

REVIEW

Role of Sugars in Senescence and Biosynthesis of Ethylene in Cut Flowers

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Abstract

The role of sugars in the prolongation of the vase life of cut flowers was reviewed. Beneficial effect of sugars on the supply of substrates for respiration and, therefore, on longer life of cut flowers is generally recognized. This widely accepted role of sugars as providers of additional substrates for respiration has perhaps largely over-shadowed other important roles. In this review, attempts were made to study the role of sugars in the prolongation of the vase life of cut flowers in general, and in the delay in ethylene biosynthesis or decrease in sensitivity to ethylene in particular.

Discipline: Postharvest technology

Additional key words: vase life, sensitivity to ethylene, substrates for respiration, water balance

Introduction

Role of sugars in the senescence of cut flowers had been extensively reviewed previously⁹ and has been updated recently³⁰. However, very little coverage has been given to the role of sucrose in the biosynthesis of ethylene⁵ or sensitivity to ethylene²⁴. Very recently, however, the beneficial effect of sugars on the prolongation of the flower vase life in several species has been attributed to the suppression of ethylene biosynthesis or sensitivity to ethylene. Thus, it appears that the role of sucrose in the senescence of cut flower species is not fully understood.

Longevity of flower has been associated with the sugar content of the flower since the late 1950s¹. The vase life of flowers with a higher sugar content was longer, whereas that of flowers with a lower sugar content was shorter¹². This beneficial effect of sugars on flower senescence was attributed to the supply of substrates for respiration, structural materials and osmoticum⁹. This holds true for cut flowers too because cut flowers are devoid of food, hormones and water supply after detachment from the plant³¹ and depend solely

on stored food at the time of harvest and on the application of exogenous sugars. Exogenous application of sucrose supplies the flower with much needed substrates for respiration and not only prolongs the vase life¹³ but also enables cut flowers harvested at the bud stage to open, which otherwise would not occur naturally⁷. Thus, sugars with biocides have become an important commercial preservative for several cut flowers.

Recently, the beneficial effect of sugars during senescence of many types of cut flowers; namely sweet pea¹⁷, *Delphinium*¹⁵, *Gentiana*³², snapdragon¹⁴, rose²¹ and *Oncidium*⁴ has been attributed to the suppression of ethylene biosynthesis or sensitivity to ethylene. The role of sugars in the senescence of cut flowers, in particular ethylene-sensitive flowers is in sharp contrast with the conventional wisdom according to which sugars are “suppliers of substrates for respiration”, although some earlier reports indicated the suppression of ethylene biosynthesis or sensitivity to ethylene by sucrose in carnation flowers. Thus, the role of sugars in flower senescence should be elucidated. Do sugars provide only substrates for respiration, structural support and improvement of the water balance or do they, in addition, interfere with ethylene biosynthesis or sensitivity? No

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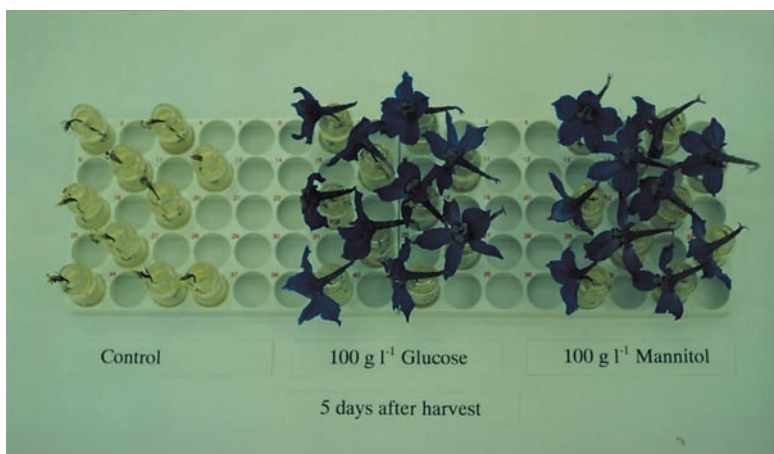


Fig. 1. Effects of glucose and mannitol on the abscission of cut *Delphinium* sepals
 Cut flowers were placed in a solution containing 200 mg L⁻¹ 8-hydroxyquinoline sulfate (HQS, a germicide) and 100 g L⁻¹ glucose (middle), 100 g L⁻¹ mannitol (right) or lacking carbohydrates (control; left) at 23°C for 5 days.



Fig. 2. Cut 'Wendy' roses treated with water (left) and 10 g L⁻¹ glucose and 10 g L⁻¹ fructose supplemented with 200 mg L⁻¹ HQS for 7 days (right)

paper had addressed this issue (interference of sugars with ethylene biosynthesis or sensitivity) to understand biochemical or molecular mechanisms, when this review was prepared.

In the present context, it is more important to understand the role of sugars in the delay of flower senescence. Research is currently focused on pre-harvest factors such as light that is known to influence the sugar content of flowers during the growth period and consequently to influence postharvest longevity. The prolongation of the vase life of cut flowers at high light intensities during the growth period has been associated with the increase in the carbohydrate content of flowers²⁶. Further supporting

this hypothesis, recently, the prolongation of the vase life of *Delphinium* cut flowers at high light intensities (70 or 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) during the growth period has been attributed to the increase in the sugar content (personal communication, K. Tanase and K. Ichimura, 2003) and decrease in ethylene production (personal communication, K. Tanase and K. Ichimura, 2003). Similarly, supplementary pre-harvest irradiance (100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) influenced the quality and opening of campanula (*Campanula carpatica*) flowers and decreased endogenous ethylene production²⁸. These factors suggest the existence of some relationships between sugars and ethylene production during flower senescence. Previous investi-

gations on cut flowers showed that in the flowers grown at a higher light intensity, longevity was extended in carnation²⁴ and chrysanthemum¹⁹.

In this review, therefore, attempts were made to examine the role of sugars in the senescence of cut flowers, with reference to their role in the suppression of ethylene biosynthesis or sensitivity to ethylene. For the sake of simplicity, the role of the sugars was classified into the following 4 categories: supply of substrates for respiration, maintenance of an adequate water balance, decrease in sensitivity to ethylene, delay in climacteric ethylene biosynthesis.

Supply of substrates for respiration

Exogenous sugars extended the vase life of several cut flowers; namely *Heuchera sanguinea* Engelm flowers¹¹, *Limonium*⁵, spray carnations², *Liatris spicata*¹⁰, sweet pea¹⁷, *Delphinium*¹⁵, *Gentiana*³², snapdragon¹⁴, carnations⁵, *Eustoma*¹⁶, rose²¹ and *Oncidium*⁴. The prolongation of the vase life was attributed to the additional supply of sugars that provide extra food or substrates for respiration to flowers. Additional supply of substrates for respiration resulted in a higher respiration rate and in a longer vase life, thereby increasing the longevity of carnation flowers²⁵. Sugars also supplied materials for building structures for the plant organs and contributed to cell wall synthesis. Several types of sugars (glucose, mannitol) are beneficial to the prolongation of the vase life of cut flowers (Fig. 1). Prolongation of the vase life of several cut flowers by sugars was attributed to the synthesis of cell walls¹³. Among the different types of sugars, sucrose has been found to be the most commonly used sugar in prolonging the vase life of cut flowers.

Sucrose also promoted bud opening of several cut flowers such as spray carnations², *Liatris spicata*¹⁰, *Gypsophila*⁷, *Heuchera sanguinea* Engelm flowers¹¹, hybrid *Limonium*⁶, gladiolus floret¹⁸, and rose (Fig. 2, K. Ichimura, unpublished data) by supplying much needed food for petal expansion. Sugars during bud opening supply energy and the carbon skeleton required for the floral structure⁶.

Maintenance of an adequate water balance

The prolongation of the vase life of cut flowers by sugar application has also been attributed to the increase in the uptake of water by the flowers. Sucrose at lower concentrations prolonged the vase life of gladiolus florets by increasing the uptake, whereas higher concentrations seemed to impede the uptake³. It is suggested that the increase in the water uptake by sucrose treatments could

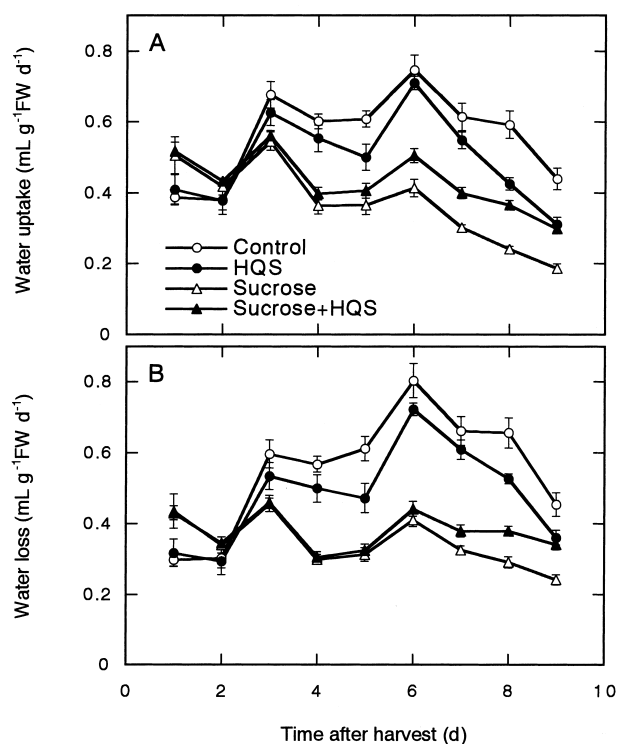


Fig. 3. Water uptake (A) by and loss (B) from cut 'Sonia' rose flowers treated with water (control), 200 mg L⁻¹ HQS, 20 g L⁻¹ sucrose or 20 g L⁻¹ sucrose + 200 mg L⁻¹ HQS

Values are means of 4 measurements \pm SE.
FW: Flower fresh weight.

be due to the increase in the osmotic concentration of the florets and leaves. In contrast, the uptake of solution with sucrose was not increased in rose except at day 1 (Fig. 3, K. Ichimura, unpublished data) or in *Grevillea*²² flowers. However, sucrose has been found to decrease water loss from the gladiolus leaves³ or rose petals (Fig. 3, K. Ichimura, unpublished data), thereby maintaining a positive water balance in the spike³ or flower. It is suggested that sucrose induces the closure of stomata, eventually reducing the loss of water in gladiolus leaves³ or rose petals²³, thereby reducing transpiration and maintaining the fresh weight. Similarly, in another cut rose cv. Cara Mia, application of sucrose during initial hydration was found to reduce the uptake⁸. It is, therefore, suggested that sugars may be effective in the maintenance of an adequate water balance in cut flowers by the reduction in the loss of water and not due to the increase in uptake⁸.

Decrease in sensitivity to ethylene

The decrease in the sensitivity to ethylene in carnation flowers treated with sucrose was recorded as early as in the mid-seventies²⁴. Besides, other sugars (glucose

Table 1. Effects of glucose and mannitol on the sensitivity to ethylene of cut *Delphinium*

Carbohydrate	Ethylene concentration ($\mu\text{L L}^{-1}$)	Time to sepal abscission (days)
Control	0	1.3 \pm 0.2
	2.5	0.3 \pm 0.2
	5	0.0 \pm 0.0
Glucose	0	7.2 \pm 0.3
	2.5	7.3 \pm 0.4
	5	6.9 \pm 0.4
Mannitol	0	7.4 \pm 0.4
	2.5	7.3 \pm 0.7
	5	6.8 \pm 0.7

All the carbohydrates were applied at 0.55 M. Cut flowers were exposed to 2.5 or 5 $\mu\text{L L}^{-1}$ ethylene for 24 h. Values are means of 12 flowers \pm SE.

and mannitol) have been found to reduce the sensitivity to ethylene of *Delphinium* flowers (Table 1)¹⁵. The mode of action of ethylene sensitivity reduction by sugars is unclear. It has, however, been suggested that the reduction in sensitivity to ethylene may be due to the accumulation of carbohydrates and not to the increase in osmolarity alone or suppression of the expression of the genes responsible for the sensitivity to ethylene¹⁵.

Delay in climacteric ethylene biosynthesis

Although, since the mid-seventies, sucrose has been reported to delay auto-catalytic ethylene production in carnation flowers⁵, few studies have been carried out in this field for more than 25 years. This is presumably because of the "strong notion" that sugars act in prolonging the vase life of cut flowers by providing "additional food" or "substrates" for respiration. Recently, it has been suggested that the beneficial effect of sugars could also be due to a delay in climacteric ethylene production and decrease in sensitivity to ethylene. Sugars delayed ethylene production in sweet pea (Fig. 4)¹⁷, *Delphinium*¹⁵, *Gentiana*³², snapdragon¹⁴, carnations⁵, rose²¹, and *Oncidium*⁴. However, the mode of action of the delay in ethylene biosynthesis by sugars has not been elucidated²⁷.

Current knowledge suggests that sugars are effective in prolonging the vase life of cut flowers by providing additional substrates for respiration, improving the water balance, delaying ethylene production and decreasing the sensitivity to ethylene. There is however, a lack of understanding of the mechanism of action of sugars in the delay in climacteric ethylene production or decrease in sensitivity to ethylene. The delay in climacteric ethylene

production may involve some inter-relationships between sugars and ethylene.

The senescence pattern of sucrose-treated spray carnation cv. Barbara was associated with a delay in the climacteric ethylene peak, followed by loosening and or drying of the outer or innermost petals or both (Pun and Ichimura, unpublished data). The lack of in-rolling of carnation petals (typical in-rolling when ethylene is involved) treated with sucrose may suggest the existence of a delay in the cysteine proteinase activity by sucrose. Previously, the increase in the cysteine proteinase activity had been attributed to the in-rolling of carnation petals²⁹ and it had been suggested that sugars delayed the expression of a protease gene³⁰. Does this mean that sucrose plays a dual role in the delay of ethylene production and inhibition of in-rolling of petals? Several other questions can also be raised such as: Do petal drying symptoms in sucrose-treated flowers (lack of typical in-rolling of petals) appear as a consequence of exhaustion of sugars and hence are petals sacrificed during relocation of food (priority being ovary and not petals)? Is the inhibition of in-rolling in petals due to a delay in or inhibition of the cysteine proteinase activity?

A recent report indicated that two separate genes are responsible for ethylene production and in-rolling of petals in carnation²⁰. It is suggested that sucrose may temporarily impair the activity of the enzymes involved in ethylene biosynthesis; namely 1-aminocyclopropane-1-carboxylic acid (ACC) synthase or ACC oxidase or both,

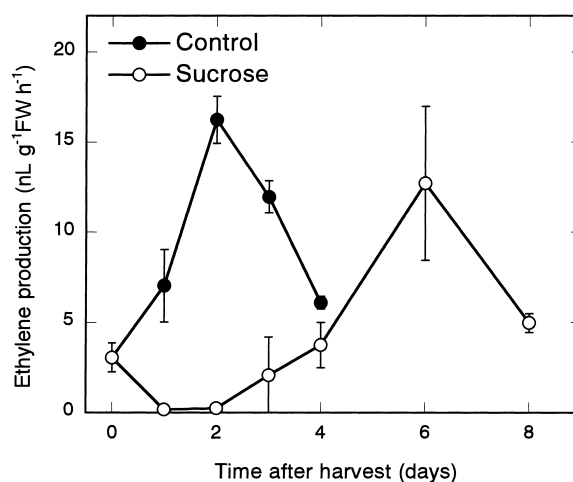


Fig. 4. Changes in ethylene production of cut sweet pea florets with time

Cut flower spikes with single florets were put in the vase water containing 200 mg L⁻¹ HQS (control), and 100 g L⁻¹ sucrose was added to the solution throughout the experimental period (sucrose). Values are means of 4 replications \pm SE. FW: Flower fresh weight.

thereby delaying ethylene production and prolonging the vase life. Similarly, sucrose may delay the expression of the genes responsible for in-rolling in carnation petals because sucrose-treated flowers do not display in-rolling of petals but the petals become loose and dry from the tips in the outer or the inner petals or both. The senescence pattern of the sucrose-treated petals is intermediate between that of control carnation flowers showing typical in-rolling and that of flowers treated with silver thiosulphate (STS) that exhibit drying of petals or necrosis, implying the suppression of typical in-rolling of petals.

Conclusion

This review highlighted the important role of sugars in extending the longevity of cut flowers. In addition to other roles of sugars, it is apparent that the influence of sugars on the delay in ethylene biosynthesis or decrease in sensitivity to ethylene is important for extending flower longevity. However, there is a lack of information about the mechanism(s) of action of sugars in the biosynthesis of or sensitivity to ethylene during the senescence of cut flowers. To fully understand the role of sucrose in the delay of senescence in cut flowers, the biochemical and molecular role of sucrose in the biosynthesis of ethylene or sensitivity to ethylene should be elucidated.

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