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Development of Flowers and Changes in Various Sugars during Opening of Cut Carnations[1]

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Abstract. **Bud-cut carnations kept in opening solutions had about the same diameter, weight, and vase-life as those cut when mature. For opening solutions, sucrose (30g/liter) appeared to be more efficient than glucose. The flower quality at full opening was better with sucrose although the vase-life was slightly longer with glucose. The flower development seemed to depend on the exogenous sugar supply and on the concomitant accumulation of soluble reducing sugars. When cut carnation flowers were supplied with a solution of ^{14}C glucose, only a fraction of the glucose was transformed into sucrose in the stem. The level of ^{14}C hexoses rose in petals, resulting from sucrose hydrolysis in the petals and from glucose directly translocated. A strong isomerase activity occurred in the petals. The leaves had no particular function in the translocation and transformation of sugars. These results are different from those reported earlier for roses.**

For some time, it has been recommended that carnations be harvested in the bud stage (2, 7). Although flowers harvested in the tight bud stage offer numerous advantages, they are incapable of developing to the commercial stage if placed in only water (13). To open and develop, they must be provided with a suitable nutritive solution (opening solution). Such solutions have been perfected, but their mechanism of action is not well known.

Since senescence of cut flowers is closely related to depletion of energy required for synthetic reactions (16), an exogenous sugar supply is recommended as the most efficient means to delay their senescence (1, 5, 8, 9, 11). A glucose supply prevents a sharp decrease in the amount of soluble proteins in petals (14). Kaltaler and Steponkus (6) suggested that the main effect of applied sugars is to maintain mitochondrial structure and function. Variations on the water balance also influence the senescence of cut flowers. When cut flowers are placed in water, the rate of water uptake declines rapidly, while the rate of transpiration continues relatively unchanged until there is a loss of turgor. The reduction in water uptake by the stem is often due to vascular blockage, particularly at the stem base. To maintain water uptake and meet energy requirements of the developing flowers, opening solutions contain a sugar, usually glucose or sucrose, and other substances (acidifying agent, antiseptic agent and an agent to precipitate calcium carbonate and fluorides) to inhibit vascular blockage (18).

The purpose of this work was twofold: first, to compare the morphology of flowers opening on the plant and ones opening in solution, and second, since the mode of action of the nutritive solutions is not well known, to study changes in sugars in various portions of the flower during bud opening.

Methods and Materials

Plant material. All experiments were performed with carnations (*Dianthus caryophyllus* L. cv Scania). The plants were grown under standard cultural practices in a polyethylene greenhouse. Cut flower stems (45 cm in length) were placed in opening or basic solution immediately after cutting and opened in a controlled temperature room at 23°C. A 12 hr photoperiod was provided by fluorescent lights (Phillips daylight BBdt 65/35) with a light intensity of 12 w/m^2 at the top of the corolla. The relative humidity was maintained at 40%. The bud opening solution used was the commercial preservative Sevaflor (Elysees 2000, Paris) containing an antiseptic agent, an acidifying agent, and a precipitating agent, to which were added 30 g of glucose (0.16M) or sucrose (0.08M) per liter. For the control lots a basic solution containing the same substances except sucrose or glucose was used.

For the morphological study, the rate of opening, the quality of opened flowers, and the vase-life of blooms were measured. The quality of open flowers was determined by measuring the diameter and weight of the fully opened flower, cut at the base of the ovary. Four stages characterized the flower opening:

Stage 0: very tight bud: 10 to 15mm of petals emerging from the calyx. The bud was pointed. This stage corresponds to that of early harvest.

Stage 1: tight bud: the bud was no longer pointed. The sepals enclosed the floral bud over half its length.

Stage 2: opening bud: the petals beginning to open.

Stage 3: pre-blooming: the outer petals were opened and horizontal, and perpendicular to the stem. This is the commercial stage.

The vase-life was estimated (12) giving the flower a grade each day between 0 and 2 according to its developmental stage (Table 1). The eventual anomalies (change in color, crumpling, etc.) gave rise to a decrease in the score (1/2 to 1 grade). The vase-life was considered to be over when the total grade fell below 15 (for a sample of 15 flowers).

Analytical techniques. Five flowers at each stage, 0 to 3, were sampled. Flowers were cut at the base of the ovary, and the stem

Table 1. Method of grading flower development.

Stage	Grade
Opening bud	1
Pre-blooming	2
Blooming	2
Pre-wilting[z]	1

[z]Petals lose their turgitity; ends were wilted.

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and leaves together were used in analyses. At the time of sampling, the organs were frozen in liquid nitrogen and lyophilized. The dry matter was determined by weighing lyophilized tissue. Sugars were extracted with 80% ethanol. Sucrose was hydrolyzed enzymatically. Titrations were done according to the Nelson colorimetric method (15).

The uptake and transformation of sugars was tested by allowing uptake of radioactive solution for stage 0 to stage 3. Glucose or sucrose uniformly labelled with ^{14}C was added to the solution (6.5×10^{-5} mole/ml of ^{14}C glucose or ^{14}C sucrose). The initial radioactivity was 3.10^6 cpm/ml. The radioactive sugars (glucose, fructose, sucrose) were separated by TLC using cellulose MN 300 (19). The developing solvent was formic acid: tertiary butanol: methyl-ethylketone: acetone: water (15; 30; 40; 15; 15 by volume). Sugars were visualized by spraying with anisidine phosphate reagent. The spots corresponding to the sugars and their cellulose supports were solubilized in water and measured for radioactivity by liquid scintillation counting (SL 30 Intertechnique). The scintillation liquid was "Rialuma" of Kontron.

The results for sugars are expressed in g or cpm for 5 organs. Their expression per g or as cpm/mg dry weight gave essentially the same curves.

Enzymes involved in sucrose hydrolysis (invertase and sucrose synthetase) were extracted at 2°C using 0.25 M tris buffer at pH 8.5. Enzyme extraction, purification and measurement of activity were carried out according to the method of Hawker et al. (3). Sucrohydrolytic enzymate activity is expressed in absorbance / min 5 organs at 37°.

Results and Discussion

Morphological development. The quality of opened blooms was compared as a function of the method of the opening and of the nature of the sugar supply. There were no overall differences in the diameters and weights between the 2 types of opening (Table 2). The nutritive solutions prepared contained either glucose or sucrose, and for the carnations, both diameter and weight of the flowers were greater when sucrose was used rather than glucose. Flowers opened in glucose were smaller than ones opening on the plant, while ones opening in sucrose were larger than those opened on the plants.

The vase-life of blooms was 17 and 19 days for flowers supplied with a sucrose and glucose solution, respectively. The vase-life of flowers harvested normally was 19 days.

Sugar changes during opening. When flowers were supplied with a glucose solution a regular increase in the total soluble reducing sugars and hexoses occurred in the flower (Fig. 1). In comparison, the increase in sucrose in the flowers, which occurred only from stage 2 to stage 3, remained very limited. In the basic solution (without sugar), a steady loss in the total soluble reducing sugars and hexoses was observed. Very little sucrose was present during the experiment. The flowers supplied with the basic solution did not open completely and wilted prematurely.

Table 2. Quality of opened carnations as functions of the mode of opening and the type of sugar supplied, means of 50 flowers.

Quality characteristic	Mode of opening: On the plant	Mode of opening: In opening solution	Type of sugar: Glucose	Type of sugar: Sucrose
Diam (cm)	9.22b[z]	9.39b	9.05a	9.52c
Weight (g)	9.38b	9.71b	8.56a	9.84c

[z]Mean separation within rows by Duncan's multiple range tests, 5% level.

Cut flower development from buds appeared to depend on the exogenous sugar supply and the concomitant accumulation of reducing sugars.

Sugar changes as a function of the nutritive solution composition. We wanted to know in which chemical form the sugars were transported and what relative roles the stems, leaves and flowers played when supplied with glucose or sucrose. Two treatments of sugar solutions were prepared: a treatment G (with glucose + ^{14}C glucose) and a treatment S (with sucrose + ^{14}C sucrose). Only sucrose, glucose and fructose were determined from the tissue, and the stems and leaves were analyzed separately.

Fig. 2 shows changes in each of the ^{14}C sugars in the various portions of the flower. Radioactivity of sucrose in the stems was almost the same with either glucose or sucrose uptake. This observation supports the idea that with the 'Scania' carnation, synthesis of sucrose from glucose occurs rapidly in the stem, as in the 'Carina' rose (17). This sucrose synthesis seems to be saturated, since ^{14}C glucose accumulates in the same way as ^{14}C sucrose in the stems of the treatment G. Such a phenomenon was not observed with the 'Carina' rose (16, 17). Fructose incorporated little radioactivity, although it was slightly higher in the stems of the treatment G. This may suggest a preferential isomerisation of glucose into fructose.

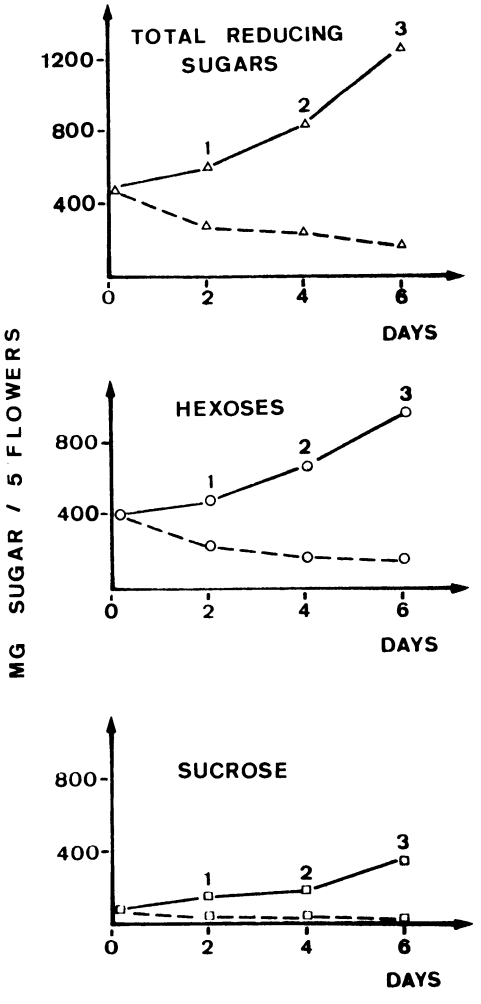

Fig. 1. — Sugar changes in flowers of cut carnations opened in a glucose solution (30g/liter) (————) and in a solution without glucose (— — — —) The notation 1, 2, 3 refers to the developmental stage of the flower.

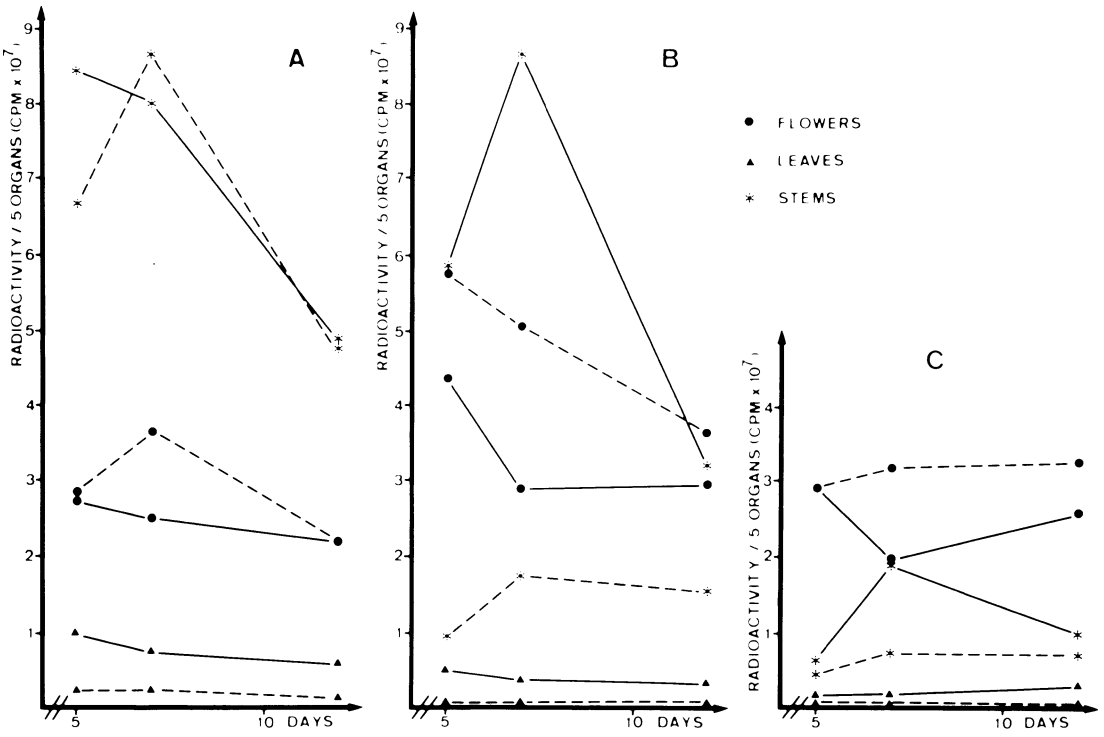

Fig. 2. —Sugar radioactivity in flowers, leaves and stem during opening. (————) flowers supplied with a glucose solution (+ ^{14}C glucose). (— — — —) flowers supplied with a sucrose solution (+ ^{14}C sucrose). The notation 1, 2, 3 refers to the developmental stage of flower. A: Sucrose. B: glucose. C: fructose.

Whatever sugar was supplied, the leaves accumulated very little ^{14}C sucrose, ^{14}C glucose, or ^{14}C fructose. The sugars were not transported to the leaves which hence did not play a great role in accumulation or hydrolysis, as they did in the 'Carina' rose (16, 17).

In flowers opened in sucrose, more radioactivity appeared in gluclose, which suggests a strong hydrolytic activity (confirmed by data in Table 3). At stage 1 the radioactivity in fructose represented about 50% of that in glucose. At stage 3 the amounts of ^{14}C recovered in glucose and fructose were similar. When opened in glucose, it was also glucose which presented the highest radioactivity (stage 1). At stages 2 and 3 the radioactivities incorporated into glucose, fructose and sucrose were almost equal. The chemical analysis of sugar showed a net accumulation in flowers when sugar was fed exogenously, but ^{14}C sucrose, ^{14}C glucose and ^{14}C fructose did not appear to accumulate in flowers when fed in the radioactive form. This may be explained by the fact that a fraction of sugars is being probably transformed into starch. Starch accumulates through most of the corolla development (4, 10).

Table 3. Suchrohydrolytic activity of cut carnation flowers and stems in relation to developmental stage and exogenous sugar source during opening.

Developmental stage	Sugar source	Enzyme activity (A/min - 5 organs) Flowers	Stems
0		17.0 ± 1.6z	1.6 ± 0.6
1	Glucose	12.3 ± 0.6	0.7 ± 0.2
2	Glucose	8.3 ± 1.1	1.2 ± 0.2
1	Sucrose	13.5 ± 0.5	1.0 ± 0.1
2	Sucrose	12.8 ± 1.5	0.7 ± 0.1

z± SE of 3 replications.

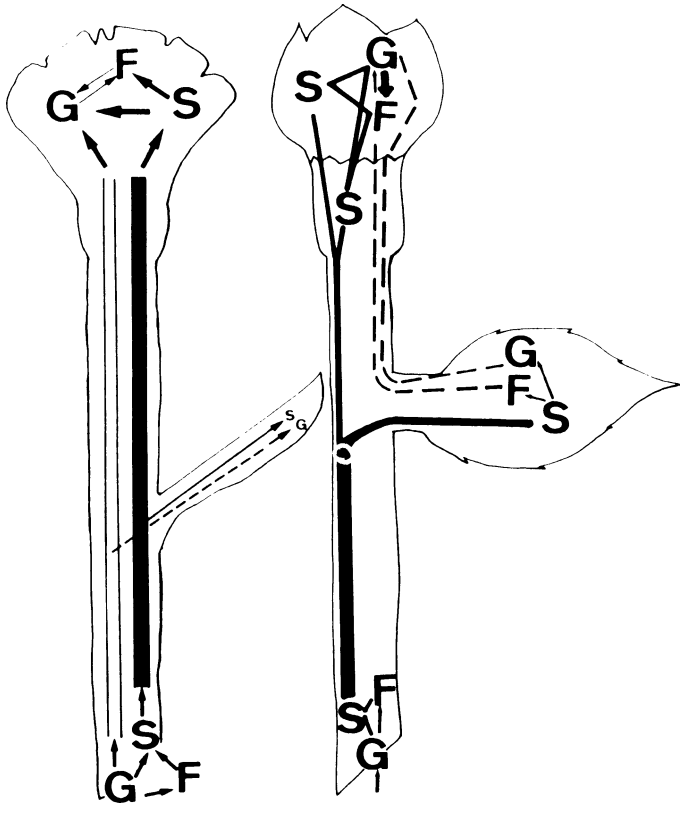

Fig. 3. — Schematic representation of interconversion of sugars in cut 'Scania' carnation (on the left) and of 'Carina' rose (on the right) supplied with a glucose solution (30g/liter).

When comparing the changes in the sugars in carnation with those in 'Carina' rose (17), one notes significant differences. Thus, with carnations the flower is a sink not only of hexoses, but also of sucrose. Such is not the case with 'Carina' rose. A very stong hydrolytic activity was measured in the carnation floral tissues. With the 'Carina' rose, inversion of sucrose was lower but also occurred in the leaves which accumulated and hydrolysed sucrose. With the carnation, the rise of hexoses in the flower seemed to result from a direct glucose migration and from a sucrose hydrolysis *in situ*, without the leaves playing an important role. Figure 3 schematically represents the sugar uptake for these 2 species. The data indicate that the sugar metabolism of cut flowers receiving an exogenous sugar supply is still not fully understood. In all cases, an increase in the hexose content of the flowers was observed, but the process leading to this may vary from 1 species to another. So, if glucose is in general transformed into sucrose in the stem tissues, this process may be adequate for sucrose to reach the flower, and there may or may not be a direct transport to the flower. The leaves may or may not play a role in sugar accumulation and sucrose hydrolysis. These phenomena are governed by enzymes whose activities vary significantly from 1 species to another.

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