose	30.35		55.25	
	Sucrose	33.84		47.68	
	Water	33.03		48.35	
6	Fructose	32.46	a	69.86	a
	Glucose	31.83	ab	67.74	a
	Sucrose	34.96	a	67.03	a
	Water	21.52	b	44.19	b
Effect					
Pulse		**		***	
Vase Solution	*			***	
Pulse* Vase Solution		NS		NS	
Day		NS		***	
Day*Pulse	NS			NS	
Day*Vase Solution		*		***	
Day*Pulse*Vase Solution		NS		NS	

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 18. Pulse solution by vase solution interaction affecting relative leakage ratio (RLR) of stems pulsed in Colombia with abscisic acid, ascorbic acid, ethanol, giberellic acid, indole acetic acid, quercetin, and tap water, then treated with fructose, glucose, sucrose, each at 10 $g \cdot L^{-1}$, or with water as vase solutions upon arrival in Raleigh, NC. Relative leakage ratio (RLR) was calculated as electrical conductivity (EC) of fresh tissue divided by EC of frozen tissue.

Pulse solution	Vase solution	RLR	
Abscisic acid	Fructose	0.13590	a[z]
	Glucose	0.07173	ab
	Sucrose	0.06277	b
	Water	0.07722	ab
Ascorbic acid	Fructose	0.06837	
	Glucose	0.09070	
	Sucrose	0.08245	
	Water	0.08172	
Ethanol	Fructose	0.09364	
	Glucose	0.09207	
	Sucrose	0.09417	
	Water	0.07736	
Giberellic acid	Fructose	0.08054	
	Glucose	0.08743	
	Sucrose	0.05502	
	Water	0.10590	
Indole acetic acid	Fructose	0.09547	
	Glucose	0.11220	
	Sucrose	0.08137	
	Water	0.09536	
Quercetin	Fructose	0.07963	
	Glucose	0.07996	
	Sucrose	0.05836	
	Water	0.06299	

Table 18 Continued.

Tap water	Fructose	0.06529
	Glucose	0.08753
	Sucrose	0.09135
	Water	0.09448
Effect		
Pulse		NS
Vase Solution		NS
Pulse* Vase Solution		*

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 19. Main effects of vase solutions using fructose or sucrose as a main carbohydrate in combination with mannitol (5 or 10 mg·L^{-1}), mannose (5 g·L^{-1}), raffinose (5 or 10 g·L^{-1}), sorbitol (1 or 5 g·L^{-1}), Splenda® (25 mg·L^{-1}), or trehalose (200 mg·L^{-1}) as protective carbohydrate sources on postharvest characteristics of cut *Rosa* 'Freedom' for Experiment 12. The senescence criteria petal wilting (WP), petal blueing (PB), and petal blackening (black.) were rated on a scale of 0-10 (0, best; 10, poor) at vase life termination. Stage of flower opening was 0=tight, 1=medium, 2=open, 3=blown and was also taken at vase life termination. Neck rot caused by botrytis infection was noted when present at termination and is presented as percentage of stems affected. Water was used as a control.

Carbohydrate	WP (0-10)	PB (0-10)	Petal black. (0-10)
		Primary Carbohydrate	
Fructose	6.7 b[Z]	6.3	2.6 a
Sucrose	6.9 ab	6.2	2.6 a
Water	7.2 a	6.3	2.3 b
Effect			
Primary	*	NS	***
Protective	NS	*	NS
Primary*Protective	NS	NS	NS

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 20. Primary by protective carbohydrate interactions for cut *Rosa* 'Freedom' treated with fructose or sucrose as primary vase solutions in combination with mannitol (5 or 10 $mg \cdot L^{-1}$), mannose (5 $g \cdot L^{-1}$), raffinose (5 or 10 $g \cdot L^{-1}$), sorbitol (1 or 5 $g \cdot L^{-1}$), Splenda® (25 $mg \cdot L^{-1}$), or trehalose (200 $mg \cdot L^{-1}$) as protective carbohydrate sources in Experiment 12. Water was used as a control. Vase life was the number of days until flowers reached an unacceptable level of senescence. The senescence parameters overall appearance (AP) petal discoloration (PD), and bent neck were rated on a scale of 0-10 (0, symptom not present; 10, symptom severe) at vase life termination. Stem blackening (black.) and leaf drop were noted at vase life termination if present. Water uptake was measured on day 4 of vase life evaluation.

Primary	Protective	Vase life (days)		AP (0-10)	PD (0-10)	Bent neck (0-10)	Stem black. (%)	Leaf drop (%)	
Fructose	Mannitol 5 $mg \cdot L^{-1}$	14.2	a[Z]	7.8	4.5	0.7	0	0	
	Mannitol 10 $mg \cdot L^{-1}$	13.1	ab	8.1	4.7	0.5	0	6.7	
	Mannose 5 $g \cdot L^{-1}$	12.1	ab	7.7	4.2	1.7	0	20.0	
	Raffinose 5 $g \cdot L^{-1}$	11.5	b	7.8	3.7	1.3	6.7	6.7	
	Raffinose 10 $g \cdot L^{-1}$	13.0	ab	7.4	4.4	0.6	0	0	
	Sorbitol 1 $g \cdot L^{-1}$	12.9	ab	7.8	4.5	0.7	0	0	
	Sorbitol 5 $g \cdot L^{-1}$	13.9	ab	7.9	4.9	0.5	0	0	
	Splenda 25 $mg \cdot L^{-1}$	13.6	ab	7.5	4.3	0.5	6.7	6.7	
	Trehalose 200 $mg \cdot L^{-1}$	14.1	a	7.2	4.3	0.2	0	0	
	Water	13.5	ab	7.6	4.6	0.6	6.7	13.3	
Sucrose	Mannitol 5 $mg \cdot L^{-1}$	13.5		7.4	4.3	0.5	6.7	6.7	b
	Mannitol 10 $mg \cdot L^{-1}$	13.3		7.5	4.5	0.6	0	0.0	b
	Mannose 5 $g \cdot L^{-1}$	12.2		7.9	4.1	0.9	6.7	73.3	a
	Raffinose 5 $g \cdot L^{-1}$	13.3		8.1	4.6	0.7	6.7	6.7	b
	Raffinose 10 $g \cdot L^{-1}$	12.4		7.3	3.7	0.5	0	13.3	b
	Sorbitol 1 $g \cdot L^{-1}$	11.5		6.9	3.5	0.8	0	0	b
	Sorbitol 5 $g \cdot L^{-1}$	12.9		8.0	4.7	1.1	0	0	b

Table 20 Continued.

	Splenda 25 mg·L^{-1}	13.1	8.1	4.9	0.6	0	0 b
	Trehalose 200 mg·L^{-1}	13.1	7.8	4.1	0.1	0	0 b
	Water	13.3	7.8	4.5	0.6	6.7	6.7 b
Water	Mannitol 5 mg·L^{-1}	11.7 ab	8.0	4.7 ab	1.1 ab	66.7 a	86.7 a
	Mannitol 10 mg·L^{-1}	11.6 ab	7.9	4.5 ab	1.3 ab	73.3 a	80.0 a
	Mannose 5 g·L^{-1}	10.9 b	7.8	3.8 b	1.5 ab	20.0 bc	100.0 a
	Raffinose 5 g·L^{-1}	13.9 a	7.4	4.3 ab	0.3 b	0 c	13.3 b
	Raffinose 10 g·L^{-1}	12.3 ab	8.3	5.1 ab	1.6 ab	0 c	6.7 b
	Sorbitol 1 g·L^{-1}	11.8 ab	8.7	6.0 ab	1.4 ab	60.0 ab	73.3 a
	Sorbitol 5 g·L^{-1}	11.4 b	8.0	4.7 ab	1.3 ab	13.3 c	20.0 b
	Splenda 25 mg·L^{-1}	11.6 ab	8.0	4.9 ab	1.4 ab	66.7 a	86.7 a
	Trehalose 200 mg·L^{-1}	11.7 ab	8.2	5.5 a	1.5 ab	73.3 a	80.0 a
	Water	11.1 b	8.5	4.1 ab	2.1 a	73.3 a	80.0 a
Effect							
Primary		***	**	**	***	***	***
Protective		**	NS	NS	NS	***	***
Primary*Protective		***	*	**	**	***	**

[Z]Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively.

Table 21. Pearson correlation and probability of significance for petal blackening, stem blackening, leaf drop, and neck rot correlated to vase life in cut *Rosa* for all experiments presented here.

Experiment	Petal black.		Stem black.		Leaf drop		Neck rot	
and cultivar	p	*r*	p	*r*	p	*r*	p	*r*
1	-0.0012	0.9818	-0.0797	0.1161	0.0013	0.9795	-0.0241	0.6354
2	0.3752	<0.0001	-0.0633	0.2306	-0.0603	0.2541	-0.1605	0.0023
3	0.5592	<0.0001	-0.0522	0.3927	-0.0231	0.7060	-0.0035	0.9548
4 Freedom	0.2311	0.0042	0.2331	0.0039	0.2001	0.0135	0.1016	0.2130
4 Judy	0.6598	<0.0001	ND[Z]		0.1111	0.1674	-0.0844	0.2948
4 Polo	0.2135	0.0078	ND		0.1085	0.1803	-0.0636	0.4331
4 Verdi	0.3330	<0.0001	0.3404	<0.0001	0.0656	0.4160	-0.3466	<0.0001
4 Versilia	0.4004	<0.0001	0.2409	0.0025	-0.0213	0.7926	-0.1083	0.1798
5 Freedom	0.0142	0.8442	0.4553	<0.0001	0.2347	0.0010	-0.3613	<0.0001
5 Judy	0.4337	<0.0001	-0.0361	0.6165	0.0571	0.4280	0.0863	0.2305
5 Polo	0.1664	0.0211	ND		0.2194	0.0021	-0.3891	<0.0001
5 Verdi	0.2290	0.0013	0.1572	0.0282	0.3097	<0.0001	-0.4565	<0.0001
5 Versilia	0.1604	0.0255	0.2467	0.0005	0.1672	0.0195	-0.5552	<0.0001
6	0.2594	0.0008	-0.2195	0.0046	-0.3207	<0.0001	-0.2345	0.0024
7 Freedom	0.3948	0.0046	0.7885	<0.0001	0.5344	<0.0001	ND	
7 Judy	0.6903	<0.0001	ND		ND		ND	
7 Polo	0.0320	0.8253	ND		-0.0150	0.9178	ND	
7 Verdi	-0.3287	0.0198	-0.3934	0.0047	0.1540	0.2858	ND	
7 Versilia	0.1336	0.3602	-0.1383	0.3433	-0.1961	0.1768	-0.1968	0.1753
8 Charlotte	0.5364	0.0007	ND		ND		ND	
8 Freedom	0.4273	0.0093	-0.0077	0.9645	-0.0677	0.6947	ND	
9	0.2760	0.0012	-0.1484	0.0858	-0.2435	0.0044	ND	
10 Charlotte	0.2340	0.0264	-0.2969	0.0045	ND	-0.0859	0.4206	
10 Freedom	0.3960	0.0001	-0.3291	0.0015	-0.1141	0.2844	-0.2816	0.0072
11	0.0606	0.2161	-0.1819	0.0002	-0.2591	<0.0001	-0.2132	<0.0001
12	0.2633	<0.0001	-0.1593	0.0007	-0.3046	<0.0001	-0.1140	0.0158

[Z]ND: postharvest characteristic not detected in cultivar

Ethylene tolerance of hybrid lilies: carbohydrate content affected by storage and pretreatment with silver thiosulfate or 1-methylcyclopropene

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Subject Category: Postharvest

Ethylene sensitivity and vase life of hybrid lilies: carbohydrate content affected by cold storage and pretreatment with silver thiosulfate or 1-methylcyclopropene

Additional index words. *Lilium*, anti-ethylene agent, STS, 1-MCP, starch hydrolysis, sucrose, glucose, fructose, vase life, cut flower

Abstract. Some reports suggest *Lilium* species are not sensitive to ethylene, while other reports indicate *Lilium* are sensitive to ethylene. A previous report indicated that 'Stargazer' had increased sensitivity to ethylene after cold storage. We speculated that differences in sensitivity were due to carbohydrate status, particularly starch levels, which may change as a result of cold exposure. To investigate the hypothesis that *Lilium* species exhibit increased sensitivity to ethylene due to altered carbohydrate levels after cold storage, we pretreated *Lilium* of different genetic backgrounds with 1-methylcyclopropene (1-MCP) or silver thiosulfate (STS) before exposing them to a two-week cold storage period and subsequent treatment with 10 $\mu L \cdot L^{-1}$ ethylene. Storage decreased vase life of cut *Lilium* 'Princess Amalia', 'Red Alert', 'Renoir', and 'Stargazer' by 4.1, 5.5, 5.8, and 2.0 days, respectively. Storage decreased tepal starch content and leaf sucrose content, but increased tepal sucrose and fructose content. The magnitude of changes in carbohydrate content was dependent on cultivar. Vase life was positively correlated with starch in tepals and

stems plus carpels, and with sucrose in leaves, but was negatively correlated with sucrose in tepals. Ethylene treatment reduced vase life in ‘Red Alert’ while treatment with either 1-MCP or STS increased vase life in both ‘Red Alert’ and ‘Renoir’. Postharvest bud blast during vase life evaluation differed only by cultivar, ranging from 0 to 0.24 buds per stem for ‘Red Alert’ and ‘Renoir’, respectively.

Ethylene sensitivity is of great concern to growers of floriculture crops. Ethylene exposure has numerous symptoms; the most problematic for cut flower growers are abscission of leaves, flowers, and buds; bud abortion; and premature floral senescence (Dole and Wilkins, 1999; Elgar et al., 1999). Ethylene sensitivity varies widely by crop. Lilies have been characterized as sensitive (Dole and Wilkins, 1999), although there is apparently varying sensitivity based on genetic background (Elgar et al., 1999; Ranwala and Miller, 2005). Asiatic lilies, for instance, are reported to be more sensitive than Oriental lilies (Elgar et al., 1999). However, after cold storage, bud opening in Oriental lily 'Stargazer' was reduced in flowers treated with ethylene (Han and Miller, 2003). Questions regarding ethylene sensitivity are important because cut lilies are a high value floriculture crop. In 2008, the wholesale value of cut lilies produced in the U.S. by growers with over $100,000 of total floriculture sales was estimated at $72 million (NASS, 2009), the highest wholesale value of any domestic U.S. cut flower crop.

Ethylene sensitivity in lily is not well understood, despite several studies on the subject (Elgar et al., 1999; Han and Miller, 2003; Dole et al., 2005). Treatment with the anti-ethylene agents silver thiosulfate (STS) and 1-methylcyclopropene (1-MCP) increased vase life of Asiatic lily 'Polyanna' (Dole et al., 2005). In another study, STS and 1-MCP increased vase life of Asiatic lily 'Cordelia' in summer-grown stems but not in winter-grown stems (Elgar et al., 1999). Treatment with STS or 1-MCP did not affect the vase life of Asiatic lily 'Elite' or *Lilium longiflorum*

'Lorena'. The same study found that exogenous ethylene decreased vase life of Asiatic lily hybrids 'Cordelia', 'Apeldoorn', 'Goldena', and 'Mona' as well as Oriental lily 'Casablanca' and *Lilium longiflorum* 'Lorena'. However, ethylene did not decrease vase life of Asiatic hybrids 'Romano', 'Grand Paradiso', and 'Nova Cento'; Oriental hybrids 'Cassandra' and 'Stargazer'; or *Lilium longiflorum* 'Gelria' and 'Princess Gracia' (Elgar et al., 1999).

A carbohydrate surplus was associated with increased longevity in Asiatic lily (van der Meulen-Muisers et al., 2001), which had previously been attributed to increased substrate for respiration. However, studies with vegetative cuttings indicated that higher levels of endogenous carbohydrates reduce sensitivity to ethylene, but do not reduce ethylene production (Rapaka and Faust, 2007; Rapaka et al., 2007a; 2007b). Therefore, in cut flowers, increased endogenous carbohydrates may not only increase vase life by increasing respirable substrate, but might also decrease ethylene sensitivity. The difference in response to treatment with STS and 1-MCP, where treatments increased vase life in summer but not in winter, in Asiatic lily 'Cordelia' (Elgar et al., 1999) also points to a possible link between carbohydrate status and ethylene sensitivity. Higher summer temperatures might decrease endogenous carbohydrates, thus increasing ethylene sensitivity and thereby decreasing effectiveness of anti-ethylene agents.

In cuttings of *Portulaca grandiflora* and *Lantana camara* used for vegetative propagation, ethylene sensitivity decreased while starch levels continued to increase after levels of the soluble carbohydrates sucrose, fructose, and glucose had peaked

and steadied, indicating that either starch or total carbohydrates may be linked to ethylene sensitivity (Rapaka et al., 2007a; 2007b). Glucose, fructose, and sucrose were higher in petals of the long-lived rose cultivar 'Delilah' than in the short-lived cultivar 'Sonia', while starch concentrations were higher in the petals of the short-lived cultivar and in the leaves of the long-lived cultivar (Ichimura et al., 2005). Interestingly, the long-lived cultivar was more sensitive to ethylene (Ichimura et al., 2005). In many species, *Solanum tuberosum* (potato) being the most characterized, cold storage of tubers results in the hydrolysis of starch to soluble sugars (Chen et al., 2008). We speculate that cold storage increases sensitivity to ethylene, as was seen in Oriental lily 'Stargazer' (Han and Miller, 2003), by increasing the relative levels of soluble sugars to starch.

Our research objectives were to determine (1) if cold storage increases ethylene sensitivity in lily hybrids, (2) if STS or 1-MCP prevent occurrence of ethylene sensitivity as a result of cold storage, and (3) the effect of cold storage on levels of soluble sugars and starch in lily hybrids.

Materials and Methods

Four hybrid lily varieties, L.A. *Lilium* 'Princess Amalia', L.A. *L.* 'Red Alert', Asiatic *L.* 'Renoir', and Oriental *L* . 'Stargazer', were received as precooled, frozen bulbs. After arrival, bulbs were planted on 26 September 2008 and held at 2 °C for rooting for three weeks before the temperature was raised to 6°C for 12 days until emergence, then growth was slowed by holding at 2°C for 12 days. Plants were

moved to a glass-covered greenhouse on 10 November 2008 set at 15/20 °C night/day minimum temperatures under natural light.

'Stargazer' lilies received 1.4 $g \cdot L^{-1}$ calcium chloride sprays one to two times per week starting 2 December 2008 to alleviate calcium deficiency symptoms. Additionally, fertilizer was changed from 250 $mg \cdot L^{-1}$ N from 20-10-20 (Peters Professional, Scotts Co., Marysville, OH) to 250 $mg \cdot L^{-1}$ N from 15-0-15 (Peters Professional, Scotts Co., Marysville, OH) on 22 December 2008 for all varieties as 15-0-15 is a base forming fertilizer with nitrogen source of calcium nitrate to increase calcium availability. Visible bud was seen on 'Princess Amalia on 26 November, on 'Red Alert' and 'Renoir' on 8 December, and on 'Stargazer' on 17 December 2008.

Stems were harvested at fully colored puffy bud stage. After harvest, stems were recut to 50 cm for 'Princess Amalia', 'Red Alert', and 'Renoir', and to 60 cm for 'Stargazer'. After recutting, stems were sorted by flower number per stem into twelve treatment groups by cultivar to form a 3 (pretreatment) x 2 (storage) x 2 (ethylene) factorial, and placed by treatment into either 0.5 L deionized water (DI) or 0.2 mM STS from 0.5 mL Chrysal AVB (Chrysal USA, Miami, FL) diluted in 0.5 L DI for 4 hours at room temperature. Stems in deionized water were either treated with 2.7 $\mu g \cdot L^{-1}$ 1-MCP or left in ambient conditions (pretreatment control) for 4 hours. For 1-MCP treatment, 400 mg Ethylbloc (Floralife, Inc., Walterboro, SC) were placed in a beaker and dissolved in 50 mL DI within a 210 L barrel, a battery operated fan was placed above the beaker, and the barrel was immediately sealed; for uniform conditions, STS and control stems were sealed in separate barrels with

ambient air also containing fans. The actual concentration of 1-MCP, as measured using isobutylene as a standard, ranged from 0.04 $\mu L \cdot L^{-1}$ at treatment initiation to 0.977 $\mu L \cdot L^{-1}$ after four hours.

After pretreatment, stems were divided into two groups and treated with either 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours or stored in DI at 3.3 °C for two weeks. After ethylene treatment, stems were placed in 0.5 L deionized water and evaluated daily to determine vase life. Vase life was the number of days until half of each stem's last flower's tepals had wilted with water-soaked lesions or had abscised or when the main stem had broken (Figure 1). Prior to the start of vase life, the number of viable buds per stem number of viable buds per stem was counted, and, at the termination of vase life, the number of flowers that had opened was counted; the difference between these counts, buds which did not open, was termed "postharvest bud blast". Stems stored at 3.3 °C were removed after 2 weeks, treated with ethylene at 0 or 10 $\mu L \cdot L^{-1}$ for 18 hours and evaluated for vase life as described for non-stored stems. Three stems of each variety from all treatments not pretreated with either 1-MCP or STS and all cold-stored treatments were removed before vase life evaluation for carbohydrate analysis. Ethylene concentrations for the 0 and 10 $\mu L \cdot L^{-1}$ treatments averaged 0.03 and 9.50 $\mu L \cdot L^{-1}$ at treatment initiation, respectively, and 0.41 and 9.41 $\mu L \cdot L^{-1}$ at treatment end, respectively.

Stems removed for carbohydrate analysis were divided into three samples: tepals, leaves, and stems plus carpels, weighed, flash frozen with liquid N_2, and lyophilized. Dried tissue was pulverized and approximately 100 mg was extracted in

3 ml 80% ethanol (ETOH) and 1 ml 8 mM sorbitol as an internal standard. Samples were vortexed to suspend dried tissue, placed in a sonicating water bath for 5 min. and heated in 80 °C water bath for 5 min. before being centrifuged at 3000xg for 5 min. at 4 °C. The supernatant was removed to a new tube. The pellet was resupended in 3 ml ETOH, vortexed, sonicated, heated in 80 °C water bath, centrifuged, and the supernatant removed twice more. Total supernatant for each sample was 10 ml (9 ml ETOH + 1 ml sorbitol solution). The pellet remaining after centrifugation and removal of the supernatant was stored at 4 °C for subsequent starch determination. Aliquots (500 µL) of the supernatant were taken and dried in a rotary evaporator then stored at -20 °C until reconstitution and analysis. Samples were reconstituted in 500 µL H_2O, centrifuged to remove remaining particulate matter, and analyzed by HPLC (LaChrom Elite, Hitachi, Pleasanton, CA) using an isocratic gradient of distilled/DI water with a flow rate of 0.4 ml·min^{-1}. A calcium column (BP-100 Ca^{++}, Benson Polymeric, Reno, NV) was used for separation. A standard curve containing sucrose, glucose, fructose, mannitol, and sorbitol was used for peak quanitification. Calculations were based on peak height and the sorbitol internal standard was used to normalize peak heights.

Starch in pellet left from soluble sugar extraction was quantified after Ranwala and Miller (2008 and 2009). The pellet left from soluble carbohydrate extraction was boiled for 30 min in 4 ml 100 mM Na-acetate buffer adjusted to pH 4.5 with 1 N acetic acid and subsequently cooled to room temperature. One ml amyloglucosidase solution (50 units·ml^{-1} in Na-acetate buffer, pH 4.5) was added to

digest each sample and left in an incubator (50 to 55 °C) for 2 days. After digestion, samples were centrifuged at 3000xg. A 500 µl (100 or 50 µl for high starch samples) aliquot of the cleared solution was removed to a new tube and 5 ml of cold phosphate buffer containing 5 units·ml^{-1} glucose oxidase, 1 unit·ml^{-1} horseradish peroxiase, and 40 µg·ml^{-1} *o*-dianisidine were added. Samples were incubated at 30 °C for 30 min before absorbance was measured in a spectrophotometer (Lambda Bio20, Perkin Elmer, Waltham, MA) at 450 nm. Absorbance was calculated against a glucose standard curve. Due to evaporation of liquid during the digestion process, a concentration factor was calculated based on the approximated remaining volume of liquid after digestion for each sample and used in final starch calculations. Amyloglucosidase blanks and potato starch digests were used as controls. All enzymes used for starch digestion were obtained from Sigma (St. Louis, MO).

Stems sampled for carbohydrates were subsetted into two factorial analyses. Stems not treated with either STS or 1-MCP but that were either stored or non-stored and either treated with 0 or 10 µL·L^{-1} ethylene were analyzed in a 3 (cultivar) x 2 (storage) x 2 (ethylene) x 3 (organ sampled) factorial. Stems that were stored and pretreated with 1-MCP or STS or not pretreated were analyzed in a 4 (cultivar) x 3 (pretreatment) x 2 (ethylene) x 3 (organ sampled) factorial. Because of inadequate numbers of stems available for 'Princess Amalia', one replicate of stems was used for the factorial on stored stems including STS and 1-MCP pretreatments, but non-stored stems of 'Princess Amalia' were not taken for analysis in the factorial including both stored and non-stored stems without pretreatments.

PROC MIXED in SAS (SAS Institute, Cary, NC) was used for statistical analysis as unequal replication existed. The Kenward-Roger method was used to calculate dominator degrees of freedom and Tukey's LSD was used for multiple comparisons.

Results

Vase life was affected by pretreatment ($p=0.0006$), storage ($p\leq0.0001$), ethylene ($p=0.0130$), cultivar ($p<0.0001$), and a storage by cultivar interaction ($p=0.0001$). Because of the interaction, we presented the data by cultivar (Table 1) here. Over all postharvest treatments, vase life was higher in 'Princess Amalia' and 'Renoir' than in 'Red Alert' and 'Stargazer', averaging 8.3, 8.7, 6.1, and 6.0 days, respectively ($p\leq0.0001$).

Storage decreased vase life in all cultivars, where vase life began the day each stem was removed from ethylene treatments and after all pretreatment and storage treatments were completed. Vase life decreased 4.1, 5.5, 5.8, and 1.9 days with storage for 'Princess Amalia', 'Red Alert', 'Renoir', and 'Stargazer', respectively (Table 1). For 'Red Alert', vase life increased with 1-MCP and STS treatments by 1.3 and 1.0 days, respectively, compared to the control. Vase life decreased 0.7 days due to exogenous ethylene treatment in 'Red Alert' compared to the control. Pretreatment also affected 'Renoir', where vase life was 2.5 and 2.8 days longer for 1-MCP and STS treated stems, respectively, compared to control stems (Table 1).

Stems of ‘Stargazer’ and ‘Renoir’ had a tendency to bend and break during postharvest, which we termed “bent stems” (Figure 1). We speculate that the weight of the flowers caused this in ‘Stargazer’; we are unsure of the cause in ‘Renoir’. When we treated bent stems as a dependent variable, an interaction existed between storage and cultivar ($p \leq 0.0001$), where the percentage of bent stems increased from 13% to 33% with storage in ‘Renoir’ and decreased from 70% to 44% with storage in ‘Stargazer’. Neither ‘Princess Amalia’ nor ‘Red Alert’ had any bent stems. Because of this trend, we correlated vase life with bent stems for ‘Stargazer’ (r=-0.6074, $p \leq 0.0001$) and for ‘Renoir’ (r=-0.7723, $p \leq 0.0001$); the negative slope indicates that bent stems were terminated first for both cultivars. Neither pretreatment with 1-MCP or STS nor treatment with ethylene had an effect on the number of bent stems.

We measured postharvest bud blast as a potential indicator of ethylene sensitivity; however, this measure varied only by cultivar, where ‘Renoir’ had increased blasted flowers per stem compared to‘Red Alert’ and ‘Stargazer’, while ‘Princess Amalia’ was intermediate (0.24, 0, 0.07, and 0.15 blasted flowers per stem, respectively, $p \leq 0.0001$). Thus, this postharvest problem appears to be controlled by genetic background.

High levels of bud abortion occurred on ‘Princess Amalia’ stems during production, which may have resulted from low winter light levels. This led to a low number of replicates for this cultivar. Therefore, no attempt was made to categorize ethylene sensitivity based on lily hybrid groupings of L.A., Oriental, and Asiatic.

Carbohydrate analysis-storage. Glucose content was affected by a storage by ethylene concentration interaction (p=0.0272). Glucose contents of stems averaged over organ (leaves, stems plus carpels, and tepals) and cultivar were 28.0 and 33.4 $mg \cdot g^{-1}$ dry weight for non-stored stems treated with 0 and 10 $\mu L \cdot L^{-1}$ ethylene, and 35.8 and 30.7 $mg \cdot g^{-1}$ dry weight for stored stems treated with 0 and 10 $\mu L \cdot L^{-1}$ ethylene, respectively.

Stored samples treated with 0 $\mu L \cdot L^{-1}$ ethylene of 'Red Alert' and 'Renoir' had higher fructose concentrations than stored 'Stargazer' treated with 0 $\mu L \cdot L^{-1}$ ethylene (Table 2). For stored samples treated with 10 $\mu L \cdot L^{-1}$ ethylene, 'Red Alert' had higher levels of fructose than 'Stargazer' (Table 2). Stored samples of 'Renoir' treated with 0 $\mu L \cdot L^{-1}$ ethylene had more fructose than non-stored samples. In the stored stems of 'Renoir', stems treated with 10 $\mu L \cdot L^{-1}$ ethylene had decreased fructose compared to the 0 $\mu L \cdot L^{-1}$ treatment (Table 2).

Sucrose was highest in leaves of all cultivars, though it was not significantly different in the tepal sample of 'Red Alert' (Table 3). For 'Stargazer', sucrose in the stem plus carpels was lower than in tepals. Sucrose in the stems plus carpels was higher in 'Red Alert' than in 'Stargazer'. Sucrose in tepals was higher in 'Red Alert' and 'Stargazer' than in 'Renoir'.

Glucose was highest in the tepals of all cultivars (Table 3). Glucose was lower in leaves than in stems plus carpels of 'Renoir'. Glucose in stems plus carpels and tepals of 'Stargazer' was lower than of 'Renoir' and lower in tepals in 'Stargazer' than in 'Red Alert' (Table 3).

Fructose was higher in tepals of ‘Red Alert’ and ‘Renoir’ than in ‘Stargazer’ and higher in stems plus carpels of ‘Renoir’ than ‘Stargazer’ (Table 3). For all cultivars, tepals had the highest level of fructose. For ‘Renoir’, leaves had a lower concentration than stems plus carpels.

Sucrose was higher in non-stored leaves than in stored leaves; however, sucrose was lower non-stored tepals than in stored tepals (Table 4). Sucrose in stems plus carpels was the same for non-stored and stored stems (Table 4).

Fructose was higher in tepals of stored stems than of non-stored stems (Table 4). Fructose was highest in tepals compared to stems plus carpels and leaves for both stored and non-stored stems (Table 4).

Tepals of non-stored ‘Stargazer’ had the highest starch concentrations among cultivars, regardless of ethylene treatment (Table 5). In the non-stored, 0 $\mu L \cdot L^{-1}$ ethylene treatment combination, tepals of ‘Red Alert’ had a higher level of starch than ‘Renoir’, while for the 10 $\mu L \cdot L^{-1}$ ethylene treatment, tepals of ‘Red Alert’ had less starch than ‘Renoir’ tepals (Table 5). Storage decreased starch concentrations in 0 $\mu L \cdot L^{-1}$ tepals of ‘Red Alert’ and in both 0 $\mu L \cdot L^{-1}$ and 10 $\mu L \cdot L^{-1}$ treatments of ‘Renoir’ and ‘Stargazer’. Tepals of non-stored ‘Red Alert’ treated with 10 $\mu L \cdot L^{-1}$ ethylene had decreased starch compared to the 0 $\mu L \cdot L^{-1}$ treatment (Table 5). Tepals of non-stored ‘Stargazer’ and ‘Renoir’ for both ethylene concentrations had higher levels of starch than did the leaves or stem plus carpels while this was only statistically significant for non-stored ‘Red Alert’ treated with 0 $\mu L \cdot L^{-1}$ ethylene. For non-stored ‘Red Alert’ treated with 10 $\mu L \cdot L^{-1}$ ethylene, starch was higher in tepals than in leaves (Table 5).

Carbohydrate analysis-Pretreatment prior to storage. For the 1-MCP and 0 $\mu L \cdot L^{-1}$ ethylene treatment combination averaged over organs, fructose was higher in 'Princess Amalia' and 'Red Alert' than in 'Stargazer' (Table 6). In the 1-MCP, 10 $\mu L \cdot L^{-1}$ ethylene treatment combination, fructose was higher in 'Princess Amalia' than in 'Red Alert' and 'Stargazer' and was higher in 'Renoir' than 'Stargazer' (Table 6).

For STS pretreated stems, 'Renoir' had higher fructose than did 'Stargazer' for both ethylene concentrations, and 'Princess Amalia' had higher fructose than 'Stargazer' for the 0 $\mu L \cdot L^{-1}$ ethylene treatment. For stems without a pretreatment, 'Princess Amalia' had higher fructose levels than 'Stargazer' and for the 0 $\mu L \cdot L^{-1}$ ethylene treatment, 'Renoir' also had higher fructose than 'Stargazer' (Table 6).

When analyzed within cultivar, only 'Renoir' showed differences in fructose between pretreatment and ethylene treatment combinations. For stems not pretreated with 1-MCP or STS, stems treated with 0 $\mu L \cdot L^{-1}$ ethylene had higher fructose than stems treated with 10 $\mu L \cdot L^{-1}$ ethylene (Table 6). Stems pretreated with 1-MCP exposed to 0 $\mu L \cdot L^{-1}$ ethylene had lower fructose than those not pretreated and to those pretreated with STS and treated with 10 $\mu L \cdot L^{-1}$ ethylene (Table 6).

Starch was highest in tepals of 'Stargazer' compared to the other cultivars. For 'Renoir' and 'Stargazer', starch was higher in tepals than stems plus carpels or leaves (Table 7).

Sucrose was higher in tepals of 'Stargazer' and 'Red Alert' than 'Princess Amalia' and 'Renoir'. Sucrose was lower in 'Stargazer' than in stems plus carpels of the other cultivars. Sucrose was higher in leaves of 'Stargazer' than leaves of 'Red

Alert' (Table 7). For 'Red Alert', sucrose was higher in tepals than leaves, but for 'Renoir', sucrose was higher in leaves than in tepals or stems plus carpels. Sucrose was higher in 'Stargazer' tepals and leaves than in stems plus carpels (Table 7).

'Princess Amalia' tepals had the highest fructose over other cultivars; 'Red Alert' and 'Renoir' tepals had higher fructose than 'Stargazer' tepals (Table 7). For stems plus carpels, 'Princess Amalia' and 'Renoir' had higher levels of fructose than 'Stargazer'(Table 7). Fructose in leaves did not differ between cultivars. For each cultivar, there was more fructose in tepals than in leaves or stems plus carpels. In 'Renoir', there was higher fructose in stems plus carpels than in the leaves (Table 7).

For tepals of stems pretreated with 1-MCP and treated with 0 $\mu L \cdot L^{-1}$ ethylene, glucose was higher in 'Princess Amalia' than the other cultivars and was higher in 'Red Alert' than in 'Stargazer' (Table 8). Glucose was higher in 'Princess Amalia' and 'Renoir' tepals of stems treated with 1-MCP and 10 $\mu L \cdot L^{-1}$ ethylene than in tepals of 'Stargazer'. For tepals of stems pretreated with STS and treated with 0 $\mu L \cdot L^{-1}$ ethylene, glucose was higher in 'Princess Amalia' than the other cultivars and was higher in 'Renoir' than in 'Stargazer' (Table 8). For stems treated with STS and 10 $\mu L \cdot L^{-1}$ ethylene, glucose was higher in tepals of 'Red Alert' and 'Renoir' than in tepals of 'Princess Amalia' and 'Stargazer'. For stems not pretreated and treated with 0 $\mu L \cdot L^{-1}$ ethylene, glucose was higher in 'Princess Amalia' and 'Renoir' than in 'Stargazer'. For stems not pretreated and treated with 10 $\mu L \cdot L^{-1}$ ethylene, glucose was higher in 'Princess Amalia' and 'Red Alert' than in 'Stargazer' (Table 8).

Glucose was higher in tepals than leaves or stems plus carpels for all treatment combinations of 'Red Alert' (Table 8). Glucose was higher in 'Renoir' tepals than in leaves and stems plus carpels for treatment combinations of 1-MCP and STS plus 10 $\mu L \cdot L^{-1}$ ethylene and no pretreatment plus 0 $\mu L \cdot L^{-1}$ ethylene. Glucose was higher in 'Renoir' tepals than in leaves for the remaining treatment combinations (Table 8). Glucose was higher in 'Stargazer' tepals than in stems plus carpels for all treatment combinations except for stems pretreated with STS and exposed to 10 $\mu L \cdot L^{-1}$ ethylene. Glucose was higher in 'Stargazer' tepals than in leaves for all treatment combinations except MCP pretreated stems exposed to 0 $\mu L \cdot L^{-1}$ ethylene (Table 8).

Carbohydrate correlations for non-stored and stored stems. In correlations between means of vase life and carbohydrate levels for each treatment and cultivar combination, vase life was positively correlated with leaf sucrose (r=0.4698, p=0.0088), stem starch (r=0.5640, p=0.0012), and tepal starch (r=0.3967, p=0.03) and negatively correlated with tepal sucrose (r=-0.5602, p=0.0013). There were also a number of significant correlations between carbohydrate levels.

Discussion

Cut flower producers, wholesalers, and florists use cold storage to hold flowers until they are marketed. This might be overnight or for several weeks, in the case of peonies (*Paeonia*). Cold temperatures reduce respiration and allow photoassimilates to remain at high levels in tissues. Although cold storage generally

increases the total length of time flowers remain viable after harvest in non-chilling sensitive species, the length of time flowers are viable for consumers, vase life, might be decreased in some species, as occurred in our work.

We hypothesized that cold storage increases ethylene sensitivity in lilies as a direct result of starch hydrolysis. Our results directly show that vase life is decreased as a result of storage and that this decrease in vase life is linked to starch hydrolysis in tepals; however, vase life following storage was not shortened more in ethylene treated stems compared to stems not treated with ethylene. While vase life is not the only indicator of ethylene sensitivity, another measure of ethylene sensitivity we used, flower bud abscission during postharvest, which we term "postharvest bud blast", differed only by cultivar. Differences in postharvest bud blast might be more influenced by reallocation patterns for carbohydrates between cultivars than by ethylene sensitivity. Van der Meulen-Muisers et al. (2001) indicate that tepal carbohydrate status at harvest, which is directly linked to stage of maturity, is predictive of bud opening. 'Stargazer' had low levels of postharvest bud blast but also had altered carbohydrate allocation patterns compared to other cultivars, as discussed below.

Starch in stems plus carpels was positively associated with vase life. Leaf sucrose and tepal starch were positively correlated with both vase life and stem plus carpel starch while tepal sucrose was negatively correlated with both vase life and stem plus carpel starch. Despite this strong evidence that stem and/or carpel starch levels are important in vase life, starch in stems plus carpels was not affected by

storage, pretreatment, or by ethylene; however, the amount of carbohydrates held in the stems plus carpels was relatively low compared to carbohydrates in the tepals. Thus, changes in the carbohydrate content of stems plus carpels might have been statistically undetectable because of the large magnitude of change in carbohydrate content in the tepals.

Starch in tepals was also positively correlated with vase life and with leaf sucrose and stem plus carpel starch. Storage decreased starch in tepals and ethylene treatment might also have decreased starch in non-stored 'Red Alert' tepals.

Vase life was positively correlated with leaf sucrose and negatively correlated with tepal sucrose. Storage decreased sucrose in leaves and increased sucrose in tepals, indicating that decreases in vase life associated with storage are correlated to changes in sucrose levels. Sucrose was only affected by cultivar by organ sampled and by storage by organ sampled interactions. These changes in sucrose in leaves and tepals after storage are likely directly linked to starch status. Because of the time of treatment with 1-MCP/STS and with ethylene, samples of non-stored organs were flash frozen approximately 22-24 hours after harvest, so sucrose in leaves would not have been newly photosynthesized, but was probably the result of transitory starch in leaves being hydrolyzed for transport to sink organs such as tepals. We did not see a correlation between tepal starch and tepal sucrose, but that is not surprising given that we would not expect tepal sucrose to be depleted in non-stored samples. van der Meulen-Muisers et al. (2001) found that sucrose in tepals (non-stored) averaged roughly 7% of total tepal carbohydrate (by weight), until the onset of wilting, when

the percentage rose, which is likely due to preparation of export to developing buds. We do not feel that high levels of tepal sucrose cause low vase life, unless sucrose acts as a senescence signal, but that high levels of tepal sucrose result from starch hydrolysis and that the depletion of starch does not allow vase life to be sustained.

In a recent review, van Doorn and Woltering (2008) characterize lilies as non-sensitive to ethylene; however, our data increases evidence indicating that ethylene sensitivity varies within the *Lilium* genus (Table 9). 'Nellie White' has consistently been reported as ethylene sensitive, while 'Stargazer' has been found sensitive in only two of four reports (Table 9), thus ethylene might have marked effects in some cultivars while others might be marginally sensitive.

Statistically, exogenous ethylene exposure decreased vase life only in 'Red Alert' in our work; however, pretreatment with either STS or 1-MCP increased vase life in both 'Red Alert' and 'Renoir', indicating that endogenous ethylene production might be more important than exogenous exposure. When ethylene inhibitors and ethylene treatment both affect vase life, we would expect that pretreatment with STS or 1-MCP would increase vase life in ethylene treated flowers to levels near vase life of flowers not treated with ethylene. We did not see this; however, new ethylene receptors might be synthesized very quickly in lilies, as Cameron and Reid (2001) demonstrated that 1-MCP efficacy declined over time, indicating the synthesis of new receptor molecules. Alternatively, in *Pelargonium*, complete prevention of ethylene damage, when ethylene is applied shortly after 1-MCP, required only 1 $\mu l \cdot L^{-1}$ 1-MCP (Cameron and Reid, 2001); the required concentration in *Lilium* might be greater.

During ethylene treatment in our study, we detected an average of 0.41 $\mu L \cdot L^{-1}$ ethylene in the 0 $\mu L \cdot L^{-1}$ chamber in the sample taken after the overnight treatment was complete, but no ethylene at the start of treatment. Thus, some endogenous ethylene production might have occurred prior to complete release of 1-MCP during treatment, which might have decreased the efficacy of the 1-MCP treatment (Reid and Çelikel, 2008). Cameron and Reid (2001) further showed that holding plants (*Pelargonium*) at low temperatures (12 °C compared to 21 and 25 °C) after 1-MCP treatment lengthened the effective period; however, temperatures of at least 20 °C were required for effective treatment of carnation (Reid and Çelikel, 2008). Thus, the conditions during our treatments were consistent with conditions from these reports for maximum efficacy of 1-MCP.

Although tepal glucose levels differed with pretreatment with STS or 1-MCP prior to cold storage in combination with ethylene treatment after cold storage, tepal glucose was not correlated with vase life or with any of the carbohydrate fractions correlated to vase life. Our data indicate that some lily cultivars are ethylene sensitive and further show that endogenous carbohydrates are correlated to vase life. The bulk of publications on the subject indicates that exogenous carbohydrate application represses ethylene sensitivity in sensitive species (Attri et al., 2008; Ichimura et al., 2000; van Doorn and Woltering, 2008).

Numerous studies have indicated that carbohydrates can act as signaling molecules (Rolland et al., 2002). Hexokinase has been the most characterized as a sensor in this role (Hanson and Smeekens, 2009) so links between fructose and

glucose concentrations and vase life might be possible even though they were not directly correlated. There were strong correlations between glucose and fructose in every tissue we sampled, which indicates that the ratio of the two might be tightly regulated.

Although neither glucose nor fructose in any tissue was correlated with vase life, fructose in cold-stored 'Renoir' was high in all tissues of cuts pretreated with STS in combination with 10 $\mu L \cdot L^{-1}$ ethylene and in stems not pretreated in combination with 0 $\mu L \cdot L^{-1}$ ethylene, but was low in tissues pretreated with 1-MCP in combination with 0 $\mu L \cdot L^{-1}$ ethylene and in cuts not pretreated and treated with 10 $\mu L \cdot L^{-1}$ ethylene. Glucose levels in cold-stored 'Renoir' followed a similar trend, which was further complicated by differences between tissue types. Pollination induces ethylene production and senescence in carnation (van Doorn and Woltering, 2008) and in *Petunia* (Bai et al., 2010). In *Cymbidium*, pollinated flowers senesced 10-13 days before unpollinated flowers; however, when treated with silver nitrate, senescence rate and carbohydrate levels in pollinated flowers were similar to unpollinated flowers (Attri et al., 2008). This, along with the effect on glucose and fructose of the interaction between 1-MCP or STS treatment in combination with ethylene treatment in our study indicates that glucose and ethylene signaling might be interconnected in lilies, as has been shown in tobacco and *Arabidopsis* (Li et al., 2009; Rolland et al., 2002). Although we have do not have evidence that carbohydrate levels and ethylene sensitivity are linked in *Lilium*, we feel that further research is warranted on the subject.

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Table 1. Vase life separated by cultivar. Stems were pretreated with 0.5 $\mu L \cdot L^{-1}$ 1-MCP, 0.2 mM STS, or ambient air and water for four hours, then stored at 3.3 °C for two weeks or not stored, then treated with 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours. Means are an average of 4 to 10 stems. Means are separated within storage, pretreatment, and ethylene for each cultivar. Significance is presented only for effects with significance for at least one cultivar. Overall significance for experiment using cultivar as an effect is included.

Effect		Princess Amalia	Red Alert	Renoir	Stargazer
Storage	Non-Stored	10.4 a[Z]	8.9 a	11.6 a	7.0 a
	Stored	6.3 b	3.4 b	5.8 b	5.0 b
Pretreatment	MCP	9.3 a	6.7 a	9.4 a	6.5 a
	STS	7.6 a	6.4 a	9.7 a	6.1 a
	Control	8.1 a	5.4 b	6.9 b	5.3 a
Ethylene	0	8.5 a	6.5 a	9.3 a	6.5 a
	10	8.1 a	5.8 b	7.9 a	5.5 a
Significance					
Storage (S)		***	***	***	*
Pretreatment (P)		NS	***	**	NS
Ethylene (E)		NS	*	NS	NS
Overall significance					
Storage (S)		***			
Pretreatment (P)		***			
Ethylene (E)		*			
Cultivar (C)		***			
S*C		***			

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 2. Fructose content ($mg \cdot g^{-1}$ dry weight) affected by a cultivar by storage by ethylene interaction. Means are averaged over leaves, stems plus carpels, and tepals for cut stems pretreated with ambient air and water for four hours, then stored at 3.3 °C for two weeks or not stored, then treated with 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours.

Cultivar	Storage	Ethylene concentration	Fructose
Red Alert	Non-Stored	0	34.8 bcd[Z]
		10	39.0 bcd
	Stored	0	44.4 abc
		10	46.0 ab
Renoir	Non-Stored	0	34.9 bcd
		10	40.6 abcd
	Stored	0	57.7 a
		10	39.4 bcd
Stargazer	Non-Stored	0	26.6 cd
		10	26.1 d
	Stored	0	25.9 d
		10	26.9 cd
Significance			
Cultivar			***
Storage			**
Ethylene			NS
C*S*E			*

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

Table 3. Sucrose, glucose, and fructose contents ($mg \cdot g^{-1}$ dry weight) affected by a cultivar by organ interaction. Means of leaves, stems plus carpels, and tepals are averaged over storage and ethylene concentration for cut stems pretreated with ambient air and water for four hours, then stored at 3.3 °C for two weeks or not stored, then treated with 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours.

Cultivar	Organ	Sucrose	Glucose	Fructose
Red Alert	Leaves	18.1 ab[Z]	14.6 d	15.4 d
	Stems and carpels	10.5 cd	17.2 cd	18.7 cd
	Tepals	14.4 bc	78.2 a	89.0 a
Renoir	Leaves	18.5 ab	13.7 d	11.5 d
	Stems and carpels	6.6 de	33.2 bc	32.0 c
	Tepals	7.3 de	72.7 a	85.8 a
Stargazer	Leaves	23.0 a	11.1 d	14.5 d
	Stems and carpels	2.2 e	10.3 d	13.5 d
	Tepals	14.5 bc	36.5 b	51.1 b
Significance				
Cultivar		*	***	***
Organ		***	***	***
C*O		***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

Table 4. Sucrose and fructose concentrations ($mg \cdot g^{-1}$ dry weight) affected by the storage by organ sampled interaction. Means of leaves, stems plus carpels, and tepals are averaged over ethylene concentration and cultivar (Red Alert, Renoir, and Stargazer) for cut stems pretreated with ambient air and water for four hours, then stored at 3.3 °C for two weeks or not stored, then treated with 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours.

Storage	Organ	Sucrose	Fructose
Non-Stored	Leaves	26.1 a[Z]	15.6 c
	Stems and carpels	6.2 d	20.2 c
	Tepals	7.9 cd	64.5 b
Stored	Leaves	13.6 bc	11.6 c
	Stems and carpels	6.6 d	22.3 c
	Tepals	16.3 b	86.1 a
Significance			
Storage (S)		NS	*
Ethylene (E)		NS	NS
Organ (O)		***	***
S*O		***	**

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

Table 5. Starch concentrations ($mg \cdot g^{-1}$ dry weight) affected by cultivar by storage by ethylene by organ interaction. Means of leaves, stems plus carpels, and tepals are separated within cultivar. Cut stems pretreated with ambient air and water for four hours, then stored at 3.3 °C for two weeks or not stored, then treated with 0 or 10 $\mu L \cdot L^{-1}$ ethylene (ethylene conc.) for 18 hours. Significance for main effects and significant simple effects is presented for each cultivar and overall for the cultivar by storage by ethylene concentration by organ factorial.

Storage	Ethylene conc.	Organ	Red Alert	Renoir	Stargazer
Non-Stored	0	Leaves	2.05 c[Z]	3.32 b	1.90 b
		Stems and carpels	5.13 bc	5.23 b	3.09 b
		Tepals	54.02 a	31.35 a	83.72 a
	10	Leaves	2.12 c	2.27 b	1.92 b
		Stems and carpels	3.15 bc	4.96 b	5.45 b
		Tepals	14.62 b	37.49 a	79.69 a
Stored	0	Leaves	1.19 c	1.72 b	1.56 b
		Stems and carpels	1.59 c	1.73 b	1.00 b
		Tepals	2.72 bc	3.16 b	10.71 b
	10	Leaves	1.72 c	1.90 b	0.99 b
		Stems and carpels	0.41 c	3.09 b	1.03 b
		Tepals	3.31 bc	3.17 b	12.19 b
Significance					
Storage (S)			***	***	***
Ethylene (E)			***	NS	NS
S*E			***	NS	NS
Organ (O)			***	***	***
S*O			***	***	***
E*O			***	NS	NS
S*E*O			***	NS	NS

Table 5 Continued.

Overall Significance	
Cultivar (C)	***
Storage (S)	***
Ethylene (E)	NS
Organ (O)	***
C*S*E*O	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

Table 6. Fructose affected by cultivar by pretreatment by ethylene interaction. Cut stems were pretreated with 0.5 $\mu L \cdot L^{-1}$ 1-methylcyclopropene (MCP), 0.2 mM silver thiosulfate (STS), or ambient air plus water (none) for four hours (pretmt.), then stored at 3.3 °C for two weeks, then treated with either 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours. Fructose content ($mg \cdot g^{-1}$ dry weight) averaged over leaves, stems plus carpels is separated within each cultivar. Significance of main effects and significant simple effects is presented within cultivar and overall for the cultivar by pretreatment by ethylene by organ factorial.

Pretmt.	Ethylene concentration	Princess Amalia	Red Alert	Renoir	Stargazer
MCP	0	60.6 a[Z]	43.2 a	37.1 b	22.2 a
	10	71.2 a	39.2 a	46.1 ab	23.8 a
STS	0	65.4 a	40.4 a	45.6 ab	21.9 a
	10	40.0 a	42.0 a	55.6 a	22.2 a
None	0	55.6 a	44.4 a	57.7 a	25.9 a
	10	57.4 a	46.0 a	39.4 b	26.9 a
Significance					
Pretreatment (P)		NS	NS	NS	NS
Ethylene (E)		NS	NS	NS	NS
P*E		NS	NS	***	NS
Overall significance					
Cultivar (C)		***			
Pretreatment (P)		NS			
Ethylene (E)		NS			
C*P*E		**			
Organ (O)		***			
C*O		***			

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

Table 7. Starch, sucrose, and fructose affected by cultivar by organ sampled interaction. Means ($mg \cdot g^{-1}$ dry weight) are separated for each carbohydrate. Cut stems were pretreated with 0.5 $\mu L \cdot L^{-1}$ 1-methylcyclopropene (MCP), 0.2 mM silver thiosulfate (STS), or ambient air plus water for four hours, then stored at 3.3 °C for two weeks, then treated with either 0 or 10 $\mu L \cdot L^{-1}$ ethylene for 18 hours. Means are averaged over pretreatment and ethylene concentration.

Cultivar	Organ	Starch	Sucrose	Fructose
Princess Amalia	Leaves	1.16 c[Z]	15.5 abc	18.6 def
	Stems and carpels	0.87 c	10.6 bcd	25.6 de
	Tepals	4.23 bc	9.4 cd	131.0 a
Red Alert	Leaves	1.63 c	9.6 cd	14.8 ef
	Stems and carpels	0.91 c	11.5 bcd	21.0 def
	Tepals	3.02 bc	17.3 ab	91.8 b
Renoir	Leaves	1.89 c	15.5 abc	12.2 ef
	Stems and carpels	2.42 c	8.4 d	30.4 d
	Tepals	5.92 b	8.7 d	98.1 b
Stargazer	Leaves	1.11 c	17.8 a	10.7 ef
	Stems and carpels	0.96 c	1.5 e	9.5 f
	Tepals	10.35 a	16.1 ab	51.3 c
Significance				
Cultivar (C)		**	NS	***
Organ (O)		***	***	***
C*O		***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

Table 8. Glucose content ($mg \cdot g^{-1}$ dry weight) affected by cultivar by pretreatment by ethylene by organ interaction. Cut stems were pretreated with 0.5 $\mu L \cdot L^{-1}$ 1-methylcyclopropene (MCP), 0.2 mM silver thiosulfate (STS), or ambient air plus water (none) for four hours (pretmt.), then stored at 3.3 °C for two weeks, then treated with either 0 or 10 $\mu L \cdot L^{-1}$ ethylene (ethylene conc.) for 18 hours. Means are separated within each cultivar. Significance of main effects and significant simple effects is presented within cultivar and overall for the cultivar by pretreatment by ethylene concentration by organ factorial.

Pretmt.	Ethylene conc.	Organ	Princess Amalia	Red Alert	Renoir	Stargazer
MCP	0	Leaves	15.5 a[Z]	14.0 b	9.9 e	10.6 bcdef
		Stems and carpels	27.2 a	26.0 b	17.2 de	6.8 ef
		Tepals	133.2 a	71.7 a	54.6 abcd	32.1 abc
	10	Leaves	24.4 a	10.7 b	11.7 de	8.0 cdef
		Stems and carpels	34.4 a	14.6 b	25.7 de	4.7 f
		Tepals	124.5 a	70.9 a	83.6 ab	33.2 ab
STS	0	Leaves	11.0 a	18.3 b	14.0 de	3.7 f
		Stems and carpels	26.6 a	20.1 b	31.7 cde	3.4 f
		Tepals	127.5 a	58.5 a	69.4 abc	30.6 abcde
	10	Leaves	10.6 a	21.2 b	14.7 de	2.8 f
		Stems and carpels	14.5 a	20.1 b	39.5 cde	8.8 cdef
		Tepals	28.8 a	82.3 a	89.3 a	31.6 abcd
None	0	Leaves	25.1 a	18.3 b	13.9 de	8.8 cdef
		Stems and carpels	22.1 a	21.0 b	45.5 bcde	8.6 cdef
		Tepals	98.2 a	73.1 a	93.4 a	39.6 a
	10	Leaves	7.5 a	19.8 b	12.6 de	7.9 def
		Stems and carpels	25.7 a	24.1 b	29.6 cde	8.9 cdef
		Tepals	93.4 a	79.1 a	53.5 abcd	40.6 a

Table 8 Continued.

Significance				
Pretreatment (P)	NS	NS	NS	NS
Ethylene (E)	NS	NS	NS	NS
Organ (O)	***	***	***	***
P*E*O	[Y]	NS	*	NS
Overall significance				
Cultivar (C)	***			
Pretreatment (P)	NS			
Ethylene (E)	NS			
Organ (O)	***			
C*P*E*O	***			

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z]Means followed by the same letter are not significant according to Tukey's LSD.

[Y]Insufficient denominator degrees of freedom for 'Princess Amalia' did not allow simple effects to be analyzed.

Table 9. Variation in ethylene sensitivity seen among lily cultivars.

Variety	Group	Ethylene sensitive	Use	Reported by
'Apeldoorn'	Asiatic	Yes	Cut	Elgar et al., 1999
'Brussels'	Asiatic	Yes	Cut	Song and Peng, 2004
'Casablanca'	Oriental	Yes	Cut	Elgar et al., 1999
'Cassandra'	Oriental	No	Cut	Elgar et al., 1999
'Cordelia'	Asiatic	Yes	Cut	Elgar et al., 1999
'Elite'	Asiatic	No	Cut	Elgar et al., 1999
'Enchantment'	Mid-century	Yes	Potted	Simmonds and Cumming, 1977
'Gelria'	*L. longiflorum*	No	Cut	Elgar et al., 1999
'Goldena'	Asiatic	Yes	Cut	Elgar et al., 1999
'Grand Paradiso'	Asiatic	No	Cut	Elgar et al., 1999
'Harmony'	Mid-century	Yes	Potted	Simmonds and Cumming, 1977
'Lorena'	*L. longiflorum*	No	Cut	Elgar et al., 1999
'Mona'	Asiatic	Yes	Cut	Elgar et al., 1999
'Mona Lisa'	Oriental	Yes	Potted	Çelikel et al., 2002
'Nellie White'	*L. longiflorum*	Yes	Potted	Blankenship et al., 1993
'Nellie White'	*L. longiflorum*	Yes	Potted	Mason and Miller, 1991
'Nellie White'	*L. longiflorum*	Yes	Potted	Wees, 1993
'Nova Centro'	Asiatic	No	Cut	Elgar et al., 1999
'Polyanna'	Asiatic	Yes	Cut	Dole et al., 2005
'Princess Amalia'	L.A.	No	Cut	Locke et al., 2010
'Princess Gracia'	*L. longiflorum*	No	Cut	Elgar et al., 1999
'Red Alert'	L.A.	Yes	Cut	Locke et al., 2010
'Renoir'	Asiatic	Yes	Cut	Locke et al., 2010
'Romano'	Asiatic	No	Cut	Elgar et al., 1999
'Simplon'	Oriental	No	Cut	Badiyan et al., 2004
'Stargazer'	Oriental	Yes	Potted	Çelikel et al., 2002
'Stargazer'	Oriental	No	Cut	Elgar et al., 1999
'Stargazer'	Oriental	Yes	Cut	Han and Miller., 2003
'Stargazer'	Oriental	No	Cut	Locke et al., 2010

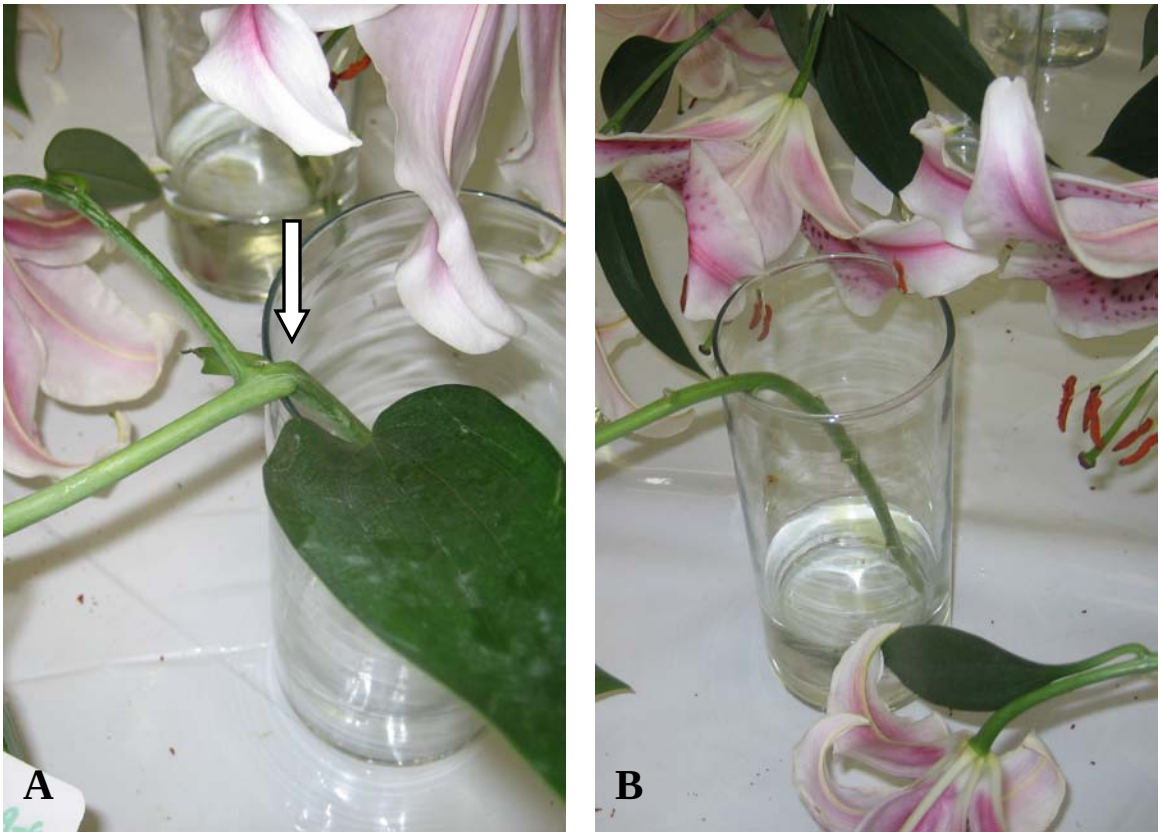

Figure 1. Lilies were terminated if stems bent, as shown in (A). Stems that leaned but were not bent were not terminated (B).

Vase life and quality of cut *Lilium* and *Helianthus* are affected by production light and temperature

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Additional index words. Lily, sunflower, cut flower, greenhouse environment, carbohydrate, starch, sucrose, glucose, fructose

Abstract. Vase life of *Lilium* 'Vermeer' and 'Dazzle' was decreased by high production temperature, but not by low light. Differences between vase life of 'Vermeer' in year 1 and 'Dazzle' in years 2 and 3 between high and low temperatures were 0.5, 3.0, and 1.2 days, respectively. However, both low light and high production temperature decreased the number of marketable stems (stems with three or more buds). Out of 20 stems per crate, low light reduced the number of marketable stems by 4.5 and 5.0 stems in years 2 and 3, respectively, while high temperature decreased marketable stems by 10.2 and 12.4 stems in years 2 and 3, respectively. High temperature in year one of the study shortened vase life of *Helianthus* 'Sunbright by 2.6 days. Vase life was affected by a light and temperature interaction in year 2, where vase life tended to be decreased at high temperatures and shade promoted vase life at lower temperatures but decreased vase life at higher temperatures. The longest vase life for *Helianthus* grown during year 2 was 15.5 days for stems grown at 10 °C night temperature in 30% shade, while the shortest vase life was 10.2 days for stems grown at 20 °C in 30% shade. Neither temperature nor light affected vase life of *Helianthus* in year 3.

Temperature and light affected carbohydrate content of tissues sampled during years 2 and 3 in both *Lilium* and *Helianthus*, but specific carbohydrates had a more striking correlation with vase life and quality in *Lilium* than in *Helianthus*. When buds from a *Lilium* stem were pooled for sampling, vase life did not correlate with tepal carbohydrate content, but correlated with specific carbohydrates from leaves, stems, and non-tepal inflorescence tissue. In year 2, *Helianthus* was correlated with a number of carbohydrates in leaf, stem, ray floret, and non-ray floret inflorescence tissues, but in year 3, vase life was only positively correlated with sucrose in ray florets.

A long postharvest vase life ensures that the customers – wholesalers, retailers and final consumers – will be satisfied and will return to purchase more flowers. Furthermore, consumers may be willing to pay a greater higher price for flowers perceived as long-lasting. Unfortunately, cut flower vase life is difficult to predict, varying by season (Van Gorsel, 1993), and by production source (Slootweg, 2005).

Four major factors that influence vase life are water relations, carbohydrate status, ethylene, and pathogens (Darras et al., 2004; Schroeder and Stimart, 2005; Slootweg, 2005). Carbohydrate status likely affects at least two of the other major factors contributing to vase life. Soluble sugars not only provide substrates for respiration but also act as osmotic adjusters and may suppress ethylene biosynthesis and lower ethylene sensitivity (Pun and Ichimura, 2003).

Many studies have demonstrated that adding exogenous soluble sugars to a vase solution, sucrose in particular, tends to increase cut flower vase life (Shimamura et al., 1997; Liao et al., 2000), although effects are species specific (Han, 2003). Halevy and Mayak (1979) and Slootweg (2005) have speculated that preharvest environmental factors that tend to alter endogenous carbohydrate status also alter vase life. Despite support for this hypothesis from early research, preharvest effects on vase life are not well understood, conflicting reports exist, and new tools have been developed to understand biochemical mechanisms. The effects of light, temperature, mineral nutrition, and water status have been studied previously (Halevy and Mayak, 1979). High light levels during production led to longer vase life in *Dianthus* and *Dendranthemum.* In addition, supplementing flowers grown under low light levels with exogenous sugars during bud opening reduced vase life the

difference in vase life of cut stems grown at low light versus high light, further supporting the hypothesis that light affects vase life through carbohydrates (Halevy and Mayak, 1979).

In contrast to high light, high temperatures during production tend to reduce vase life (Halevy and Mayak, 1979), likely by increasing respiration rates and preventing build-up of carbohydrate reserves. However, this temperature effect is not well defined. Some reports indicated that increasing temperatures impaired vase life only at temperatures above approximately 25°C (Halevy and Mayak, 1979). In addition, possible interactions between temperature and other factors complicate understanding temperature effects on vase life. For example, at low temperatures, carbohydrate reserves can increase, but pigments can also increase with at low temperatures (Halevy and Mayak, 1979; Chalker-Scott, 1999), causing depletion of carbohydrate reserves for pigment biosynthesis. Flavonoid biosynthesis is induced by glucose, fructose, and sucrose (Weiss, 2000) and requires acetyl-CoA as a precursor (Koes et al., 1994). Although the resulting depletion of carbohydrate reserves likely decreases vase life, anthocyanins are often induced by osmotic stress, and some have speculated that anthocyanins are osmoregulators (Chalker-Scott, 1999).

Interactions among environmental factors also occur in the production greenhouse or field. During the winter when light levels are low, the temperature is also low, retarding loss of carbohydrates. On the other hand, in the summer, the loss of carbohydrates from increased respiration may be partially or completely offset by higher carbon fixation rates at higher light levels. During late summer and early fall, as light levels decrease but temperatures remain high, vase life of some species also appears to decline. This may be due to decreasing carbohydrates, as photosynthetic rates decline but respiration rates remain high.

In recent work with field-grown *Zinnia*, the vase life decreased from 15 days during the summer (July and August) to 7 days during the fall (September and early October) (Dole, unpublished data). This decrease in vase life occurred even with flowers held in floral preservatives containing sugars, demonstrating that although sucrose-containing solutions alleviated endogenous carbohydrate shortages in previous studies, factors may exist that complicate these findings (Halevy and Mayak, 1979). For example, optimum vase life of *Zinnia* was obtained by using only water during the summer and by using floral holding preservatives during the fall (Dole, unpublished data).

As noted earlier, soluble sugars increase cut flower postharvest vase life by providing energy for respiration and by decreasing osmotic values for increased water uptake (Halevy and Mayak, 1979; van der Meulen-Muisers et al., 2001; Pun and Ichimura, 2003). In Asiatic *Lilium*, a carbohydrate surplus was associated with increased longevity (van der Meulen-Muisers et al., 2001). Environmental factors such as high CO_2 and high light levels lead to increased carbohydrate reserves. In turn, these climate factors correlate with longer vase life in *Freesia* (Slootweg, 2005). Furthermore, the environment during the last two weeks prior to harvest were the most important to vase life in *Freesia* (Slootweg, 2005).

Further support of the hypothesis that soluble sugars increase vase life comes from reports that glucose, fructose, sucrose, and methyl glucoside were higher in petals of the long-lived *Rosa* cultivar 'Delilah' than in the short-lived cultivar 'Sonia'. In contrast, *myo*-inositol and xylose concentrations were the same (Ichimura et al., 2005), while starch concentrations were higher in the petals of the short-lived cultivar and in the leaves in the long-lived cultivar (Ichimura et al., 2005). Interestingly, the long-lived cultivar 'Delilah' was

more sensitive to ethylene (Ichimura et al., 2005). Furthermore, reduced quality in *Delphinium* occurs when sepal sucrose reserves become a source for the pistil, leading to reduced sepal turgor (Kikuchi et al., 2003).

Many have researched studied the effects of vase solution components on endogenous carbohydrates in cut flowers. For instance, the addition of sucrose to vase solutions lengthened vase life of 'Sonia' *Rosa* more than adding the germistat 8-hydroxyquinoline sulphate (HQS), suggesting that for this cultivar, an available carbohydrate pool is more important to vase life than xylem hydraulic conductance (Ichimura et al., 2003). In those studies, the addition of sucrose treatments led to higher levels of internal glucose, fructose, sucrose, and methyl glucoside than was present in cuts treated with distilled water or HQS. This suggests that sucrose catabolism improves water status as the monosaccharides glucose and fructose lower osmotic potential more than the disaccharide sucrose. In contrast, sucrose in the vase solution of 'Stargazer' *Lilium* did not lead to increased vase life, but did increase opening of secondary buds and increased anthocyanin content (Han, 2003).

We hypothesized that changes in internal carbohydrates resulting from varying production light and temperature levels might have an effect on postharvest vase life of cut *Helianthus* and Asiatic *Lilium*. Furthermore, we hypothesized that the conditions during the last two weeks of production are most important in determining postharvest vase life. The objectives of this study were to 1) determine the optimum preharvest temperature and light conditions for maximum vase life of cut *Helianthus* and *Lilium* and 2) determine if and how these conditions correlate with endogenous carbohydrate levels. The answers to these questions are valuable to greenhouse growers, who must make a choice between shading to

keep a greenhouse cool and not shading and allowing solar radiation to heat a greenhouse above desirable temperatures.

Materials and Methods

Year 1: Light and Temperature

Helianthus 'Sunbright' (sunflower) from seed and *Lilium* 'Vermeer' (lily) from bulbs were grown in bulb crates measuring 56.5 x 36.5 x 16 cm (for sunflower) and 56.5 x 36.5 x 20 cm (for lily) at 24 and 20 plants per crate, respectively. Sunflowers were sown into crates on 20 Nov. 2006 and germinated under ambient greenhouse conditions with 15/23 °C night/day temperature set points. Lilies were planted on 2 Nov. and placed in 5.6 °C cold storage for rooting. The storage temperature was raised to 12.8 °C on 22 Nov. to speed rooting and shoot growth, then lowered to 5.6 °C on 24 Nov. before lilies were moved to the greenhouse on 27 Nov. Five one-crate replications were used for each treatment described below. Stem length (both species) and the number of marketable stems per crate (for lilies only, defined as stems with three or more viable buds) were recorded.

Light

Greenhouse-grown plants were irrigated as needed, grown at ambient humidity, with night temperature set at 15°C/23 °C day temperature (average daily temperature was 19.1 °C) and placed in the following treatments on 6 Dec. 2006: (1-3) 0, 30, and 60% shade for the duration of the harvest cycle, (4) 0% shade followed by 60% shade for the final two weeks of the harvest cycle, (5) 60% shade followed by 0% shade for the final two weeks of the harvest

cycle, (6) 0% shade followed by 60 % shade for the final two days of the harvest cycle, (7) 60% shade followed by 0% shade for the final two days of the harvest cycle, and (8) 0% shade supplemented with 8 hours per day of 100 µmol·m^{-2}s^{-1} by HID lamps concurrent with day light. Daily light integrals for 0, 30, and 60% shade averaged 14.0, 9.1, and 5.4 mol·m·$^{-2}$·day^{-1}, respectively.

Temperature

Plants were grown under ambient light and grown under the following seven night temperature treatments starting 5 Dec. 2006: (1-3) 10, 15, or 20°C, (4) 10°C followed by 20°C for the last two weeks prior to harvest, (5) 20°C followed by 10°C for the last two weeks prior to harvest, (6) 10°C followed by 20°C for the last two days prior to harvest, and (7) 20°C followed by 10°C for the last two days prior to harvest. The set points (°C night/day) and ADT °C during production for 10, 15 and 20 °C treatments were 10/21 and 15.2 °C, 15/23 and 19.1, and 20/27 and 22.3, respectively.

Year 2: Light and Temperature Interactions

Helianthus 'Sunbright' seeds and *Lilium* 'Dazzle' bulbs were planted at 24 and 20 plants per crate respectively. Sunflowers were sown on 30 Nov. 2007 and germinated under ambient greenhouse conditions at 15 °C night temperature with night interruption lighting from 10:00 PM to 2:00 AM starting 5 Dec. and ending 17 Dec. Lilies were planted on 2 Nov. 2007 and placed in 1.5 °C storage for rooting. On 19 Nov., the storage temperature was

increased to 7.8 °C to speed rooting and shoot growth. Lilies were moved to the greenhouse on 5 Dec. Treatments were imposed beginning 21 Dec.

Treatments were (1-3) 10, 15, or 20 °C night temperature with no shade, (4-6) 10, 15, or 20 °C night temperature with 30% shade, (7-8) plants started at 15 °C in no shade and 30% shade were moved to 30% shade and no shade, respectively, two weeks prior to harvest, (9-10) plants started in 30% shade at 10 or 20 °C were moved to no shade at 20 or 10° C, respectively, two weeks prior to harvest, and (11-14) plants started in no shade at 10 or 20° C were moved two weeks prior to harvest to 20 or 10° C, respectively, in no shade or 30% shade. The set points (°C night/day) and ADT °C during production for 10, 15 and 20 °C treatments were 10/22 and 15.7; 15/24 and 19.7; and 20/30 and 24.5, respectively. The daily light integrals for 0 and 30% shade averaged 8.8 and 5.8 $mol \cdot m^{-2} \cdot day^{-1}$, respectively.

Year 3: Light and Temperature Interactions

Helianthus 'Sunbright' and *Lilium* 'Dazzle' were planted at 24 and 20 plants per crate respectively. Sunflowers were sown on 1 Dec. 2008 and germinated at 15° C night temperature in ambient greenhouse conditions with a night temperature of 10° C. Lilies were planted on 20 Oct. 2008 and placed in 6° C storage. The storage temperature was lowered to 2° C on 28 Oct. and raised to 6° C on 20 Nov., then lowered again on 27 Nov. Lilies were placed in the greenhouse on 8 Dec. Temperature treatments began 31 Dec. 2008. Light treatments began 1 Jan. 2009.

Treatments were (1-3) 10, 15, or 20 °C night temperature with no shade, (4-5) 10 or 20 °C night temperature with 30% shade, (6-7) plants started in 30% shade at 10 or 20 °C

were moved to no shade at 20 or 10° C, respectively, two weeks prior to harvest, (8-11) plants started in no shade at 10 or 20° C were moved to 20 or 10° C, respectively, in no shade or 30% shade two weeks prior to harvest. Due to insufficient replications, one lily treatment had four replicates, three sunflower treatments had four replicates, and one sunflower treatment had three replicates; all remaining treatments had five replicates. The set points (°C night/day) and ADT °C during production for 10, 15 and 20 °C treatments were 10/24 and 14.8, 15/25 and 18.6, and 20/28 and 22.2, respectively. The daily light integral in 0% shade was 7.6 $mol \cdot m^{-2} \cdot day^{-1}$.

Harvest criteria and postharvest handling

Sunflowers were harvested when ray florets ranged were perpendicular to fully expanded with the disk and when 0-3 rows of disk florets were open. Lilies were harvested at the first fully colored puffy bud stage, with the exception of the year 1 temperature study, which were harvested when the first flower on each stem opened. Marketable stems (those with at least three viable buds) were used first, but stems with one or two buds were used if a crate had insufficient marketable stems.

After harvest, stems were transported to a postharvest evaluation room, recut to 30 cm (year 1) or 35 cm (year 2) for sunflowers or to 45 cm for lilies, and placed in 22 °C deionized (DI) water at 22 °C under 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light for 12 hours per day at 40 to 60% relative humidity. For year 1, sunflowers were placed in 50 ml water in culture tubes and water was refilled as necessary. For year 2 and year 3, stems were placed in 1L jars with

either 300 ml water (year 2) or 400 ml water (year 3). Lilies were placed in 1L jars with 400 ml water (year 1) or 500 ml water (years 2 and 3).

For sunflowers, vase life was defined as the number of days from harvest until half of the ray florets had wilted or abscised. For lilies harvested in year 1, vase life was the number of days from harvest until half of the flowers on a stem had wilted or abscised. For lilies harvested in years 2 and 3, vase life was the number of days from harvest until half of the last viable flower had wilted or abscised.

Postharvest data included stem length before recutting, stage of opening (sunflowers), flower or bud number per stem (lilies), stem caliper measured at cut end after recutting, disk diameter (sunflowers) or bud length (lilies), vase life, water uptake measured on the day of termination for year 1 and on day 7 of vase life for years 2 and 3, initial fresh weight after recutting, and dry weight. For lilies grown in years 2 and 3, we counted the number of flowers on each stem that opened during vase life to determine the number of buds that blasted during vase life, which we termed postharvest bud blast to distinguish this characteristic from bud blast during production. Postharvest bud blast was calculated as the number of buds at harvest minus the number of flowers that opened during vase life. Also for years two and three, unmarketable stems, which we defined as stems with fewer than three viable buds, in each crate of lilies were tallied as sampling was completed.

Carbohydrate analysis

For years 2 and 3, one stem from each replication on day 0 was used for carbohydrate analysis. Stems were sectioned as follows for sample preparation and analysis: tepals

(*Lilium*) or ray florets (*Helianthus*), remaining part of the inflorescence, leaves, and stem. Each section was weighed, flash frozen in liquid nitrogen, and freeze dried. Dried tissue was pulverized and approximately 20 mg was extracted in 3 ml ethanol (ETOH) plus 1 ml 8 mM lactose as an internal standard. Samples were vortexed to suspend dried tissue, placed in sonicating water bath for 5 min. and heated in 80 °C water bath for 5 min. before being centrifuged at 3000xg for 5 min at 4 °C. The supernatant was removed to a new tube. The pellet was resupended in 3 ml ETOH, vortexed, sonicated, heated in 80 °C water bath, centrifuged, and the supernatant removed twice more. Total supernatant for each sample was 10 ml (9 ml ETOH + 1 ml lactose solution). Aliquots (200 µL) of the supernatant were taken and dried in a rotary evaporator then stored at -20 °C prior to reconstitution and analysis. Samples were reconstituted in 1 mL H_2O and centrifuged to remove remaining particulate matter. The extracts were analyzed using a Dionex BioLC (Dionex Corporation, Sunnyvale, CA) at a controlled temperature of 25 °C. The system consisted of a gradient pump, an autosampler, and a Pulsed Amperometric Detector (PAD). The mobile phase was 200 mM NaOH at an isocratic flow rate of 1.0 mL/min. The column used was a Dionex PA-1, 250 mm length and 4 mm i.d., fitted with a Dionex PA-1 Guard column. The detector was programmed to run a quadruple waveform as recommended by the manufacturer. The detector range was 1 µC. The injection volume was 10 :L. Each sugar was quantified by calculating a ratio of the peak height of the unknown to the peak height of lactose. Carbohydrate identity was determined by comigration with known carbohydrate standards. All the reference standards were purchased from Sigma Chemical Corp. (St. Louis, MO).

Residual starch in pellet left from soluble sugar extractions was quantified as described by Ranwala and Miller (2008 and 2009). The pellet remaining from soluble carbohydrate extraction was boiled for 30 min. in 4 ml 100 mM Na-acetate buffer adjusted to pH 4.5 with 1 N acetic acid and subsequently cooled to room temperature. One ml amyloglucosidase solution (50 units·ml^{-1} in Na-acetate buffer, pH 4.5) was added to digest each sample which was then incubated at 50-55 °C for 2 days. After digestion, samples were centrifuged at 3000xg. 500 µl (100 or 50 µl for high starch samples) of the cleared solution was removed to a new tube and 5 ml of cold phosphate buffer containing 5 units·ml^{-1} glucose oxidase, 1 unit·ml^{-1} horseradish peroxiase, and 40 µg·ml^{-1} *o*-dianisidine were added. Samples were incubated at 30 °C for 30 min before absorbance was read in a spectrophotometer (Lambda Bio20, Perkin Elmer, Waltham, MA) at 450 nm. Absorbance was converted to glucose concentration calculated against a glucose standard curve. Amyloglucosidase blanks and potato starch digests were used as controls. All enzymes used for starch digestion were obtained from Sigma (St. Louis, MO).

Statistical analysis

From each crate, we used five subsamples for vase life determination, one sample for carbohydrate analysis, and two subsamples for dry weight. We used PROC MIXED in SAS (SAS Institute, Cary, NC) because of the unequal replication in year 3 and also because of high rates of lily bud abortion in certain treatments. PROC CORR was used to determine relationships between dependent variables.

For light and temperature interaction studies in years 2 and 3, plants in treatments 1 through 6 and 1 through 5, respectively, which were not moved between environments, were analyzed first to determine if there was an interaction between light and temperature for each dependent variable. If there was an interaction, means were separated for each treatment in the full experiment. If there was not an interaction, the additional treatments were analyzed for main effects only by combining them into the treatments "Started at 10" and "Started at 20" for temperature main effects, and into the treatments "Started in 0% shade" and "Started in 30% shade" or merged into the existing "0% shade" treatment for light main effects.

Results

Lilium

For all three years, vase life of lilies was affected by production temperature but not by light. Vase life was greatest longest for stems grown entirely at 10 or 15 °C compared to those grown at 20 °C (Tables 1, 2, and 3). In year 1, *Lilium* 'Vermeer' stems with a two-week finishing period at 10 °C following production at 20 °C had the same vase life as stems grown entirely at 10 or 15 °C, but this was not true for 'Dazzle' in years 2 and 3 (Tables 1, 2, and 3). In year 2, stems started at either 10 or 20 °C and then transferred to 20 and 10, respectively, had longer vase life than those grown entirely at 20 °C (Table 2). In year 3, stems started at 10 and 20 °C had similar vase life compared to stems grown entirely at 20 °C (Table 3). Vase life averaged over light treatments was 10.1, 12.5, and 12.7 days, respectively, for years 1, 2 and 3.

In years 2 and 3, unmarketable stems were affected by both temperature and light main effects (Tables 2 and 3). For temperature, either growing entirely or starting lilies at 10 °C yielded the lowest number of unmarketable stems (Tables 2 and 3). For years 2 and 3, crates grown entirely at 15 °C had fewer unmarketable stems than crates grown entirely at 20 °C and in year 3, crates grown entirely at 15 °C had the same number of unmarketable stems as crates grown entirely at or started at 10 °C (Tables2 and 3). In year 2, growing entirely in 0% shade yielded the lowest number of unmarketable stems, while in year 3, either growing entirely or starting in 0% shade yielded the lowest number of unmarketable stems (Tables 2 and 3).

Water uptake was affected by temperature only in year 1 and by a temperature by light interaction in years 2 and 3 (Tables 1, 4, and 5). In year 1, water uptake averaged 167.4 ml over all light treatments. Water uptake was greatest in stems grown entirely at 10 °C, started at 10 °C but finished at 20 °C for two days, and in stems started at 20 °C but finished at 10 °C for two weeks (Table 1). In year 2, uptake was greater in stems started at 20 °C and finished at 10 °C in 0% shade than in stems grown entirely at 15 °C and 0% shade or than those started at 15 °C in 30% shade (Table 4). Uptake was also high in several treatments either started at 20 °C or finished in 30% shade (Table 4). For year 3, stems grown entirely or started at 20 and 15°C had greater water uptake than stems grown entirely or started at 10 °C, with the exception of stems grown entirely at 10 °C in 0% shade, which were not different from stems grown entirely at 15 °C in 0% shade and stems started at 20 °C in 0% shade then moved to 10 °C in 30% shade (Table 5).

Appearance ratings recorded on day 7 of vase life were affected by temperature but not light in year 2. Appearance over all light treatments in year 2 averaged 4.8 on a scale of 0-10. Appearance was better for stems grown entirely at 20 °C (4.4) compared to stems grown entirely at 15 °C (5.4) (Table 2). In year 3, appearance was worse for stems grown entirely at 20 °C in 0% shade than in all stems either grown entirely at or started at 10 °C or 15° C with the exceptions of those moved to 20 °C in 0% shade (Table 5). Treatments started at 10 °C and moved to 20 °C in 0% shade had a poor appearance (3.0) compared to stems grown entirely at 10 °C in 0% shade (1.1) (Table 5).

For year 1, stem length was affected by temperature but not by light (Table 1). Over all light treatments, stem length averaged 99.8 cm. In years 2 and 3, stem length was affected by both temperature and light main effects. For both years 1 and 2, stems grown entirely at or started at 10 °C were longer than stems grown entirely or started at 15 °C or 20 °C (Tables 1 and 2). Stems grown entirely at 15 °C were longer than stems grown entirely at 20 °C but not longer than stems started at 20 °C and moved to 10 °C (Tables 1 and 2). For year 2, stems grown entirely under 30% shade were longer than stems grown entirely under 0% shade (Table 2). In year 3, stems grown entirely or started at 10 °C were longer than stems grown entirely at 15 °C (Table 3). Stems grown entirely at 15 °C were longer than stems grown entirely or started at 20 °C (Table 3). Stems grown entirely in 0% shade were longer than stems started in 30% shade (Table 3).

Stem caliper was affected by neither light nor temperature in year 1 (data not presented), averaging 0.76 cm over treatments for both light and temperature. However, caliper was affected by light and temperature main effects in years 2 and 3. For year 2,

caliper was larger in stems started at 10 °C than in stems grown entirely or started at 15 or 20 °C and was larger in stems grown entirely at 10 °C than in stems grown entirely at 15 °C or started at 20 °C (Table 2). Caliper was larger in stems grown entirely or started at 0% shade than in stems grown entirely or started in 30% shade (Table 2). For year 3, caliper was also larger for stems started at 10 °C than those started at 20 °C, and larger in stems grown entirely or started in 0% shade than in those started in 30% shade (Table 3).

For all years, flower length was affected by temperature but not by light (data not presented), which averaged 7.2, 9.7, and 9.5 cm long in years 1, 2, and 3, respectively. In year 1, flowers were longer for stems grown entirely at 20 °C than for stems grown entirely at 15 °C or stems started at 20 °C and moved to 10 °C for two weeks (Table 1). In year 2, flowers grown entirely at 15 or 20 °C were longer than flowers grown entirely at 10 °C, or those started at 10 or 20 °C (Table 2). In year 3, flowers were longer on stems grown entirely at 20 °C than on stems grown entirely at 10 or 15 °C or started at 10 or 20 °C (Table 3).

In year 1 bud count per stem was affected by light but not by temperature (data not presented), which averaged 3.6 buds per stem over all treatments. Bud count was higher for stems grown entirely in 0% shade than in 30% shade (Table 6). Bud counts for stems grown entirely and started under 60% shade were lower than for those grown entirely in 30% shade but were not significantly different from stems grown entirely in 0% shade (Table 6).

Bud count per stem was affected by both temperature and light main effects in year 2. Stems grown entirely at 10 °C had more buds than those grown entirely at 15 or 20 °C or than those started at 20 °C (Table 2). Stems started at 10 °C had more buds than those grown

entirely or started at 20 °C (Table 2). Stems grown entirely at 15 °C had more buds than those grown entirely at 20 °C (Table 2). Stems grown entirely in 0% shade had more buds than those grown under 30% shade or started in 0% shade (Table 2).

In year 3, stems grown entirely at 10 °C in 0% shade had more buds per stem than did stems grown entirely or started at 20 °C under either light regime (Table 5). Stems started at 10 °C and 0% shade and stems grown entirely at 15 °C had more buds per stem than did stems grown or started at 20 °C except those grown entirely at 20 °C under 30% shade (Table 5). All remaining treatments grown or started at 10 °C had more buds per stem than stems grown entirely at 20 °C under 0% shade, or stems started at 20 °C under 0% and 30% shade and moved to 10 °C under 0% shade (Table 5).

In year 2, bud count change was affected by both light and temperature where stems started at 10 °C had increased bud blasting compared to stems started at 20 °C and stems started at 0% shade had increased bud blasting compared to stems started at 30% shade (Table 2). In year 3, stems started at 10 °C had increased bud blasting compared to stems grown entirely at 10, 15, or 20 °C or stems started at 20 °C. Stems grown entirely in 0 or 30% shade had increased bud blasting over stems started in 30% shade (Table 3).

Fresh weight was affected by light but not temperature in year 1. Fresh weight at harvest and termination fresh weight were 53.0 and 48.0, respectively, for temperature treatments in year 1. Fresh weight was higher for stems grown entirely in 0% shade than for stems grown entirely in 30 or 60% shade (Table 6). Fresh weight at termination was affected similarly, with fresh weight being higher for stems grown entirely in 0% shade than for stems grown entirely in 30 or 60% shade. Termination fresh weight was also higher for stems

started in 0% shade and moved to 60% shade two days or two weeks before harvest (Table 6). Fresh weight was affected by both temperature and light in year 2. Fresh weight was higher in stems grown entirely at 10 °C than in stems grown entirely at 15 °C or those grown entirely or started at 20 °C (Table 2). Fresh weight was higher in stems started at 10 °C than in those grown entirely or started at 20 °C (Table 2). Fresh weight was higher in stems grown entirely in 0% shade than in those grown entirely or started in 30% shade (Table 2). In year 3, an interaction between light and temperature occurred where stems grown entirely or started at 10 °C in 0% shade had higher fresh weight than those grown entirely or started at 10 °C and 30% shade as well as treatments grown entirely or started at 20 °C for all light conditions (Table 5). Stems grown entirely at 15 °C in 0% shade had higher fresh weight than treatments grown entirely or started at 20 °C in 0% shade or than stems started at 20 °C in 30% shade and moved to 10 °C in 0% shade (Table 5).

Dry weight was affected by both temperature and light in all three years. In year 1, dry weight was higher in stems grown entirely at 10 °C than in stems grown entirely at 15 or 20 °C, than in those started at 10 ° C and moved to 20 °C approximately two weeks prior to harvest, as well as those started at 20 °C and moved to 10 °C two days before harvest (Table 1). Dry weight was higher for stems grown entirely in 0% shade than for those started in 0% shade and moved to 60% shade two days or two weeks prior to harvest (Table 6). Stems grown entirely in 0% shade also had higher dry weight than those grown entirely in 30 or 60% shade and those grown under HID supplemental lighting (Table 6). Stems started in 0% shade and moved to 60% shade two days or two weeks before harvest and those grown with

supplemental HID lighting had higher dry weight than those grown entirely in 60% shade (Table 6).

For year 2, stems grown entirely at 10 °C had higher dry weight than those grown entirely at 15 or 20 °C and those started at 10 or 20 °C (Table 2). Stems started in 0% shade had higher dry weight than those grown entirely under 30% shade or those started in 0% shade and moved to 30% shade (Table 2). For year 3, stems grown entirely at 10 °C had higher dry weight than those grown entirely or started at 20 °C and stems grown entirely at 15 °C and those started at 10 °C had higher dry weight than those started at 20 °C (Table 3). Stems started in 0% shade had higher fresh weight than those grown entirely in 30% shade (Table 3).

Percent dry weight, a measure of photosynthetic efficiency, was not affected by temperature or by light in year 1 and by both temperature and light in years 2 and 3. In year 1, percent dry weight averaged 10.9 over temperature treatments and 11.6 over light treatments. In year 2, stems grown entirely at 10 °C had higher percent dry weight than those grown entirely at 15 or 20 °C and than those started at 10 °C (Table 2). Stems started at 20 °C had higher percent dry weight than those grown entirely at 15 °C or those started at 10 °C (Table 2). Stems grown entirely in 0% shade had higher percent dry weight than those grown entirely in 30% shade and than those started in 0% shade (Table 2). Stems started in 30% shade had higher percent dry weight than those started in 0% shade (Table 2). In year 3, stems grown entirely at 10 °C had a higher percent dry weight than those grown entirely or started at 20 °C and those started at 10 °C (Table 3). Stems grown entirely at 15 °C had a higher percent dry weight than those grown entirely or started at 20 °C (Table 3). Stems

grown entirely in 0% shade had a higher percent dry weight than those grown entirely in 30% shade (Table 3).

Water uptake was corrected for fresh weight of plant material and, for year 1, the number of days of vase life. Water uptake was measured on day 7 of vase life for all stems in years 2 and 3. Corrected water uptake varied by temperature and light in years 1 and 2 and by temperature in year 3. In year 1, stems started at 10 °C and moved to 20 °C two weeks before harvest had increased water uptake compared to those grown entirely at 15 or 20 °C as well as those started at 20 °C and moved to 10 °C two days prior to harvest (Table 1). Stems started at 10 °C and moved to 20 °C two days before harvest and those started at 20 °C and moved to 10 °C two weeks before harvest had increased water uptake compared to those grown entirely at 15 °C and those started at 20 °C and moved to 10 °C two days before harvest (Table 1). Stems started in 30% shade had higher water uptake over those grown entirely in 0% shade as well as those started in 0% shade and moved to 60% shade two days before harvest (Table 6).

For years 2 and 3, water uptake was greater in stems grown entirely or started at 20 °C than in those grown entirely or started at 10 °C and those grown entirely at 15 °C (Tables 2 and 3). For year 2, stems grown entirely in 30% shade had higher uptake than those grown entirely in 0% shade and those started at 30% shade (Table 2).

Lilium carbohydrate content

In year 2, light and temperature did not affect glucose, fructose, or starch content of the inflorescence minus tepals, averaging 47.8, 39.0, and 14.5 mg per gram dry weight

($mg \cdot g^{-1}dw$) over all treatments, respectively. Temperature and light both affected levels of sucrose and the carbohydrate tentatively identified as glycerol glucoside 1. Glycerol glucoside 1 and sucrose were both higher in stems grown entirely at 10 than at 15 °C, and for glycerol glucoside 1, also higher in stems grown entirely at 10 than at 20 °C (Table 7). Glycerol glucoside 1 and sucrose were higher in stems started under 30% shade than those grown entirely under 0% shade, and sucrose content was also higher in stems started under 30% shade than for stems grown entirely under 30% shade (Table 7). Inflorescence inositol and a second carbohydrate tentatively identified as glycerol glucoside 2 contents were affected by a light by temperature interaction. Inositol content was higher in stems grown entirely at 10 °C under 0% shade than in stems grown entirely at 10 °C under 30% shade (Table 8). Glycerol glucoside 2 content was higher in stems either grown entirely or finished at 10 °C under 0% shade than in stems grown entirely at 20 °C under 0% shade (Table 8).

Pearson correlations between postharvest characteristics and inflorescence carbohydrates for year 2 did not reveal a relationship between vase life and any carbohydrate; however, several other characteristics were correlated to inflorescence carbohydrates levels. Flower length, which was greatest at high temperatures for all three years, was negatively correlated with glycerol glucoside 2 content (r=-0.5652, p=0.03). Water uptake was positively correlated with glucose (r=0.6177, p=0.02). Percent dry weight was positively correlated with glycerol glucoside 1 (r=0.5335, p=0.0494) and glycerol glucoside 2 (r=0.7069, p=0.0047). In the inflorescence, several carbohydrates were positively associated with each other. Inositol was associated with glycerol glucoside 1 (r=0.5420, p=0.0453), glycerol glucoside 2 (r=0.6881, p=0.0065), and sucrose (r=0.6161, p=0.019). Glycerol

glucoside 1 was also associated with glycerol glucoside 2 (r=0.8145, p=0.0004), glucose (r=0.5720, p=0.0326), and sucrose (r=0.6034, p=0.0223). Glucose was also correlated with fructose (r=0.5623, p=0.0364). Starch was associated with fructose (r=0.6082, p=0.021) and stachyose (r=0.5711, p=0.0329).

Year 2 leaf inositol and starch were affected by temperature. Inositol was higher in leaves of stems grown entirely at 10 °C than in those grown entirely at 15 or 20 °C or started at 10 °C (Table 7). Starch was higher in stems grown entirely at 15 °C or started at 20 °C than in those started at 10 °C (Table 7). Inositol and starch contents were not affected by light. In addition, while glycerol glucoside 1, glycerol glucoside 2, glucose, and fructose contents were affected by neither temperature nor light, with mean contents of 5.1, 2.7, 4.4, 0.73, 37.4, and 32.0 $mg \cdot g^{-1}$ dw over all treatments, respectively. Sucrose in leaves was affected by treatment with sucrose being higher in stems grown entirely at 10 °C under 0% shade than in stems grown entirely at 15 °C under 0% shade as well as being higher than in stems grown entirely at 20 °C under 30% shade (Table 8).

For year 2 leaves, vase life was correlated with inositol (r=0.5507, p=0.0413) and glycerol glucoside 2 (r=0.5811, p=0.0293). The number of unmarketable stems per crate was negatively associated with glycerol glucoside 2 (r=-0.5756, p=0.0313). Flower length was again negatively associated with both glycerol glucoside 1 (r=-0.7131, p=0.0042) and glycerol glucoside 2 (r=-.7654, p=0.0014). Bud count per stem was positively associated with glycerol glucoside 2 (r=0.5397, p=0.0464). Bud blasting was negatively associated with glucose (r=-0.6914, p=0.0062) and fructose (r=-0.6805, p=0.0074). Fresh weight was negatively associated with fructose (r=-0.5797, p=0.0298). Percent dry weight was

positively associated with inositol (r=0.5436, p=0.0445) and glycerol glucoside 2 (r=5809, p=0.0294). Inositol was associated with sucrose (r=0.5863, p=0.0275), glycerol glucoside 1 with glycerol glucoside 2 (r=0.8533, p=0.0001), and glucose with fructose (r=0.8343, p=0.0002).

During year 2, glycerol glucoside 1 was higher in stems started at 10 °C than in stems grown entirely or started at 20 °C and was higher in stems grown entirely at 10 than at 20 °C (Table 7). Glycerol glucoside 2 was higher in stems grown entirely at 10 or 15 °C or started at 10 °C than in stems grown entirely at 20 °C (Table 7). Neither inositol nor starch was affected by light or temperature (averaging 1.5 and 1.7 $mg \cdot g^{-1}$ dw, respectively). Glycerol glucoside 1 and glycerol glucoside 2 were not affected by light, averaging 23.2 and 6.6 $mg \cdot g^{-1}$ dw over all treatments, respectively. Sucrose averaged 7.1 $mg \cdot g^{-1}$ dw over all treatments. Glucose was highest in stems grown entirely at 10 °C in 0% shade and lowest in stems started at 10 °C and moved to 20 °C in 0% shade for both temperatures and in those grown entirely at 15 °C and moved form 0 to 30% shade (Table 8). Treatments started at 20 °C and moved to 10 °C in 0% shade also had higher glucose than several other treatments either grown entirely at or moved to 20 °C or started and grown entirely at 15 °C (Table 8). Fructose was highest in stems grown entirely at 10 °C in 0% shade (Table 8). These stems had a higher fructose content than all other treatments grown entirely or started at 10 °C or grown entirely at 15 or 20 °C. Stems started at 20 °C in 30% shade and moved to 10 °C in 0% shade also had higher fructose than stems started at 10 °C in 0% shade and moved to 20 °C in 0 or 30% shade, those grown entirely at 20 °C under either 0 or 30% shade, and those

grown entirely at 15 °C with the exception of those started under 30% shade and moved to 0% shade (Table 8).

For *Lilium* grown during year 2, vase life was positively correlated with both glycerol glucoside 1 (r=0.8352, p=0.0002) and glycerol glucoside 2 (r=0.8594, p<0.0001) in the stems. Stem glycerol glucoside 1 and glycerol glucoside 2 were negatively associated with the number of unmarketable stems (r=-0.7825, p=0.0009) and (r=-0.6354, p=0.0146), positively associated with bud count (r=0.8349, p=0.0002) and (r=0.7324, p=0.8349), positively associated with bud blasting (r=0.6239, p=0.0171) and (r=0.5552, p=0.0393), positively associated with fresh weight (r=0.7765, p=0.0011) and (r=0.6906, p=0.0062). Stem glycerol glucoside 1 was also correlated with dry weight (r=0.5424, p=0.0451). Percent dry weight was correlated with glucose (r=0.7608, p=0.0016) and fructose (r=0.6584, and p=0.0105). For carbohydrates, glycerol glucoside 2 was positively associated with glycerol glucoside 1 (r=0.9096, p<0.0001) and negatively associated with stachyose (r=-0.5605, p=0.0371). Glucose was positively correlated with fructose (r=0.9362, p<0.0001) and sucrose (r=0.5939, p=0.0251). Fructose and sucrose were also positively correlated (r=0.6958, p=0.0057).

In tepals of year 2 stems, glycerol glucoside 2, glycerol glucoside 1, and glucose were all affected by temperature. Glycerol glucoside 1 was also affected by light. Glycerol glucoside 2 was higher in stems started at 20 °C than in those grown entirely at 15 or 20 °C and than those started at 10 °C; glycerol glucoside 2 was higher in stems grown entirely at 10 than at 20 °C (Table 7). Glycerol glucoside 1 was higher in stems started at 20 °C than in those grown entirely at 20 °C or started at 10 °C. Glycerol glucoside 1 was higher in stems

grown entirely at 10 than at 20 °C (Table 7). Glycerol glucoside 1 was higher in stems started in 30% shade than in those grown entirely or started in 0% shade (Table 7). Tepal glycerol glucoside 2, glucose, and sucrose contents averaged over all treatments were 14.8, 98.4 and 7.9 $mg \cdot g^{-1}$ dw, respectively. Inositol, fructose, and starch were affected by treatment, but only means for inositol could be separated. Tepal inositol was higher in stems started at 10 °C in 0% shade and moved to 20 °C in 30% shade and in stems started at 10 °C in 30% shade and moved to 20 °C in 0% shade than in stems grown entirely at 10 °C in 30% shade (Table 8).

In year 2 tepals, vase life did not correlate with any carbohydrate. Starch was negatively associated with flower length (r=-.8308, p=0.0002). Bud count change was negatively correlated to glucose (r=-0.6496, p=0.0119) and fructose (r=-0.5645, p=0.0355). Percent dry weight was correlated with glycerol glucoside 2 (r=0.6492, p=0.012) and starch (r=0.5802, p=0.0296). Glycerol glucoside 2 was correlated positively with glycerol glucoside 1 (r=0.9343, p<0.0001), glucose (r=0.6716, p=0.0085), and fructose (r=0.6816, p=0.0073). Fructose was also associated with glycerol glucoside 1 (r=0.5839, p=0.0283) and glucose (r=0.7823, p=0.0009).

In year 3, inflorescence inositol, glycerol glucoside 2, and glycerol glucoside 1 were affected by temperature. Tepal carbohydrates were not affected by light or by the interaction of temperature and light. Inositol was higher in stems grown entirely at 20 than at 10 °C (Table 9). Glycerol glucoside 2 and glycerol glucoside 1 were higher in tepals of stems grown entirely at 15 °C and, for glycerol glucoside 1, those grown entirely at 10 °C than in those grown entirely or started at 20 °C (Table 9). For glycerol glucoside 2 and glycerol

glucoside 1, tepals of stems started at 10 °C had higher contents than those started at 20 °C (Table 9). Over all treatments, inositol, glycerol glucoside 1, glycerol glucoside 2, glucose, fructose, sucrose, stachyose, and starch contents were 3.7, 17.2, 63.9, 122.5, 76.9, 7.4, 0.21, and 22.5 $mg \cdot g^{-1}$ dw, respectively.

For year 3 inflorescences, vase life was positively correlated with glycerol glucoside 1 (r=0.07983, p=0.0032) and glycerol glucoside 2 (r=0.7756, p=0.005). Glycerol glucoside 1 and glycerol glucoside 2 had negative correlations with unmarketable stems (r=-0.9062, p=0.0001) and (r=-0.7223, p=0.0121), and positive correlations with bud count per stem (r=0.9267, p<0.0001) and (r=0.7824, p=0.0044), with fresh weight (r=0.8624, p=0.0006) and (r=0.6671, p=0.0249), and with dry weight (r=0.8739, p=0.0004) and (r=0.7153, p=0.0133). Water uptake was negatively correlated with glycerol glucoside 1 (r=-0.6201, p=0.0418) but positively correlated with starch (r=0.6587, p=0.0275). Inositol was negatively correlated with percent dry weight (r=-0.6301, p=0.0377). Glycerol glucoside 1 and glycerol glucoside 2 were positively correlated with each other (r=0.9280, p<0.0001) as were glucose and fructose (r=0.9795, p<0.0001).

In year 3 leaves, temperature affected inositol, glycerol glucoside 1, glycerol glucoside 2, glucose, and fructose, while only inositol was affected by light. Inositol was higher for stems grown entirely at 10 °C than for stems grown entirely at 20 °C or started at 10 or 20 °C (Table 9). Glycerol glucoside 1 and glycerol glucoside 2 were higher for stems started at 10 °C than for those started at 20 °C (Table 9). Glucose and fructose were higher for stems grown entirely at 20 than at 10 °C (Table 9). Stems grown entirely in 0% shade and those started in 30% shade had higher leaf inositol than those grown entirely in 30%

shade (Table 9). No interactions affected leaf carbohydrate contents in year 3. Neither light nor temperature affected sucrose, stachyose, or starch contents. Glycerol glucoside 1, glycerol glucoside 2, glucose, fructose, sucrose, stachyose, and starch contents were 0.24, 3.4, 33.9, 27.3, 34.5, 0.14, and 7.2 $mg \cdot g^{-1}$ dw, respectively.

For year 3 *Lilium*, vase life did not correlate with levels of any carbohydrate in leaves. The number of unmarketable stems per crate was negatively associated with glycerol glucoside 1 (r=-0.8317, p=0.0015), glycerol glucoside 2 (r=-0.6218, p=0.0411), and sucrose (r=-.07607, p=0.0066) but was positively associated with glucose (r=0.7744, p=0.0051), fructose (r=0.7834, p=0.0043), and starch (r=0.7609, p=0.0065). Conversely, bud count per stem was positively associated with glycerol glucoside 1 (r=0.8211, p=0.0019), glycerol glucoside 2 (r=0.6519, p=0.0298), and with sucrose (r=0.7267, p=0.0113), but negatively associated with glucose (r=-0.6723, p=0.0234), fructose (r=-0.6863, p=0.0197), and starch (r=0.6703, p=0.024). Water uptake followed a pattern similar to that in unmarketable stems, where water uptake was negatively associated with glycerol glucoside 1 (r=-0.7127, p=0.0138), glycerol glucoside 2 (r=-0.6521, p=0.0297), and sucrose (r=-0.7295, p=0.0108), but positively associated with glucose (r=0.6025, p=0.0498), fructose (r=0.6147, p=0.0442), and starch (r=0.8450, p=0.0011). As with bud count, fresh weight and dry weight were positively correlated with glycerol glucoside 1 (r=0.7694 and 0.7913, p=0.0056 and 0.0037, respectively), and sucrose (r=0.6099 and 0.6225, p=0.0463 and 0.0408), but were negatively correlated with glucose (r=-0.6267 and -0.7322, p=0.0391 and 0.0104) and with fructose (r=-0.6435 and -0.7551, p=0.0327 and 0.0072). Dry weight was also negatively correlated with leaf starch (r=-0.6195, p=0.0421). Glycerol glucoside 2 was correlated with glycerol

glucoside 1 (r=0.8929, p=0.002), with sucrose (r=0.6541, p=0.029), and glycerol glucoside 1 with sucrose (r=0.6993, p=0.0166). Glycerol glucoside 1 was negatively associated with starch (r=-0.6366, p=0.0352). Glucose was associated with fructose (r=0.9972, p<0.0001), with starch (r=0.7858, p=0.0041), and fructose with starch (r=0.7963, p=0.0034).

Year 3 lily stem inositol, glucose, and fructose contents were affected by temperature but not light. Inositol was higher in stems grown entirely at 10 or 20 °C or started at 20 °C than in those started at 10 °C (Table 9). Glucose and fructose were higher in stems grown entirely at 10 than at 20 °C (Table 9). Stem glycerol glucoside 1 and glycerol glucoside 2 differed by treatment. Glycerol glucoside 2 was higher in stems started at 10 °C in 0% shade and started 10 °C in 30% shade and finished at 20 °C in 30 and 0% shade, respectively, than in stems grown entirely at 20 °C in 0% shade or started at 20 °C in 0% shade and finished at 10 °C in 0% shade (Table 10). Stems grown entirely at 10 °C in 0% shade and those started in those conditions but moved to 20 °C in 0% shade had higher glycerol glucoside 2 than those grown entirely at 20 °C in 0% shade (Table 10). Glycerol glucoside 1 distribution followed a very similar pattern. Glycerol glucoside 1 was higher in stems started at 10 °C in 0% shade and finished at 20 °C in 30% shade than in all treatments grown entirely or started at 20 °C, except the one grown entirely in 30% shade for the entire crop cycle (Table 10). Stems started at 10 °C under either 0 or 30% shade and finished at 20 °C in 0% shade had higher glycerol glucoside 1 than stems grown entirely at 20 °C in 0% shade (Table 10). Sucrose, stachyose, and starch were not affected by either light or temperature. Inositol, glucose, fructose, sucrose, stachyose, and starch averaged 2.0, 42.8, 31.8, 6.1, 0.05, and 1.4, respectively, over all treatments.

For stems samples of year 3 lilies, vase life was associated with glucose (r=0.7448, p=0.0085) and fructose (r=0.7314, p=0.0105). The number of unmarketable stems per crate was associated with inositol (r=0.6535, p=0.0292), with glycerol glucoside 1 (r=-0.7901, p=0.0038), and with glycerol glucoside 2 (r=-0.7630, p=0.0063). Bud count per stem was negatively correlated with inositol (r=-0.6215, p=0.0412), but positively correlated with glycerol glucoside 1 (r=0.8668, p=0.0006), glycerol glucoside 2 (r=0.8595, p=0.0007), glucose (r=0.6224, p=0.0408), and with fructose (r=0.6250, p=0.0398). Water uptake was correlated with inositol (r=0.6806, p=0.0212), and negatively correlated with glycerol glucoside 1 (r=-0.6102, p=0.0462) and glycerol glucoside 2 (r=-0.6589, p=0.0275). Fresh weight and dry weight were positively associated with glycerol glucoside 1 (r=0.8390 and 0.7397, p=0.0012 and 0.0093), glycerol glucoside 2 (r=0.7901 and 0.7253, p=0.0038 and 0.0133), glucose (r=0.6326 and 0.7556, p=0.0367 and 0.0072), and fructose (r=0.6227 and 0.7511, p=0.0407 and 0.0077). Percent dry weight was also associated with glucose (r=0.7281, p=0.0111) and fructose (r=0.7004, p=0.0164). In stems, inositol was negatively associated with glycerol glucoside 1 (r=-0.7112, p=0.0141) and glycerol glucoside 2 (r=-0.7125, p=0.0139, while glycerol glucoside 1 and glycerol glucoside 2 were positively correlated (r=0.9850, p<0.0001). Glucose and fructose were also correlated (p=0.9969, p<0.0001).

For tepals of stems grown entirely in year 3, sucrose was affected by temperature and glucose was affected by light. Sucrose was higher in stems grown entirely at 10 °C than in stems grown entirely at 20 °C or started at either 10 or 20 °C (Table 9). Glucose was higher in tepals of stems grown entirely under 30% shade than in those grown entirely or started at

0% shade (Table 9). In year 3, no tepal carbohydrate was affected by a temperature by light interaction. Average carbohydrate content was 4.1, 9.4, 27.5, 127.6, and 65.4 $mg \cdot g^{-1}$ dw for inositol, glycerol glucoside 1, glycerol glucoside 2, fructose, and starch, respectively.

For Pearson correlations of postharvest characteristics with year 3 tepal carbohydrates, no carbohydrate showed associations with vase life. Bud count per stem was associated with tepal glycerol glucoside 1 (r=0.6490, p=0.0307) and percent dry weight was associated with starch (r=0.7530, p=0.0075). Glycerol glucoside 1, glycerol glucoside 2, glucose, fructose, and sucrose were each positively correlated with each other with r ranging from 0.6249-0.9964, and p ranging from <0.0001 to 0.0398.

Helianthus

Vase life in sunflowers was affected by temperature but not by light in year 1, by an interaction of temperature and light in year 2, and by neither temperature nor light in year 3. In year 1, vase life was greater in stems grown entirely at 10 °C than in those grown entirely at 15 or 20 °C (Table 11). In year 2, vase life was greater in stems grown entirely at 10 °C in 30% shade than in stems started at 10 °C in 30% shade and moved to 20 °C in 0% shade, those grown entirely at 15 °C and either grown entirely or started in 0% shade, and those grown entirely at 15 °C and moved from 30% shade to 0% shade two weeks before harvest (Table 12). Vase life was also greater in stems grown entirely at 10 °C in 30% shade and in those grown entirely at 15 °C in 30% shade than in stems grown entirely at 20 °C with either 0 or 30% shade (Table 12). Vase life of stems grown entirely at 20 °C in 30% shade was lower than vase life of any other treatment combination (Table 12). For the year 1 light

study, vase life average 10.1 days over all treatments and averaged 11.6 days over all treatments in year 3.

Uptake was affected by temperature and light in year 1. Uptake was greater in stems entirely grown or started at 10 °C than in stems grown entirely or started at 20 °C (Table 11). Uptake was greater in stems grown entirely at 10 °C than in stems grown entirely at 15 or 20 °C (Table 11). Uptake was greater in stems grown entirely with HID supplemental light than in stems grown entirely in 30% shade or those started in 60% shade and moved to 0% shade for two days or two weeks prior to harvest (Table 13). Uptake was also greater in stems grown entirely in 0% shade and those started in 0% shade and moved to 60% shade for two days prior to harvest than in those grown entirely in 30% shade and those started in 60% shade and moved to 0% shade for two weeks prior to harvest (Table 13). Uptake was greater for stems started in 0% shade and moved to 60% shade two weeks prior to harvest than for those started in 60% shade and moved to 0% shade for two weeks (Table 13).

For year 2, uptake was affected by both temperature and light. Uptake was greater for stems grown entirely at 10 °C than for all other temperature treatments (Table 14). Uptake was greater in stems grown entirely at 20 °C and in stems started at 10 °C than in stems started at 20 °C (Table 14). Stems grown entirely or started in 0% shade had greater uptake than those grown entirely or started in 30% shade (Table 14). For year 3, uptake was affected by a temperature by light interaction where stems started at 20 °C in 0% shade and moved to 10 °C in 0% shade had higher water uptake than stems grown entirely or started at 20 °C in 30% shade (Table 15). Stems started at 10°C in 0% shade and moved to 20 °C in

0% shade had greater water uptake than stems started at 20 °C in 30% shade and moved to 10 °C in 0% shade (Table 15).

In year 1, stems grown entirely at 10 °C were longer than those grown entirely at 15 °C and than those started at 20 °C and moved to 10 °C for two weeks (Table 11). Stems grown entirely in 0% shade and under supplemental HID light were longer than those grown entirely or started under 30 or 60% shade (Table 13). Those started under 0% shade were longer than those grown entirely under 30 or 60% shade and those started under 60% shade and moved to 0% shade for two weeks (Table 13).

Stem length was affected by a temperature by light interaction in year 2. Stems started at 15 °C in 0% shade and moved to 30% shade were longer than all treatments grown entirely or started at 20 °C (Table 12). Stems grown entirely at 10 °C under 30% shade were longer than those started in the same conditions and moved to 20 °C and 0% shade as well as treatments grown entirely or started at 20 °C in 30% shade (Table 12). Stems grown entirely at 10 °C in 0% shade and those grown entirely or started at 15 °C in 30% shade were longer than stems grown entirely or started at 20 °C in 30% shade (Table 12). Stems started at 20 °C in 30 % shade were shorter than all treatments grown entirely or started at 10 or 15 °C except the treatment started at 10 °C in 30% shade and moved to 20 °C and 0% shade (Table 12).

In year 3, stem length was affected by temperature and by light. Stems grown entirely at 10 °C were longer than those grown entirely or started at 20 °C and those started at 10 °C (Table 16). Stems grown entirely at 15 °C were longer than those grown entirely or

started at 20 °C (Table 16). Stems started at 10 °C were longer than those started at 20 °C (Table 16).

Caliper was affected by temperature and light for all three years. In year 1, stems grown entirely at 10 °C or started at 10 °C and moved to 20 °C for two days before harvest were larger than those grown entirely at 15 or 20 °C (Table 11). Stems started at 10 °C and moved to 20 °C two weeks prior to harvest were larger than those grown entirely at 15 °C (Table 11). Caliper of stems grown entirely or started in 0% shade or with supplemental HID light were larger than those grown entirely or started under 30 or 60% shade (Table 13).

In year 2, stems grown entirely at 10 °C were larger than those grown entirely at 15 or 20 °C and than those started at 20 °C (Table 14). Stems started at 10 °C were larger than those grown entirely or started at 20 °C and stems grown entirely at 15 °C were larger than those grown entirely at 20 °C (Table 14). Stems grown entirely or started under 0% shade were larger than stems grown entirely or started in 30% shade (Table 14). In year 3, stems grown entirely at 10 °C were larger than those grown entirely or started at 20 °C (Table 16). Stems grown entirely in 0% shade were larger than those started in 30% shade (Table 16).

Flower diameter was affected by temperature and by light in years 1 and 2 and by an interaction of the two in year 3. For year 1, diameters of flowers grown entirely at 10 and 20 °C were larger than those grown entirely at 15°C (Table 11). Diameters of flowers grown entirely or started in 0% shade and under supplemental HID were larger than those grown entirely or started under 30 or 60% shade (Table 13). In year 2, flowers grown entirely or started at 10 °C were larger than those grown entirely or started at 15 or 20 °C (Table 14). Flowers grown entirely or started under 0% shade were larger than those grown entirely or

started under 30% shade (Table 14). For year 3, flower diameter was greater in stems started at 10 °C in 0% shade and finished at 20 °C in 0% shade than in stems grown entirely at 10 °C in 30% shade, those grown entirely at 15 °C, and those grown entirely or started at 20 °C under any light conditions (Table 15). Stems grown entirely at 10 °C under 0% shade and started in those conditions and moved to 20 °C with 30% shade had larger flowers than stems grown entirely at 10 °C in 30% shade and all treatments grown or started at 20 °C, regardless of light conditions (Table 15). Stems started at 10 °C under 30% shade and moved to 20 °C under 0% shade had larger flowers than those grown entirely at 10 °C under 30% shade and than those grown entirely at 20 °C and those started at 20 °C under 30% shade and moved to 10 °C under 0% shade (Table 15). Stems grown entirely at 15 °C with 0% shade had larger flowers than those grown entirely at 20 °C and those started at 20 °C under 30% shade and moved to 10 °C under 0% shade (Table 15).

Fresh weight was affected by both temperature and light for all three years. In year 1, fresh weight and termination fresh weight was higher for stems grown entirely at 10 °C and those started at 10 °C and moved to 20 °C for two days prior to harvest than for stems started at 10 °C and moved to 20 °C for two weeks, than stems grown entirely at 15 or 20 °C, and than stems started at 20 °C (Table 11). Stems started at 10 °C and moved to 20 °C for two weeks had higher fresh weight and termination fresh weight than stems grown entirely at 15 °C (Table 11). Stems grown with supplemental HID light had higher fresh weight and termination fresh weight than stems started under 0% shade and moved to 60% shade for two weeks prior to harvest and than stems grown entirely or started under 30 or 60% shade (Table 13). Stems grown entirely or started under 0% shade had higher fresh weights and

termination fresh weights than stems grown entirely or started under 30 or 60% shade (Table 13).

In year 2, fresh weight was higher for stems grown entirely at 10 °C than for all other treatments (Table 14). Stems started at 10 °C had higher fresh weight than stems grown entirely or started at 20 °C and stems grown entirely at 15 °C had higher fresh weight than stems grown entirely at 20 °C (Table 14). Stems grown entirely or started under 0% shade had higher fresh weight than stems grown entirely or started under 30% shade (Table 14). In year 3, fresh weight was higher in stems grown entirely at 10 °C than in stems grown entirely or started at 20 °C (Table 16). Fresh weight was higher in stems grown entirely at 15 °C and started at 20 °C than those grown entirely at 20 °C (Table 16). Fresh weight was higher in stems grown entirely in 0% shade than in those grown entirely or started in 30% shade (Table 16).

Dry weight was affected by both temperature and light for all three years. In year 1, stems grown entirely at 10 °C had a higher dry weight than did those started at 10 °C and moved to 20 °C for two weeks prior to harvest, as well as stems grown entirely at 15 or 20 °C and those started at 20 °C (Table 11). Dry weight was higher for treatments supplemented with HID or grown entirely or started at 0% shade than for treatments grown entirely or started in 30 or 60% shade (Table 13). In year 2, dry weight was highest for the treatment grown entirely at 10 °C (Table 14). Dry weight was higher for stems grown entirely at 15 °C and those started at 10 °C than for stems grown entirely at 20 °C (Table 14). Stems grown entirely or started in 0% shade had higher dry weight than stems grown entirely or started in 30% shade (Table 14). For year 3, stems grown entirely at 10 °C had a higher dry weight

than those grown entirely at 20 °C (Table 16). Stems grown entirely in 0% shade had higher dry weight than those started in 30% shade (Table 16).

Percent dry weight, a measure of photosynthetic efficiency, did not differ by temperature or by light for year 1. Percent dry weight averaged 10.9 for temperature treatments and 11.6 for light treatments. In year 2, temperature and light affected percent dry weight. Stems grown entirely at 10 °C had a higher percent dry weight than stems grown entirely at 20 °C or stems started at 10 °C (Table 14). Stems grown entirely at 15 °C and started at 20 °C had a higher percent dry weight than stems started at 10 °C (Table 14). Stems grown entirely or started in 0% shade had a higher percent dry weight than stems grown entirely or started in 30% shade (Table 14). In year 3, percent dry weight did not differ by temperature or by light, averaging 10.8 and 10.9, respectively.

Corrected water uptake differed by temperature and by light in year 1. Uptake per gram fresh weight per day was higher in stems grown entirely at 15 and 20 °C and those started at 20 °C and moved to 10 °C for two weeks than for stems grown entirely at 10 °C or those started at 10 °C and moved two days before harvest (Table 11). Stems moved two weeks prior to harvest from 10 °C to 20 °C and stems moved two days before harvest from 20 °C to 10 °C had increased water uptake over stems that were grown entirely at 10 °C (Table 11). Stems started at 0% shade and moved to 60% shade two weeks prior to harvest, stems grown entirely in 30% shade, and stems moved from 60% shade to 0% shade two weeks prior to harvest had increased water uptake over stems grown with supplemental HID lighting and those grown entirely in 0% shade or started in 0% shade and moved to 60% shade two days before harvest (Table 13).

Corrected water uptake differed by temperature in year 2. Stems grown entirely at 20 °C had greater water uptake per gram fresh weight than stems grown entirely at 10 or 15 °C or than those started at 10 or 20 °C (Table 14). In year 3, water uptake differed by light. Water uptake was greater in stems grown entirely in 30% shade than in those started in 0% shade (Table 16). Corrected water uptake averaged 7.2 $ml \cdot g^{-1}$ fresh weight for light treatments in year 2 and 6.0 $ml \cdot g^{-1}$ fresh weight in year 3.

Helianthus carbohydrate content

For year 2 inflorescences minus ray florets, inositol and glucose were affected by temperature. Inositol was higher in inflorescences of stems started at 20 °C than for those started at 10 °C (Table 17). Glucose was higher in stems grown entirely at 10 or 15 °C and started at 20 °C than in stems started at 10 °C (Table 17). Inflorescence carbohydrates were not affected by a temperature by light interaction. Carbohydrate contents averaged over treatments were 31.9, 16.5, 2.0, 3.3,1.3, and 1.7 $mg \cdot g^{-1}$ dw, respectively, for fructose, sucrose, stachyose, and starch and the two putative glycerol glucosides, unknown carbohydrate 1 and unknown carbohydrate 2.

In Pearson correlations between inflorescence carbohydrates and postharvest characteristics, vase life was negatively correlated with inflorescence fructose (r=-0.6161, p=0.019) and sucrose (r=-0.6527, p=0.0114). Percent dry weigh was negatively correlated with inositol (r=-0.5337, p=0.0493) and fructose (r=-0.5606, p=0.037). Percent dry weight was positively correlated with glucose (r=0.6142, p=0.0194). Unknown carbohydrate 2 was

correlated with starch (r=0.7205, p=0.0037) and fructose was correlated with sucrose (r=0.9593, p<0.0001).

Leaf sucrose was affected by light while starch was affected by temperature. Starch was higher in leaves of stems grown entirely at 10 °C than grown entirely at 20 °C (Table 17). Sucrose was higher in leaves started at 0% shade than in those started in 30% shade (Table 17). Inositol was higher in stems grown entirely at 10 °C in 30% shade than in stems started at 10 °C in 0 or 30% shade and moved to 20 °C in 0% shade, than in stems grown entirely at 15 °C in 0 or 30% shade those grown entirely at 15 °C and moved from 0% shade to 30% shade, and than in stems grown entirely at 20 °C in 30% shade (Table 18). Inositol was also higher for stems started at 20 °C in 0% shade and moved to 10 °C in either 0 or 30% shade than for stems started at 10 °C in 0% shade and moved to 20 °C in 0% shade, than for stems grown entirely at 15 °C in either 0 or 30% shade and those grown entirely at 15 °C and moved from 0 to 30% shade, and than for stems grown entirely at 20 °C in 30% shade (Table 18). Year 2 leaf unknown carbohydrate 1, unknown carbohydrate 2, glucose, fructose, and stachyose were not affected by temperature, light, or their interactions; contents averaged over treatment were 0.33, 1.8, 8.3, 6.2, and 0.22 $mg \cdot g^{-1}$ dw, respectively.

In year 2 correlations between leaf carbohydrates and postharvest characteristics, vase life was correlated with inositol (r=0.6553, p=0.011) and starch (r=0.5796, p=0.0298). Among carbohydrates, inositol was correlated with glucose, fructose, and starch; unknown carbohydrate 1, unknown carbohydrate 2, glucose, fructose, sucrose, and starch were each correlated with each other. Pearson r for these ranged from 0.5484 to 0.9748 and p was <0.0001 to 0.0423.

In year 2 ray florets, fructose was affected by temperature and starch was affected by light. Fructose was higher in stems grown entirely at 15 °C than in those grown entirely at 10 or 20 °C (Table 17). Starch was higher in ray florets of stems grown entirely in 30% shade than in those started in 30% shade (Table 17). Ray floret inositol, unknown carbohydrate 1, unknown carbohydrate 2, glucose, sucrose, and stachyose were not affected by temperature, light, or their interaction; contents were 3.7, 1.4, 3.6, 58.3, 7.3, and 0.6 $mg \cdot g^{-1}$ dw, respectively.

In year 2 ray floret correlations, vase life was associated with inositol (r=0.6565, p=0.0108) and glucose (r=0.5780, p=0.0304). Fresh weight, dry weight, and percent dry weight were correlated with stachyose (r=0.6709, 0.6916, and 0.5467; p=0.0086, 0.0061, and 0.0431, respectively). Unknown carbohydrate 1 was correlated with unknown carbohydrate 2 (r=0.9720, p<0.0001), unknown carbohydrate 1 with sucrose (r=0.5700, p=0.0297), glucose with fructose (r=0.8394, p=0.0002) and starch (r=0.6278, p=0.0162), and fructose with starch (r=0.5378, p=0.0473).

Year 2 stem glucose, fructose, and stachyose contents were affected by temperature and glucose was also affected by light. Glucose was highest in stems grown entirely at 10 °C compared to stems grown entirely at 20 °C or started at 10 °C (Table 17). Fructose was highest in stems grown entirely at 15 °C and started at 20 °C compared to those grown entirely at 20 °C and started at 10 °C (Table 17). Fructose was higher in stems grown entirely at 10 than at 20 °C (Table 17). Stachyose was higher in stems grown entirely at 10 than at 15 or 20 °C and than in those started at 20 °C (Table 17). Glucose was higher for stems grown entirely in 0% shade than in those grown entirely in 30% shade (Table 17).

Temperature, light, or their interaction did not affect inositol, unknown carbohydrate 1, unknown carbohydrate 2, sucrose, or starch. Their contents averaged 1.9, 0.20, 1.1, 4.3, and 1.3 $mg \cdot g^{-1}$ dw, respectively.

In year 2 stem samples, vase life was positively correlated with fructose (r=0.6341, p=0.0149). Water uptake was correlated with stachyose (r=0.6005, p=0.0232), which was also correlated with fresh weight (r=0.6232, p=0.0173). Percent dry weight was correlated with glucose (r=0.8159, p=0.0004) and fructose (r=0.5832, p=0.0286). Unknown carbohydrate 1 was correlated with unknown carbohydrate 2 (r=0.8642, p<0.0001) and glucose with fructose (r=0.8092, p=0.0005).

For year 3, inflorescence glucose, fructose, and sucrose were shown to be affected by a temperature by light interaction, but differences between treatments were not significant. Glucose, fructose, and sucrose averaged 55.8, 16.6, and 0.61 $mg \cdot g^{-1}$ dw, respectively. Other inflorescence carbohydrates were not affected by either temperature or light and averaged 3.7, 1.2, 0.43, 3.5, and 1.6 for inositol, unknown carbohydrate 1, unknown carbohydrate 2, stachyose, and starch, respectively. We could not analyze starch for the temperature by light interaction because of insufficient denominator degrees of freedom.

For year 3 inflorescence carbohydrate samples, vase life was not associated with any carbohydrate. Percent dry weight was correlated with unknown carbohydrate 2 (r=0.6578, p=0.0278). Among carbohydrates, unknown carbohydrate 2 was correlated with starch (r=0.9387, p<0.0001), and fructose with unknown carbohydrate 1 (r=0.7819, p=0.0045) and glucose (r=0.8818, p=0.0003).

Year 3 leaf glucose and fructose were affected by temperature. For both, stems grown entirely at 20 °C had higher contents than stems grown entirely at 10 °C (Table 19). Leaf inositol, sucrose, and stachyose were affected by a temperature by light interaction and separated by treatment. Inositol was higher in stems grown entirely at 15 °C in 0% shade than for all treatments except stems grown entirely at 10 °C in 30% shade, and stems started at 20 °C in 0 or 30% shade and moved to 10 °C in 0% shade (Table 20). Stems started at 20 ° in 0% shade and moved to 10 °C in 0% shade had higher inositol than stems grown entirely at 10 °C in 0% shade and than those started at 10 °C in 0% shade and moved to 20 °C in 0% shade (Table 20). Stems grown entirely at 10 °C in 30% shade had higher inositol than stems started at 10 °C in 0% shade and moved to 20 °C in 0% shade (Table 20). Leaf sucrose was higher in stems grown entirely at 20 °C in 30% shade than in stems started at 10 °C in 0% shade and moved to 20 °C in 30% shade, than stems grown entirely or started at 10 °C in 30% shade, and than all other treatments grown entirely or started at 20 °C (Table 20). Leaf stachyose was higher in stems started at 20 °C in 0% shade and moved to 10 °C in 30% shade than in all stems grown entirely or started at 10 or 15 °C and those grown entirely at 20 °C in 30% shade (Table 20). Leaf unknown carbohydrate 1, unknown carbohydrate 2, and starch were not affected by temperature, light, or their interaction. Their contents were 0.08, 1.2, and 1.7 when averaged over treatments.

In year 3 leaves, inositol was negatively associated with vase life (r=-0.6942, p=0.0178). Water uptake was negatively correlated to fructose (r=-0.6230, p=0.0406). Percent dry weight was correlated with glucose (r=0.6561, p=0.0284) and with fructose

(r=0.74413, p=0.0086). Unknown carbohydrate 2, glucose, fructose, and sucrose were each associated with each other with r from 0.7435 to 0.9632 and p from <0.0001 to 0.0087.

Year 3 ray floret inositol and glucose were affected by temperature and light. Unknown carbohydrate 2 was also affected by light. Inositol was higher for stems started at 20 °C than for stems grown entirely at 20 °C (Table 19). Glucose was higher for stems started at 20 °C than for stems grown entirely at 10 °C (Table 19). Inositol was higher for stems grown entirely in 30% shade than for stems started at 0 or 30% shade (Table 19). Unknown carbohydrate 2 was higher for stems grown entirely in 30 than 0% shade (Table 19). Glucose was higher in ray florets of stems grown entirely at 30% shade than for those started in 30% shade (Table 19). Unknown carbohydrate 1, fructose, sucrose, stachyose, and starch, which were not affected by temperature, light, or the interaction, averaged 1.6, 47.7, 16.9, 1.9, and 5.4 $mg \cdot g^{-1}$ dw, respectively.

For year 3 ray floret carbohydrate samples, vase life was correlated with sucrose content (r=0.6159, p=0.0437). Sucrose was also correlated with dry weight (r=0.6317, p=0.0371). Among carbohydrates, unknown carbohydrate 2 was related to stachyose (r=-0.6536, p=0.0292) and starch (r=0.6760, p=0.0224). Glucose and fructose were also correlated (r=0.8154, p=0.0022).

Year 3 stem inositol, unknown carbohydrate 2, glucose, and stachyose were affected by temperature. Inositol was also affected by light. Inositol was higher in stems started at 20 °C than in those grown entirely at 10, 15, or 20 °C (Table 19). Unknown carbohydrate 2 was higher in stems grown entirely at 10 °C than in those started at 10 or 20 °C (Table 19). Glucose was higher in stems grown entirely at 15 °C than in stems grown entirely at 20 °C

and those started at 10 or 20 °C (Table 19). Glucose was higher in stems grown entirely at 10 °C than in those started at 10 °C (Table 19). Stachyose was higher in stems grown entirely at 20 °C than in those started at 10 °C (Table 19). Inositol was higher in stems grown entirely in 30% shade than in those started in 0 or 30% shade (Table 19). Unknown carbohydrate 1, fructose, sucrose, and starch were not affected by temperature, light, or the interaction and averaged 0.16, 14.0, 2.1, and 1.4 over treatments, respectively.

Carbohydrates in stem samples of year 3 sunflowers did not reveal a relationship between vase life and any stem carbohydrate. Stachyose was negatively correlated with water uptake (r=-0.6071, p=0.0476). Unknown carbohydrate 2 was correlated with starch (r=0.6962, p=0.0173) and glucose with fructose (r=0.7616, p=0.0065).

Discussion

High temperatures decreased vase life in lilies, while low light did not, which suggests that growers should shade lilies to keep temperatures low. However, because high temperatures and low light both increased incidence of bud abortion during production, a careful balance is required to avoid reducing marketability. For lilies, where production temperature consistently had an effect on vase life, we recommend shading to achieve maximum vase life, but decreasing the number of bulbs planted per crate to maximize the light interception in the canopy interior.

In an experiment studying the effects of temperature and planting density on chrysanthemum production, van der Ploeg et al. (2009) found that low temperature delayed development by 4 to 17 days, depending on year and cultivar. We found that predicting time

to flower was difficult in both species we studied, which led to inconsistencies in the amount of time the plants spent in their final light and temperature conditions from year-to-year.

In roses, vase life was increased by supplemental lighting (Fjeld et al., 1994) but as periods of light exposure increased from 16 to 20 and from 20 to 24 hours, vase life decreased (Mortensen and Fjeld, 1998). This could indicate a requirement for a dark period for transitory starch degradation and carbohydrate export from leaves to flowers. Many factors during production complicate effects on vase life. For instance, Mortensen and Fjeld (1998) proposed that high humidity (90% or higher) conditions causes stomata to remain open, leading to poor water use efficiency during vase life. Although vase life was not measured, Mascarini et al. (2006) found that a bent shoot system in roses, which minimizes the red:far red light ratio intercepted by non-producing shoots, led to increased productivity and longer stem length. It has been proposed that by leaving the non-producing shoots on the plant, photosynthesis in these shoots can induce the productive shoots to flower. At the same time, the high far-red light perceived by the non-producing shoots signals the producing shoots to elongate. In roses, we see that production environment influences vase life but effects of production environment are complex.

For each lily experiment, vase life was positively correlated with water uptake and fresh weight, but negatively correlated with water uptake per gram fresh weight. Vase life was correlated with dry weight in year 2 and both dry weight and percent dry weight in years 1 and 3. Taken together, this suggests that stems grown in conditions that do not promote robust growth, such as low light and high temperature, are not acclimated for efficient postharvest water use, and this is strongly related to vase life.

We found high levels of what we first identified as mannitol and sorbitol in lily tissues, as the carbohydrates had retention times only slightly different than authentic standards on the PA1 HPLC column. Carbohydrates with similar retention times were present in sunflower tissues as well. One would not expect to find both mannitol and sorbitol in a single species, and particularly not at high levels (Stoop et al., 1996), and reanalysis of samples using a HA1 sugar alcohol column confirmed that these carbohydrates are not mannitol and sorbitol. We suspect that, for lily, these carbohydrates are, in fact, glycerol glucosides previously reported in lily tepals, one of them being lilioside B (van der Meulen-Muisers et al., 2001), as some glycerol glucosides migrate similarly to mannitol and sorbitol on a PA1 column (W.B. Miller and U. van Meeteren, personal communications). At the time of this publication, the putitive glycerol glucosides identity has not been positively confirmed, thus we have tentatively referred to them as glycerol glucosides 1 and 2. We are uncertain of the identity in sunflower, and have termed them unknown carbohydrates 1 and 2.

Interestingly, we did not see a relationship between tepal carbohydrates and vase life in lily for either year 2 or 3. Correlations between tepal carbohydrates and other postharvest characteristics were not consistent for both years. However, van der Meulen-Muisers et al. (2001) found that the level of tepal carbohydrates at harvest was associated with the likelihood a bud would fully develop and open. We then might expect that tepal carbohydrates would be correlated with unmarketable stems, bud count, and postharvest bud blast. The difference in our results could be that in the van der Meulen-Muisers et al. (2001) study, carbohydrates from each bud were sampled separately while we pooled buds from each stem for sampling. Van der Meulen-Muisers et al. (2001) reported that glycerol

glucoside, which we have tentatively identified in our samples, was the primary carbohydrate in lily buds until they were approximately 6 cm in size for the cultivars in their study. At this stage of development, starch became the main carbohydrate until anthesis, when glucose and fructose levels rose dramatically (van der Meulen-Muisers et al., 2001).

Vase life was correlated with leaf inositol and glycerol glucoside 2 in year 2 but not in year 3. Vase life was also associated with glycerol glucoside 1 and glycerol glucoside 2 in the inflorescence minus tepals in year 3 but not in year 2. Vase life showed a positive correlation with glycerol glucoside 1 and glycerol glucoside 2 in stem sections in year 2 and with glucose and fructose in year 3. While correlations exist between vase life and carbohydrates in other tissues, the lack of correlation between tepal carbohydrates and vase life while several correlations exist between vase life and carbohydrates in other tissues may either indicate that factors other than carbohydrate status in the tepals are primarily responsible for differences in vase life in lily or that tepal carbohydrate status is constantly in flux and that source organ carbohydrate status is most important for vase life. Since lily flowers open acropetally, carbohydrate contents are constantly in flux as a result of reallocation from senescing flowers to developing buds. Therefore, it would be unsurprising if source organs other than flowers play an integral role in carbohydrate storage for the flowers prior to flower opening.

Our results indicate that stem glucose, fructose, glycerol glucoside 1, and glycerol glucoside 2 have primary roles in bud viability and postharvest performance. If, as we suspect, the carbohydrates we have tentatively referred to as glycerol glucosides 1 and 2 are glycerol glucosides, their positive correlation with bud viability would align support the

findings of with the van der Meulen-Muisers et al. (2001) study. Although glycerol glucoside 1 and glycerol glucoside 2 were positively correlated with bud blasting in year 2, this is likely because they were also positively correlated with bud count per stem, so stems had more buds to support.

Sucrose tended to be correlated to the same postharvest characteristics as glycerol glucoside 1 and glycerol glucoside 2 while starch tended to have the same correlations as glucose and fructose. In leaves sampled during year 3, leaf glucose, fructose, and starch were positively correlated with unmarketable stems and water uptake, while glycerol glucoside 1, sucrose, and/or glycerol glucoside 2 were positively associated with bud count per stem, fresh weight, and dry weight. These differences in correlations may be due to the regulation of so-called "feast" and "famine" genes (Koch, 1996). In other words, when environmental conditions do not promote carbohydrate production (famine), carbohydrates are kept in the leaves as glucose and fructose as energy stores. Conversley, but when carbohydrates are plentiful (feast), they are converted to glycerol glucosides and/or sucrose for transport to sink tissues.

In our experiments, sunflower vase life was not consistently affected by temperature or light. Natural light levels during the third year of production were low, which may have prevented the light and temperature treatments we imposed from having an effect on vase life. In our study, vase life was not strongly or consistently correlated to flower size, but flower size was affected by growing conditions. For this reason, light is of high great importance in sunflower. Friedman et al. (2007) report that irrigation with secondary treated effluent did not alter developmental timing, yield, flower weight, or flower size in

sunflowers; however, their study does cite increased “petal browning” during vase life, which would have resulted in termination of vase life in our study. Together, these studies indicate that visual appeal at harvest may not be related to vase life in sunflower.

Interestingly, water uptake in our study did not correlate with corrected water uptake for any year, but was correlated with total water uptake in year 1. Although this may simply be that flowers with a long vase life necessarily use more water, it might also indicate that stem blockage is a primary cause of wilting in sunflowers. Chlorine tablets (Chrysal CVB, Chrysal USA, Miami, FL) have become a popular postharvest treatment among sunflower growers (Andrea Gagnon, personal communication). Sunflower stems have numerous trichomes, which may provide attachment points for microbes and microbe containing debris. Chlorine tablets may disinfect the stems and prevent bacterial plugs from forming in the stem tissue.

Sunflower vase life was correlated with fresh weight in the temperature study in years 1 and 2. In the year 1 temperature study, vase life was also correlated with dry weight and percent dry weight, but this was not true for the year 1 light study or for years 2 or 3. In the year 1 temperature study and in year 3, vase life was negatively correlated with water uptake corrected for fresh weight (and for days, in year 1), again indicating that stems that are unable to utilize water efficiently tend to have a shorter vase life.

While various sugars were correlated with vase life, our data does not indicate a clear relationship between any one carbohydrate in the organs we sampled and vase life in sunflowers in both years. This may be due to the fact that there was little variation in vase life in year 3. This study was conducted in winter, in order to achieve lower greenhouse

temperatures. Consequently, sunflowers flowered at a substandard size, and carbohydrate status may have been inadequate. Of 28 *Helianthus* cultivars tested, Yañez et al. (2005) characterized 26 as facultative short day; however, vase life was not different between flowers grown under short day and long day conditions.

Alternatively, vase life in sunflowers may not be as dependent on carbohydrate status as on other factors, such as water uptake as discussed above. Vase life in sunflowers varied by environment, but environments did not appear to have the same effect on vase life from year to year. For sunflowers, we believe that temperature might be more important than light for vase life, but not for stem quality. It might be possible, with a day-neutral cultivar, to use shade to achieve temperature control and harvest thus produce sunflowers of an acceptable size. Additionally, utilizing HID lighting before sunrise or after sunset to extend photoperiod and allow increased photosynthesis might allow temperatures to remain cool while preventing premature flower development. Seed company information on photoperiodism is often inaccurate. However, research on photoperiodism is ongoing, and information is available from cut flower commodity grower associations (Yañez et al., 2005; Association of Specialty Cut Flower Growers). At this point, we doubt that a truly day-neutral sunflower cultivar has been developed. It is likely that some cultivars are simply more sensitive to short days than others.

In summary, we recommend lowering temperatures to increase postharvest vase life and increase quality. In lily, especially, we found that production under low temperatures produces high quality stems, with high carbohydrate levels to sustain vase life. However, both species studied here are determinant and produce one flowering stem per plant. With

other cut flower species where many stems per plant are produced and profitability depends on productivity per plant more than the quality per plant, it may be more beneficial to raise temperatures, to a point, for faster production. In chrysanthemum, the number of flowers produced, tended to increase with higher temperatures. However, the size of individual flowers tended to decrease with higher temperatures (van der Ploeg, et al., 2009). The number of flowers produced per plant also decreased with increased plant density (van der Ploeg et al., 2009), supporting our finding that low light levels can limit productivity. In the van der Ploeg study, it should be noted that the temperature and light effects on flowering were highly dependent on cultivar.

Several studies, such as van der Ploeg et al. (2009), have studied production environment and productivity in various species. However, there are few studies that link growing conditions, endogenous carbohydrates, and vase life of cut flowers, as this study does. Much of the existing research has been done on rose (Fjeld et al., 1994; Mortensen and Fjeld, 1998). However, responses to light and temperature almost certainly vary between species, and the work here provides information that will help growers of two of the most important domestic cuts produced in the United States.

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Table 1. Vase life, postharvest characteristics, and quality of *Lilium* 'Vermeer' grown during year 1 at temperatures (temp.) 10, 15, or 20 °C or grown at 10 or 20 °C and moved to 20 or 10 °C two days or two weeks prior to harvest. Actual length of time in final conditions varied based on unpredictable weather patters and variation of maturity within treatments. Water uptake was taken at termination of vase life. Stem length and flower length were taken at harvest. Termination (term.) dry weight was taken on terminated stems. Percent dry weight equals (term. dry weight*100/term. fresh weight). Uptake in ml of water per gram of fresh weight (at harvest) per day ($ml \cdot g^{-1} fw \cdot d^{-1}$) of vase life was calculated to account for differences in uptake as a result of varying vase lives and differences in stem size resulting from treatments.

Temp. (°C)										
Initial	Final	Target days	Days at final temp. (mean)	Vase life (d)	Uptake (ml)	Stem length (cm)	Flower length (cm)	Term. dry weight (g)	Percent dry weight	Uptake ($ml \cdot g^{-1} fw \cdot d^{-1}$)
10		-[Z]	65	9.3 a[Y]	196.3 a	109.4 a	7.9 ab	5.2 a	10.9 a	0.41 abc
10	20	2	3	8.7 ab	198.4 a	110.4 a	8.0 ab	4.8 ab	10.5 a	0.43 ab
10	20	14	11	8.3 b	181.9 ab	109.3 a	8.1 ab	4.0 b	9.3 bc	0.46 a
15		-	48	9.3 a	148.7 b	98.9 b	7.8 b	4.0 b	8.6 cd	0.30 c
20		-	43	8.8 ab	169.2 ab	90.8 c	8.2 a	4.0 b	8.7 bcd	0.35 bc
20	10	2	3	8.8 ab	143.7 b	93.0 bc	7.9 ab	4.0 b	8.5 d	0.30 c
20	10	14	22	9.3 a	205.6 a	92.6 bc	7.8 b	4.4 ab	9.4 b	0.42 ab
Treatment				**	***	***	**	***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 1 Continued.

[Z] Plants remained in treatment for the entire experiment.

[Y] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 2. Vase life, postharvest characteristics, and quality of *Lilium* 'Dazzle' grown during winter year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for dependent variables presented here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). Unmarketable stems, stem length, caliper, flower length, bud count, and fresh weight were taken at harvest. Appearance was evaluated on day 7 where 0 is excellent and 10 is very poor. Blasted flowers per stem was the number of buds at harvest minus the number of buds that opened during vase life. Dry weight was taken on stems that were dried on the day of harvest. Percent dry weight was (dry weight*100/fresh weight). Uptake in $ml \cdot g^{-1}$ fresh weight (fw) was calculated to account for differences in size resulting from treatments.

	Vase life (d)	Unmarket-able stems (per crate)	Ap-pearance (0-10)	Stem length (cm)	Flower Caliper (cm)	Bud length (cm)	Blasted count (per stem)	Fresh flowers (per stem)	Dry weight (g)	weight (g)	Percent dry weight	Uptake ($ml \cdot g^{-1}fw$)
						Temperature						
10	13.8 a[z]	7.0 c	4.5 ab	110.8 a	0.63 ab	9.6 b	3.5 a	0.37 ab	40.5 a	3.8 a	9.7 a	3.13 b
15	12.8 ab	13.4 b	5.4 a	100.7 b	0.60 c	10.0 a	3.0 bc	0.30 ab	35.6 bc	2.8 b	8.6 c	3.33 b
20	10.8 c	17.2 ab	4.4 b	96.9 c	0.61 bc	9.9 a	2.5 d	0.19 ab	32.9 cd	2.8 b	8.7 bc	4.17 a
Started 10	12.9 ab	9.3 c	5.1 ab	108.0 a	0.63 a	9.6 b	3.3 ab	0.50 a	36.9 ab	3.0 b	8.8 c	3.47 b
Started 20	12.2 b	17.2 a	4.6 ab	99.6 bc	0.59 c	9.6 b	2.9 cd	0.05 b	32.4 d	2.7 b	9.4 ab	4.08 a

Table 2 Continued.

Light												
0%		9.6 b		101.9 b	0.62 a		3.3 a	0.31 ab	38.0 a	3.4 a	9.5 a	3.32 b
30%		14.5 a		104.6 a	0.59 b		2.9 b	0.19 ab	33.3 b	2.7 b	8.7 bc	4.15 a
Started 0%		13.6 a		103.3 ab	0.62 a		2.9 b	0.45 a	36.1 ab	2.8 b	8.7 c	3.60 ab
Started 30%		13.6 a		103.2 ab	0.60 b		3.0 ab	0.18 b	35.2 b	3.1 ab	9.3 ab	3.48 b
Significance												
Temperature (T)	***	***	*	***	***	***	***	***	***	***	***	***
Light (L)	NS	***	NS	*	***	NS	**	*	***	***	***	***
T*L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 3. Vase life, postharvest characteristics, and quality of *Lilium* 'Dazzle' grown during year 3 at 10, 15, or 20 °C in 0% shade or at 10 or 20 °C in 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for dependent variables here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). Unmarketable stems, stem length, caliper, and flower length were taken at harvest. Bud count change during vase life evaluation was the number of buds at harvest minus the number of buds that opened during vase life. Dry weight was taken on stems that were dried on the day of harvest. Percent dry weight was (dry weight*100/fresh weight). Uptake in $ml \cdot g^{-1}$ fresh weight (fw) was calculated to account for differences in size resulting from treatments.

Treatment	Vase life (d)	Unmarketable stems (per crate)	Stem length (cm)	Caliper (cm)	Flower length (cm)	Blasted flowers (per stem)	Dry weight (g)	Percent dry weight	Uptake ($ml \cdot g^{-1}$fw)
				Temperature					
10	13.1 ab[z]	4.6 b	112.0 a	0.64 ab	9.5 b	0.03 b	4.6 a	11.2 a	3.5 b
15	14.1 a	4.2 b	106.9 b	0.63 ab	9.5 b	0.00 b	4.2 ab	11.1 ab	3.9 b
20	11.9 b	17.0 a	100.5 c	0.63 ab	9.9 a	0.00 b	3.2 bc	10.2 c	4.9 a

Table 3 Continued.

Started 10	12.3 b	4.7 b	111.7 a	0.66 a	9.5 b	0.39 a	3.9 ab	10.1 c	3.3 b
Started 20	12.0 b	18.4 a	99.3 c	0.62 b	9.3 b	0.08 b	3.0 c	10.5 bc	5.3 a
				Light					
0% shade		7.6 b	107.7 a	0.65 a		0.19 a	4.0 a	11.0 a	4.0 a
30% shade		12.6 a	105.9 ab	0.63 ab		0.23 a	3.2 b	10.1 b	4.5 a
Started 0%		7.2 b	106.4 ab	0.65 a		0.03 ab	4.1 ab	10.7 ab	3.9 a
Started 30%		11.7 a	104.4 b	0.62 b		0 b	3.8 ab	10.7 ab	4.3 a
Significance									
Temperature (T)	***	***	***	**	***	***	***	***	***
Light (L)	NS	***	*	**	NS	**	*	**	**
T*L	NS	NS	NS	NS	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 4. Uncorrected water uptake for *Lilium* 'Dazzle' grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). As presented here, treatments are grouped by starting temperature and light. Actual days spent in the final environment are presented. Water uptake was taken on day 7 of vase life and was calculated as the number of milliliters starting in the vase minus the number of milliliters left in the vase.

Initial		Final		Average days at final temp./light	Uptake (ml)
Temp. (°C)	Light (% shade)	Temp. (°C)	Light (% shade)		
10	0	10	0	75	132.8 abc[z]
		20	0	16	128.6 abc
		20	30	15	135.0 ab
	30	10	30	74	133.6 ab
		20	0	15	130.3 abc
15	0	15	0	60	110.5 c
		15	30	17	120.9 abc
	30	15	30	62	139.5 ab
		15	0	18	112.6 bc
20	0	20	0	56	137.4 ab
		10	0	28	145.2 a
		10	30	27	138.6 ab
	30	20	30	56	140.2 ab
		10	0	29	129.8 abc
Treatment					***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 4 Continued.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 5. Postharvest characteristics and quality of *Lilium* 'Dazzle' affected by a light by temperature interaction grown during year 3 at 10, 15, or 20 °C in 0% shade or at 10 or 20 °C in 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Here, treatments are grouped by starting temperature and light. Water uptake in ml and overall appearance rated from 0 (excellent) to 10 (poor) were taken on day 7. Bud count per stem and fresh weight were taken at harvest.

Initial		Final		Days at final				
Temp. (C°)	Light (% shade)	Temp. (C°)	Light (% shade)	temp./light	Uptake (ml)	Day 7 appearance	Bud count	Fresh weight (g)
10	0	10	0	59	149.8 bc[z]	1.1 c	3.9 a	45.1 a
		20	0	10	138.8 cd	3.0 ab	3.8 ab	43.6 a
		20	30	9	137.8 cd	2.6 bc	3.8 ab	42.8 a
	30	10	30	58	143.6 cd	1.9 bc	3.3 abc	36.1 bc
		20	0	10	130.0 d	3.0 ab	3.3 abc	35.9 bc
15	0	15	0	49	161.3 ab	1.4 bc	3.7 ab	41.3 ab
20	0	20	0	40	169.3 a	4.5 a	2.5 d	34.1 c
		10	0	4	169.8 a	2.7 abc	2.3 d	31.4 c
		10	30	3	163.4 ab	3.2 abc	2.6 cd	32.5 c
	30	20	30	40	185.0 a	2.5 abc	2.8 bcd	35.8 bc

Table 5 Continued.

	10	0	3	170.0 a	2.0 abc	2.4 d	31.5 c
Treatment				***	***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 6. Postharvest characteristics and quality of *Lilium* 'Vermeer' grown during year 1 at 15 °C, in 0, 30, or 60% shade or under 0% shade supplemented with high intensity discharge lighting (HID) or grown at 0 or 60% shade and moved to 60 or 0% shade two days or two weeks prior to harvest. Bud count and fresh weight were taken at harvest. Termination (term.) fresh and dry weights were taken on terminated stems. Uptake in ml of water per gram of fresh weight (at harvest) per day of vase life was calculated to account for differences in uptake as a result of varying vase lives and differences in stem size resulting from treatments.

Light (% shade)		Target	Days at final light	Bud count	Fresh weight	Term. fresh weight	Term. dry weight	Uptake
Initial	Final	days	(mean)	(per stem)	(g)	(g)	(g)	($ml \cdot g^{-1} fw \cdot d^{-1}$)
0	0	-[Z]	48	3.9 a[Y]	52.5 a	51.3 a	4.4 a	0.32 b
0	60	2	2	3.3 ab	45.2 ab	42.2 b	3.6 b	0.33 b
0	60	14	12	3.6 ab	47.2 ab	42.4 b	3.5 b	0.38 ab
30	30	-	51	2.4 b	39.5 b	36.9 b	3.2 bc	0.45 a
60	60	-	48	2.2 ab	36.2 b	31.4 b	2.6 c	0.42 ab
60	0	14	11	2.0 ab	36.3 ab	40.9 ab	3.7 abc	0.40 ab
HID	HID	-	48	3.4 ab	46.2 ab	44.1 ab	3.8 b	0.36 ab
Treatment				*	**	***	***	*

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Plants remained in treatment entire time.

[Y] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 7. Effects of temperature and light on carbohydrate levels in the inflorescence (minus tepals and anthers), leaves, stem, and tepals of *Lilium* 'Dazzle' grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for carbohydrates shown here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards and are presented as mg per gram dry weight. Putative glucosides identified are glycerol glucoside 1 (glgsd. 1) and glycerol glucoside 2 (glgsd. 2)

	Inflorescence		Leaves		Stem		Tepals	
	Glgsd. 1	Sucrose	Inositol	Starch	Glgsd. 2	Glgsd. 1	Glgsd. 2	Glgsd. 1
				Temperature				
10	7.5 a[z]	28.0 a	3.8 a	5.5 ab	29.3 a	8.8 ab	16.7 ab	6.0 ab
15	3.8 b	12.7 b	2.4 b	7.2 a	26.3 a	7.0 abc	15.2 bc	5.1 abc

Table 7 Continued.

20	4.0 b	20.5 ab	2.0 b	3.6 ab	9.9 b	2.7 c	8.6 c	2.4 c
Start 10	5.2 ab	21.5 ab	2.1 b	2.2 b	29.3 a	9.5 a	11.8 bc	3.7 bc
Start 20	6.3 ab	20.5 ab	3.1 ab	6.9 a	21.1 ab	4.8 bc	21.7 a	6.6 a
				Light				
0	4.8 b	18.1 b						4.5 b
30	4.4 ab	13.1 b						4.1 ab
Start 0	5.0 ab	21.5 ab						3.6 b
Start 30	7.2 a	29.8 a						6.8 a
Significance								
Temperature (T)	**	*	**	**	**	***	***	***
Light (L)	*	*	NS	NS	NS	NS	NS	**
T*L	NS	NS	NS	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 8. Treatment effects of temperature and light on carbohydrate levels in the inflorescence (minus tepals and anthers), leaves, stem, and tepals of *Lilium* 'Dazzle' grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Here, treatments are grouped by initial temperature and light. On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards and are presented as mg per gram dry weight. Putative glucoside identified is glycerol glucoside 2.

Initial		Final							
Temp.	Light	Temp.	Light	Inflorescence		Leaves	Stem		Tepals
(°C)	(% shade)	(°C)	(% shade)	Inositol	Glycerol glucoside 2	Sucrose	Glucose	Fructose	Inositol
10	0	10	0	4.0 a[z]	28.0 a	47.2 a	60.9 a	56.8 a	3.6 ab
		20	0	3.3 ab	19.6 ab	29.3 ab	20.0 d	15.6 c	5.6 ab
		20	30	3.3 ab	17.6 ab	19.7 ab	30.2 cd	22.6 c	5.8 a
	30	10	30	2.0 b	16.2 ab	27.4 ab	40.4 abcd	30.5 bc	2.3 b
		20	0	3.3 ab	21.5 ab	37.3 ab	31.6 cd	25.9 bc	5.7 a
15	0	15	0	2.6 ab	15.9 ab	7.0 b	28.5 cd	21.7 c	3.4 ab
		15	30	2.4 ab	14.5 ab	21.8 ab	19.5 d	19.6 c	3.9 ab

Table 8 Continued.

	30	15	30	3.1 ab	17.1 ab	29.0 ab	27.5 cd	23.5 c	3.3 ab
		15	0	3.5 ab	18.3 ab	31.8 ab	32.3 bcd	32.1 bc	3.4 ab
20	0	20	0	3.3 ab	10.9 b	23.2 ab	27.5 cd	15.4 c	2.7 ab
		10	0	3.6 ab	27.0 a	13.8 ab	49.3 abc	35.2 abc	4.3 ab
		10	30	3.1 ab	22.7 ab	39.4 ab	49.1 abcd	37.2 abc	3.8 ab
	30	20	30	2.8 ab	14.5 ab	7.1 b	37.3 abcd	24.8 c	4.3 ab
		10	0	3.7 ab	30.1 a	33.7 ab	60.2 ab	48.9 ab	4.1 ab
Treatment				*	***	**	***	***	*

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 9. Effects of temperature and light on carbohydrate levels in the inflorescence (minus tepals and anthers), leaves, stem, and tepals of *Lilium* 'Dazzle' grown during year 3 at 10, 15, or 20 °C in 0% shade or at 10 or 20 °C in 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for carbohydrates shown here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards. Inositol (inostl.), glycerol glucoside 2 (glgsd. 2), glycerol glucoside 1 (glgsd. 1), glucose (gluc.), fructose (fruc.), and sucrose (suc.) contents are presented in mg per gram dry weight.

	Inflorescence			Leaves					Stem			Tepals	
	Inostl.	Glgsd. 2	Glgsd. 1	Inostl.	Glgsd. 2	Glgsd. 1	Gluc.	Fruc.	Inostl.	Gluc.	Fruc.	Gluc.	Suc.
Temp													
10	3.1 b[Z]	70.0 abc	20.8 a	3.7 a	3.5 ab	0.36 ab	16.4 b	13.7 b	2.7 a	57.6 a	42.7 a		9.7 a
15	3.2 ab	97.3 a	29.2 a	2.3 ab	4.1 ab	0.40 ab	26.1 ab	22.6 ab	0.9 ab	55.5 ab	40.3 ab		5.7 ab
20	4.5 a	45.0 bc	9.7 bc	2.3 b	3.1 ab	0.14 ab	48.2 a	37.6 a	2.9 a	29.3 b	22.4 b		3.3 b

Table 9 Continued.

Started 10	3.6	ab	68.8	ab	20.4	ab	2.3	b	4.8	a	0.33	a	33.7	ab	27.1	ab	0.8	b	37.1	ab	27.9	ab		2.6 b
Started 20	3.8	ab	38.2	c	5.8	c	2.0	b	1.4	b	0	b	44.8	ab	35.3	ab	2.6	a	34.4	ab	25.5	ab		3.2 b
Light																								
0							3.1	a															154.5	b
30							1.4	b															312.3	a
Started 0							2.6	ab															106.9	b
Started 30							3.0	a															187.8	ab
Significance																								
Temp	*		***		***		**		*		*		*		*		***		**		**		NS	**
Light	NS		NS		NS		**		NS		NS		NS		NS		NS		NS		NS		*	NS
T*L	NS		NS		NS		NS		NS		NS		NS		NS		NS		NS		NS		NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 10. Treatment effects of temperature and light on carbohydrate levels in the stem of *Lilium* 'Dazzle' grown during year 3 at 10, 15, or 20 °C in 0% shade or at 10 or 20 °C in 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Here, treatments are grouped by starting temperature and light. On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards. Glycerol glucoside 1 and glycerol glucoside 2 contents are given in mg per gram dry weight.

Initial		Final		Stem	
Temp. (°C)	Light (% shade)	Temp. (°C)	Light (% shade)	Glycerol glucoside 2	Glycerol glucoside 1
10	0	10	0	32.5 ab[Z]	10.5 abc
		20	0	34.2 ab	11.7 ab
		20	30	36.5 a	12.1 a
	30	10	30	20.2 abc	4.9 abc
		20	0	37.1 a	11.1 ab
15	0	15	0	28.3 abc	9.5 abc
20	0	20	0	8.6 c	2.4 c
		10	0	10.9 bc	3.3 bc
		10	30	13.8 abc	3.4 bc
	30	20	30	27.6 abc	8.6 abc
		10	0	12.9 abc	2.4 bc
Treatment				***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 11. Vase life, postharvest characteristics, and quality of *Helianthus* 'Sunbright' grown during year 1 at 10, 15, or 20 °C or grown at 10 or 20 °C and moved to 20 or 10 °C (10→20 and 20→10, respectively) 2 days (2D) or 2 weeks (2W) prior to harvest. Water uptake, termination (term.) fresh and dry weights were taken at termination of vase life. Stem length, caliper, flower diameter (diam.), and fresh weight were taken at harvest. Corrected uptake was calculated using harvest fresh weight (fw).

Temperature(°C)		Target	Days at final	Vase life	Uptake	Stem length	Caliper	Flower diam.	Fresh weight	Term. fresh	Term. dry	Uptake ($ml \cdot g^{-1}fw \cdot d^{-1}$)
Initial	Final	days	Temp.	(d)	(ml)	(cm)	(cm)	(cm)	(g)	weight (g)	weight (g)	
10	10	-[Z]	52	12.9 a[Y]	192.5 a	72.1 a	0.64 a	1.67 a	19.4 a	20.1 a	2.17 a	0.77 c
10	20	2	4	10.4 ab	161.7 ab	68.3 ab	0.69 a	1.59 ab	19.5 a	19.3 a	1.94 ab	0.84 bc
10	20	14	11	10.9 ab	153.5 ab	59.5 ab	0.63 ab	1.54 ab	14.2 b	14.0 b	1.42 bc	0.99 ab
15	15	-	43	10.1 b	87.9 c	56.4 b	0.51 c	1.21 b	8.2 c	8.7 c	0.93 c	1.08 a
20	20	-	35	10.3 b	123.8 bc	60.6 ab	0.54 bc	1.72 a	10.4 bc	11.4 bc	1.17 c	1.12 a
20	10	2	6	11.5 ab	131.6 bc	63.7 ab	0.59 abc	1.61 ab	12.3 bc	11.8 bc	1.35 c	1.01 ab
20	10	14	14	11.1 ab	122.4 bc	58.0 b	0.61 abc	1.40 ab	11.6 bc	10.9 bc	1.21 c	1.07 a
Treatment				*	***	**	***	*	***	***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Plants remained in treatment entire time.

[Y] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 12. Vase life and stem length of *Helianthus* 'Sunbright' grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Here, treatments are grouped by starting temperature and light. Vase life was the number of days from harvest until half of ray florets were wilted, dried, or abscised. Stem length was measured at harvest.

Initial		Final		Avg. days	Vase	Stem
Temp. (°C)	Light (% shade)	Temp. (°C)	Light (% shade)	at final temp./light	life (days)	length (cm)
10	0	10	0	70	13.5 abc[Z]	64.8 abc
		20	0	9	13.8 abc	63.5 bcd
		20	30	10	13.6 abc	63.8 bcd
	30	10	30	67	15.5 a	66.2 ab
		20	0	12	12.9 bc	59.3 cde
15	0	15	0	60	13.1 bc	63.0 bcd
		15	30	18	13.1 bc	70.7 a
	30	15	30	63	14.8 ab	66.0 abc
		15	0	20	12.7 bc	64.2 abc
20	0	20	0	56	12.3 c	62.3 bcde
		10	0	19	14.4 abc	60.9 bcde
		10	30	21	14.6 abc	61.9 bcde
	30	20	30	60	10.2 d	57.2 de
		10	0	10	14.1 abc	56.1 e
Treatment					***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 13. Vase life, postharvest characteristics, and quality of *Helianthus* 'Sunbright' grown during year 1 at 15 °C, in 0, 30, or 60% shade or under 0% shade supplemented with high intensity discharge lighting (HID) or grown at 0 or 60% shade and moved to 60 or 0% shade (0→60 and 60→0, respectively) 2 days (2D) or 2 weeks (2W) prior to harvest. Water uptake was taken at termination of vase life. Stem length, caliper, flower diameter (diam.), and fresh weight were taken at harvest. Termination (term.) fresh and dry weights were taken on terminated stems. Percent dry weight equals (term. dry weight*100/term. fresh weight). Uptake in ml of water per gram of fresh weight (at harvest) per day of vase life was calculated to account for differences in uptake as a result of varying vase lives and differences in stem size.

Light (% shade)		Target	Actual days	Uptake	Stem	Caliper	Flower	Fresh	Term. fresh	Term. dry	Uptake
Initial	Final	days	(mean)	(ml)	length (cm)	(cm)	diam. (cm)	weight (g)	weight (g)	weight (g)	($ml \cdot g^{-1} d^{-1}$)
0	0	-[Z]	39	115.6 ab[Y]	61.5 a	0.58 a	2.27 a	13.1 ab	12.5 ab	1.34 a	0.88 b
0	60	2	5	116.9 ab	57.2 ab	0.62 a	2.46 a	13.0 ab	11.7 ab	1.21 a	0.87 b
0	60	14	16	116.1 abc	54.3 abc	0.60 a	2.36 a	11.3 b	10.1 b	1.15 a	1.14 a
30	30	-	44	77.4 cd	44.5 c	0.47 b	1.76 b	6.9 c	5.7 c	0.71 b	1.16 a
60	60	-	48	68.0 abcd	41.6 c	0.40 b	1.59 b	4.2 c	4.5 c	0.51 b	1.10 ab
60	0	2	12	77.4 bcd	45.1 bc	0.43 b	1.70 b	5.2 c	5.1 c	0.61 b	1.08 ab
60	0	14	19	68.0 d	42.9 c	0.42 b	1.66 b	5.3 c	4.8 c	0.59 b	1.14 a
HID	HID	-	36	139.9 a	61.8 a	0.61 a	2.40 a	14.9 a	14.3 a	1.41 a	0.86 b
Treatment				***	***	***	***	***	***	***	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Plants remained in treatment for entire experiment.

[Y] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 14. Postharvest characteristics, and quality of *Helianthus* 'Sunbright' grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for dependent variables presented here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). Caliper, flower diameter, and fresh weight were taken at harvest. Dry weight was taken on stems that were dried on the day of harvest. Percent dry weight was (dry weight*100/fresh weight). Uptake was taken on day 7 of vase life and uptake in $ml \cdot g^{-1}$ fresh weight (fw) was calculated to account for differences in size resulting from treatments.

	Uptake (ml)	Caliper (cm)	Flower diameter (cm)	Fresh weight (g)	Dry weight (g)	Percent dry weight	Uptake ($ml \cdot g^{-1}$fw)
				Temperature			
10	122.1 a[Z]	0.64 a	1.63 a	18.3 a	1.61 a	10.2 a	6.7 b
15	88.8 bc	0.58 bc	1.42 b	13.6 bc	1.27 b	9.7 ab	6.6 b
20	102.3 b	0.51 d	1.32 bc	10.4 d	0.87 c	9.0 b	9.5 a

Table 14 Continued.

Started 10	93.0 b	0.62 ab	1.55 a	14.6 b	1.27 b	8.9 c	6.5 b
Started 20	75.9 c	0.55 cd	1.20 c	11.8 cd	1.05 bc	9.7 ab	6.6 b
			Light				
0%	113.4 a	0.64 a	1.57 a	16.5 a	1.44 a	9.8 a	
30%	80.5 b	0.52 c	1.30 b	11.2 b	0.96 b	9.3 ab	
Started 0%	105.5 a	0.59 b	1.50 a	15.0 a	1.39 a	9.9 a	
Started 30%	86.2 b	0.57 bc	1.33 b	12.3 b	1.06 b	9.1 b	
Significance							
Temperature	***	***	***	***	***	***	***
Light	***	***	***	***	***	**	NS
Temperature*Light	NS	NS	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 15. Flower diameter and uncorrected water uptake of *Helianthus* 'Sunbright' grown in year 3 at 10, 15, or 20 °C in 0% shade or at 10 or 20 °C in 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Treatments are grouped by starting temperature and light conditions. Flower diameter was measured across the inflorescence at time of harvest and uptake was taken on day 7 of vase life.

Initial		Final		Days at final temp/light	Flower diameter (cm)	Uptake (ml)
Temp. (C°)	Light (% shade)	Temp. (C°)	Light (% shade)			
10	0	10	0	43	1.54 ab[Z]	82.3 abc
		20	0	15	1.71 a	93.8 ab
		20	30	16	1.56 ab	76.0 abc
	30	10	30	46	1.15 de	91.4 abc
		20	0	16	1.44 abc	70.2 abc
15	0	15	0	36	1.36 bcd	92.2 abc
20	0	20	0	35	0.98 e	74.0 abc
		10	0	11	1.16 cde	96.6 a
		10	30	13	1.22 cde	74.6 abc
	30	20	30	36	0.97 e	60.9 bc
		10	0	14	1.00 e	62.6 c
Treatment					***	

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 16. Vase life, postharvest characteristics, and quality of *Helianthus* 'Sunbright' grown in year 3 at 10, 15, or 20 °C in 0% shade or at 10 or 20 °C in 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for dependent variables here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). Vase life was the number of days from harvest until half of ray florets were wilted, dried, or abscised. Stem length, caliper, and fresh weight were taken at harvest. Two subsample stems from each replicate were dried. Percent dry weight is (dry weight*100/fresh weight). A corrected water uptake in ml per gram fresh weight (fw) accounts for differences in size resulting from treatments.

	Stem length (cm)	Caliper (cm)	Fresh weight (g)	Dry weight (g)	Uptake ($ml \cdot g^{-1} fw$)
			Temperature		
10	44.6 a[Z]	0.69 a	15.0 a	1.51 a	
15	42.8 ab	0.66 ab	14.6 ab	1.41 ab	
20	35.1 cd	0.57 b	10.2 c	1.07 b	
Started 10	39.7 bc	0.64 ab	13.1 abc	1.33 ab	
Started 20	35.4 d	0.58 b	11.3 b	1.13 ab	
			Light		
0%	40.7 a	0.66 a	15.0 a	1.45 a	6.0 ab
30%	38.0 a	0.61 ab	11.4 b	1.15 ab	7.6 a
Started 0%	40.9 a	0.64 ab	13.7 ab	1.43 ab	5.1 b

Table 16 Continued.

Started 30%	38.4 a	0.59 b	11.2 b	1.13 b	5.6 ab
Significance					
Temperature (T)	***	***	***	**	NS
Light (L)	*	*	***	**	*
T*L	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 17. Effects of temperature and light on the carbohydrate contents of *Helianthus* 'Sunbright' inflorescences (minus ray florets), leaves, ray florets, and stems grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in and moved to 10 °C in 0% shade for all temperatures or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for carbohydrate contents presented here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards and are given in mg per gram dry weight.

	Inflorescence		Leaves		Ray Florets		Stem		
	Inositol	Glucose	Sucrose	Starch	Fructose	Starch	Glucose	Fructose	Stachyose
Temp.									
10	3.8 ab[Z]	102.1 a	6.7 a		29.6 b		107.5 a	27.7 ab	1.6 a
15	3.4 ab	96.4 a	2.2 ab		58.6 a		94.4 ab	27.8 a	0.1 b
20	4.0 ab	71.6 ab	0.1 b		26.8 b		55.4 c	12.2 c	0.3 b
Started 10	3.1 b	55.3 b	2.5 ab		54.1 ab		39.4 c	17.1 bc	0.8 ab

Table 17 Continued.

Started 20	4.5 a	93.9 a		2.5 ab	55.4 ab		81.3 bc	28.7 a	0.1 b
			Light						
0			2.5 ab			3.7 ab	90.5 a		
30			3.2 ab			19.6 a	61.3 b		
Started 0			3.7 a			0.9 ab	72.3 ab		
Started 30			0.8 b			0 b	78.3 ab		
Significance									
Temp	*	***	NS	*	**	NS	***	***	***
Light	NS	NS	*	NS	NS	*	*	NS	NS
T*L	NS	NS	NS	NS	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 18. Inositol content of *Helianthus* 'Sunbright' leaves grown during year 2 at 10, 15, or 20 °C in 0% shade or 30% shade or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in and moved to 10 °C in 0% shade for all temperatures or grown at 15 °C in 0% or 30% shade and moved to 30 or 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Treatments are grouped by starting conditions. At harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards and are presented as mg per gram dry weight.

Initial Temp. (°C)	Light (% shade)	Final Temp. (°C)	Light (% shade)	Leaves Inositol	
10	0	10	0	2.4	abc[Z]
		20	0	1.7	c
		20	30	2.6	abc
	30	10	30	3.3	a
		20	0	1.9	bc
15	0	15	0	1.7	c
		15	30	1.7	c
	30	15	30	2.0	c
		15	0	2.4	abc
20	0	20	0	2.1	abc
		10	0	2.9	ab
		10	30	3.1	ab
	30	20	30	1.6	c
		10	0	2.7	abc
Treatment				***	

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 19. Effects of temperature and light on carbohydrate levels in the inflorescence (minus ray florets), leaves, ray florets, and stem of *Helianthus* 'Sunbright' grown during year 3 at 10, 15, or 20 °C in 0% shade or 30% shade (10 and 20 °C only) or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). Simple effects were not significant for carbohydrates shown here, thus all treatments were grouped into temperature main effects (10, 15, or 20 °C or started 10 °C or started 20 °C) and light main effects (0 or 30% shade or started 0% or started 30%). On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards and are given as mg per gram dry weight. The putative glycerol glucoside is unknown carbohydrate 2 (UK 2).

	Leaves		Ray florets			Stem			
	Glucose	Fructose	Inositol	UK 2	Glucose	Inositol	UK2	Glucose	Stachyose
				Temperature					
10	2.0 b[Z]	2.3 b	4.8 ab		31.4 b	2.8 b	1.9 a	49.0 ab	4.8 ab
15	10.1 ab	6.4 ab	3.3 ab		82.5 ab	1.7 b	0.2 ab	78.2 a	4.1 ab
20	16.8 a	12.9 a	1.8 b		57.1 ab	2.2 b	1.4 ab	34.9 bc	9.4 a
Started 10	7.5 ab	7.3 ab	3.9 ab		67.3 ab	3.8 ab	0.3 b	23.5 c	2.1 b

Table 19 Continued.

Started 20	9.6 ab	8.3 ab	5.7 a		79.9 a	5.0 a	0.2 b	29.2 bc	5.2 ab
				Light					
0			4.3 ab	1.0 b	65.3 ab	3.3 ab			
30			6.6 a	6.8 a	95.1 a	4.9 a			
Started 0			2.4 b	1.6 ab	49.4 ab	2.1 b			
Started 30			2.3 b	0.8 ab	44.8 b	1.9 b			
Significance									
Temp	*	*	*	NS	*	***	*	***	*
Light	NS	NS	*	*	*	**	NS	NS	NS
T*L	NS	NS	NS	NS	NS	NS	NS	NS	NS

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

Table 20. Treatment effects on carbohydrate levels in the leaves of *Helianthus* 'Sunbright' grown during year 3 at 10, 15, or 20 °C in 0% shade or 30% shade (at 10 and 20 °C only) or started at 10 in 0 or 30% shade and moved to 20 °C in 30 or 0% shade, respectively, or started at 20 in 0 or 30% shade and moved to 10 °C in 30 or 0% shade, respectively, or started at 10 and moved to 20 °C or started at 20 in 0% shade and moved to 10 °C in 0% shade approximately 2 weeks before harvest (for all treatments that were moved between environments). On the day of harvest, tissues were flash frozen with liquid nitrogen, stored at -20 °C until they were freeze dried, then carbohydrates were extracted in 80% ethanol. Carbohydrates were identified based on retention time of authentic standards and are given in mg per gram dry weight.

Initial		Final		Leaves		
Temp. (C°)	Light (% shade)	Temp. (C°)	Light (% shade)	Inositol	Sucrose	Stachyose
10	0	10	0	2.2 cd[Z]	4.2 ab	0 b
		20	0	2.2 d	2.6 ab	0 b
		20	30	2.6 bcd	0.6 b	0 b
	30	10	30	3.8 abc	0.7 b	0 b
		20	0	2.5 bcd	0.8 b	0 b
15	0	15	0	4.8 a	2.9 ab	0 b
20	0	20	0	2.5 bcd	0.9 b	0.98 ab
		10	0	4.1 ab	1.4 b	0.30 ab
		10	30	2.8 bcd	1.6 b	1.35 a
	30	20	30	2.8 bcd	9.7 a	0 b
		10	0	3.5 abcd	0.2 b	1.01 ab
Treatment				***	*	***

[NS],*, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

[Z] Means followed by the same letter are not significantly different according to Tukey's procedure ($P \leq 0.05$).

APPENDIX

APPENDIX 1

Termination Rating Scale-*Rosa* Experiments 2-10

Openness stages

0: Tight-petals upright, some outer petals may be slightly reflexed
1: Medium – all whorls beginning to reflex
2: Open – Outer whorls completely reflexed, all whorls reflexing to a high degree
3: Blown – stamen visible

Termination reasons (0-10) *All ratings are based on 0: no problem to 10: most severe*

Bent neck (BN)—See Figure 1

0: neck tissue is hard
1: neck tissue beginning to soften
2: slight 10-20° nod
3-4: 30-80° nod
5: 90° nod
6-9: 100-150°
10: head of flower touching stem

Wilted petals (WP)—See Figure 2

0: completely firm
3: petals are slightly "soft" or velvety to touch but don't really wilt (normal non-wilted appearance after 10 days or so of vase life)
6: petals very "soft" or velvety to touch, but still don't show wilting visibly
7: tips of some of the petals are slightly limp
8: wilting is prominent on most of the petals (can be a major reason for termination of stem)
9: wilting is prominent; oxidative browning and softening are visible on a good deal of the flower
10: nearly all petals are very wilted; oxidative browning is severe

Black tips (BT)—See Figure 3

0: no black tips
1-2: 1-4 black tips
3: more than 4 black tips or one entire petal black and crispy
4: 40% of flower has black tips
5: 50% of flower has black tips or two entire petals black and crispy
6: 60% of flower has black tips
7: 70% of flower has black tips or three entire petals black and crispy

8: 80% of flower has black tips
9: 90% of flower has black tips or four entire petals black and crispy
10: 100% of flower has black tips

Petal discoloration (PD)—See Figures 4 and 5
0: no brown spots
1-2: 1-4 brown spots
3: more than 4 brown spots or one entire petal brown and crispy
4: 40% of flower has brown spots
5: 50% of flower has brown spots or two entire petals brown and crispy
6: 60% of flower has brown spots
7: 70% of flower has brown spots
8: 80% of flower has brown spots
9: 90% of flower has brown spots
10: 100% of flower has brown spots

Petal blueing (PB)—Figure 6
0: red, can be lighter or darker than came out of box
3: red, just starting to show hints of pink or purple
4: slightly more purple than 3 *or* a flower that has petal lightening and one or two outer whorls of petals that are light purple
5: flower color is still only slightly purple, is still mostly red *or* a flower that has petal lightening with fuschia inner whorls and three or four whorls of outer petals that are purple
6: flower color is dark fuschia
7: flower color is mostly purple with some red still showing *or* flower color is not a severe purple
8: flower is entirely medium purple
9: dark purple
10: very dark purple

Other symptoms:

Leaf Drop (LD) and chlorosis: Leaves fall off, usually due to phytotoxicity, also if leaves are chlorotic, or crispy, to be checked, symptom must be mostly present

Neck Rot—See Figure 7: Botrytis infection in neck and receptacle tissue; appears brown; can cause the heads to fall off, symptom checked if any brown soft tissue present

Black Stem (BS): Black areas on stems, usually at nodes or on neck when softening is present; symptom checked if condition present at slight to severe degree

Note: Rot is often present when neck of flower is still hard, while black stem is characteristics of softening of neck.

Overall appearance (0-10): 0=perfect condition, 10=severe unsightliness; may be independent of other termination reasons if stem is unsightly for another reason, i.e. split heads

All photos courtesy of Erin M. Regan

Figure 1. Bent neck, rating of 5.

Figure 3. Black tips, rating of 2.

Figure 2. Petal wilting, rating of 8.

Figure 4. Petal discoloration, brown spotting, discoloration rating of 5.

Figure 5. Petal discoloration, brown crisping, a symptom of botrytis infection, discoloration rating of 7.

Figure 7. Neck rot caused by botrytis infection.

Figure 6. Petal blueing, flower on left, blueing=6-7; flower on right, blueing=1-2.