ASPECTS OF CARBOHYDRATE BALANCE DURING FLORET OPENING IN FREESIA

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Abstract

Endogenous carbohydrates were investigated during development of florets of *Freesia hybrida* 'Polaris' from inflorescences attached to the plant as well as from cut inflorescences placed in water. During development at the plant the amount of glucose, fructose and sucrose increased about 15-20 times; maximum was reached at anthesis. For detached inflorescences, at anthesis the amount of sugars in the 5th floret (from the base of the inflorescence) was only about 20% as compared to attached inflorescences, however, opening of the florets at position 5 was normal.

The increase of sugars during development of buds of cut inflorescences could not only be accounted for by starch hydrolysis. Decreasing the stem length of cut inflorescences greatly reduced the increase in dry weight and in total carbohydrates of the buds. However, there was no influence of stem length on the number of flowering florets/inflorescence.

It is questionable whether variations in flowering percentage in cut flowers placed in water are correlated with differences in endogenous carbohydrates.

Additional index words
Flower opening, sugars, starch.

1. Introduction

Freesia flowers face upward in apparently one-sided spikes held more or less horizontally. An inflorescence on the main branch consists of 8-14 florets. Anthesis proceeds from the base to the apex of the inflorescence. In general, on the plant all buds reach anthesis. As a cut flower held in water, the number of florets/inflorescence reaching anthesis can vary to a large extent. Ten till 60% of the buds may die before they reach anthesis.

The number of fully developed freesia florets on cut inflorescences is increased by supplying exogenous sugars (Woodson, 1987; Spikman, 1989). Promotion of flower opening by placing cut flowers in sugar solutions has been successful with many other flowers, like *Gladiolus hybrids* (Mayak et al.,1973; Serek et al., 1994), *Gypsophila*, *Antirrhinum* (Apelbaum and Katchansky, 1977), carnation (Paulin and Jamain, 1982), *Liatris spicata* (Han, 1992) and rose (Van Doorn et al., 1991). The physiological role of carbohydrates in flower opening, however, is not completely understood (Evans and Reid, 1988). Parallel data of carbohydrate contents in petals during development of attached and detached flowers are rather limited. Tirosh and Mayak (1988) presented changes in starch content during development of carnation petals. The starch content declined gradually during senescence. The extent of decline was greater in cut flowers held in water in comparison to attached flowers. With 'Sonia' roses, Ho and Nichols (1977) discussed that the reducing sugar pool of the cut corolla was maintained at the expense of starch which depleted fairly quickly, in contrast to the continuous accumulation of starch found in the intact corolla. With the rose 'Madelon', during development in water only the fructose concentration increased, while all other carbohydrate concentrations decreased or remained at the same level (Marissen, 1991). During opening on

the plant all carbohydrate concentrations increased.

The purpose of the present study was to get information about the role of carbohydrates in the variation in flower opening in freesia. Therefore changes in carbohydrates during the development of freesia florets in attached and detached inflorescences were investigated. As with a detached inflorescence, besides the florets themselves, only the stem can serve as a possible source of carbohydrates, it was also investigated if differences in stem length influenced available carbohydrates and opening of the florets.

2. Material and methods

2.1. Plantmaterial.

All experiments were carried out with *Freesia* 'Polaris'.

Detached versus attached inflorescences. For this experiment plants were grown from corms in a greenhouse of the Department of Horticulture (temperature set points day/night: 10°C/8°C). Corms were planted at the end of the summer in 5 l plastic pots (4 corms/pot) filled with a commercial potting soil. Pots were digged in the soil of the greenhouse; temperature of the pots was kept at 14-15°C by cooling or heating of the soil. The experiment was started when the inflorescences had reached the commercial harvesting stage, i.e. with the basal bud (bud 1) at full colour but still tight. A randomized block design with 3 blocks was used as experimental design. For measurements at attached inflorescences pots with plants were transferred from the greenhouse to a phytotron and placed at 20°C, 60% RH, photoperiod of 12 hrs (44 Wm^{-2}) by a mixture of high pressure sodium and mercury lamps. For measurements at detached inflorescences, following harvest in the greenhouse, stems were trimmed to 30 cm length, and placed in tap water under cool-white fluorescent light, photoperiod of 12 hrs (3 Wm^{-2}), at 20°C and 60% RH.

Stem length. In these experiments cut inflorescences were obtained from a commercial grower and transported dry (40 minutes) to the Department, or were obtained from plants grown in a greenhouse of the Department of Horticulture. Inflorescences were harvested in the early morning, trimmed to the desired stem length (2 or 40 cm) and placed in tap water. The experiment about flowering percentage (table 1) was performed 3 times (exp.'s A, B, C): A.Inflorescences picked at commercial harvesting stage at the Department; B.Inflorescences picked at commercial harvesting stage at a commercial grower; C.Inflorescences picked in an early developmental stage (basal bud green and about 50% enclosed by its bracts) at a commercial grower. For measuring time course of dry weight and carbohydrates inflorescences were picked at the commercial grower with bud 3 green and about 50% enclosed by its bracts. To prevent a possible redistribution of carbohydrates between florets, all florets except bud 3 were removed at the start of vase life.

2.2. Carbohydrate analysis.

Each sampling date from each block, 3 buds (florets) from the 3 positions from one inflorescence were cut, frozen in liquid nitrogen, lyophilized and ground (pooled together). Using 15 mg of the powder, sugars were extracted by 80% ethanol (80°C). From the supernatant 1 ml was taken, dried under vacuum and dissolved in water. Sugars were measured by HPLC (Dionex CarboPac PA1 column, Dionex PED detector). After washing the remaining pallet with 80% ethanol, the pallet was used for starch analysis. After vacuum drying of the pellet a thermostable α-amylase in water was used to dissolve the starch (30 min at 90°C), followed by hydrolysis by amyloglucosidase (15 min at 60°C). Glucose was measured in the supernatant by HPLC.

3. Results

3.1. Detached versus attached inflorescence.

According to the HPLC-chromatograms the main soluble carbohydrates in the florets were glucose, fructose and sucrose. Until anthesis the amount of sucrose was about half the

amount of glucose and fructose and about 15% of the total carbohydrate amount (figure 2). The amounts of glucose and fructose were about similar at any moment during development.

During floret development at attached inflorescences the amount of sugars per floret increased about 15-20 times until anthesis; thereafter these amounts decreased (figure 2A). The amount of glucose and fructose decreased faster than the amount of sucrose. During floret development of detached inflorescences in water the increase of sugar content was much less than on attached inflorescences (figure 2B) and strongly dependent on bud position within the inflorescence. Maximum total carbohydrate content at position 1, 3 and 5 was respectively 54, 33 and 20% of the content of attached florets. Florets at all 3 positions reached anthesis; in position 6 and 7 of the cut inflorescences some florets reached anthesis, others did not. From position 8 all buds died. With attached inflorescences at least 10 florets per inflorescence reached anthesis.

Starch was only a minor compound; it represented 30% of total carbohydrate in young buds (this was 5% of dry weight), however, only about 2% from the moment the soluble sugars started to increase (<1% of dry weight). The increase in sugars could not only be accounted for by starch hydrolysis.

3.2. Stem length.

As there was an increase in the total amount of carbohydrates during development of the florets it can be expected that there is transport of carbohydrates from the flower stem to the florets. By varying stem length it was investigated if the stem served as a carbohydrate pool for the inflorescence. With 40 cm stem length the increase in dry weight of the florets was about 4 times as compared with florets at stems of 2 cm length; the increase in total carbohydrate was about 6 times (figure 3).

However, stem length had no influence on the number of florets per inflorescence that reached anthesis, whether the flowers were picked at the commercial harvesting stage or at a much earlier developmental stage (table 1).

4. Discussion

Development of freesia florets to anthesis is accompanied by an increase in the amount of soluble sugars per floret (figure 2A,B), as well as per unit of dry weight (data not shown). In cut inflorescences the increase is less for a bud position more upward to the apex of the inflorescence, probably due to the developmental stage at cutting. Most of the increase occurred during the phase of fast petal expansion. The same was found for rose corollas (Ho and Nichols, 1977; Marissen, 1991) and seems to agree with a correlation between reducing sugar content and petal expansion as demonstrated in cut carnation flowers fed with exogenous sugar (Paulin and Jamain, 1982). The increase in soluble sugars in detached freesia inflorescences during development to anthesis is in accordance with findings with detached rose (Ho and Nichols, 1977; Marissen, 1991) and gladiolus (Yamane et al.,1991) flowers, but differs from cut carnations in which all carbohydrates decrease from the moment of cutting (Paulin and Jamain, 1982).

With detached inflorescences the increase in sugar content was greatly diminished by cutting, especially for florets in an early developmental stage at cutting (figure 2B). However, even with the small increase in florets at position 5 all florets at this position reached anthesis. This disagrees with the suggested correlation between reducing sugar content and petal expansion (Paulin and Jamain, 1982). These findings suggest that the amount and concentration of sugars itself do not determine whether flower buds will open or not. This last suggestion was confirmed by the effects of varying stem length which strongly influenced the amount of available carbohydrates (figure 3), but had no effect on the number of opening florets per inflorescence (table 1). The size of the opened flowers seemed to be correlated to the amount of sugars. Although exogenous sugars greatly enhance blooming in cut flowers it is still questionable whether variations in flowering percentage in cut flowers placed in water are correlated with differences in endogenous carbohydrates.

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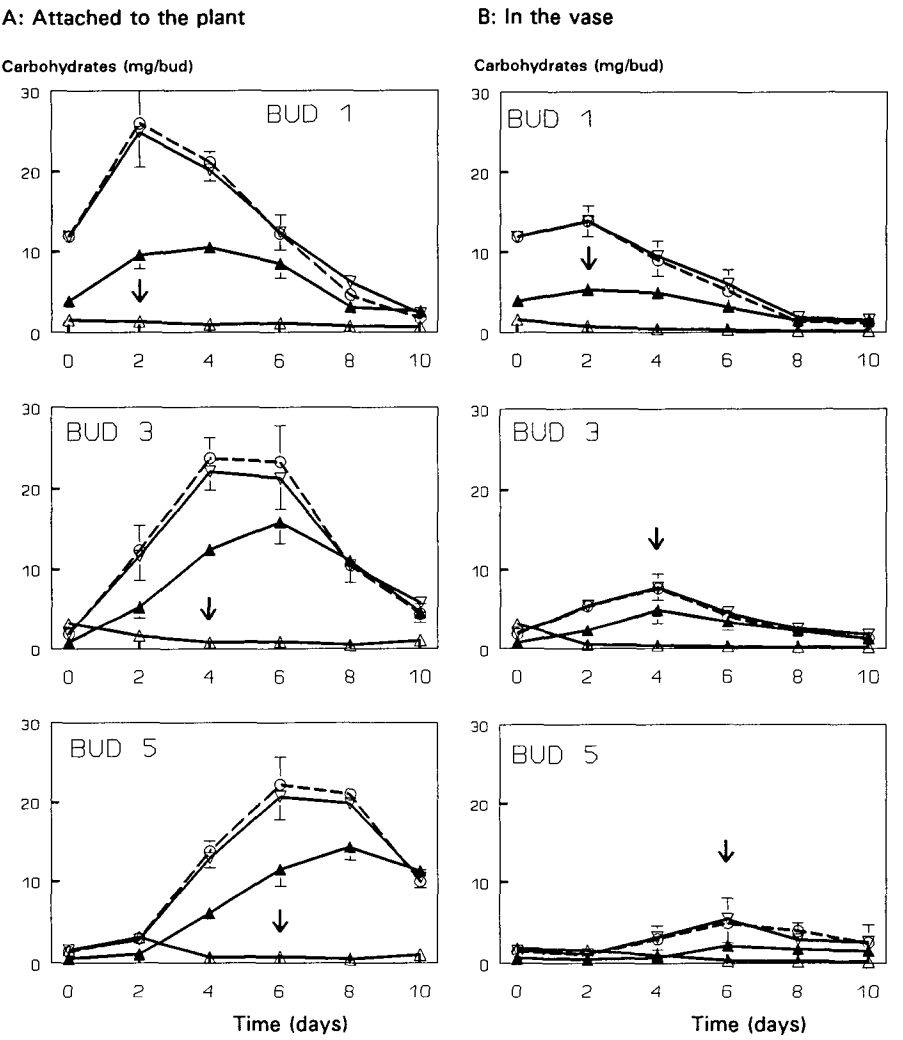

Figure 1. Amounts of carbohydrates during floret development of attached (A) and detached (B) flowers. Buds taken from position 1, 3 and 5 in the inflorescence, counted from the most basal (largest) bud to the apex of the inflorescence. On X-axes time from reaching commercial *harvesting stage (A) or start of vase life (B)*; —▲— *sucrose*; - -○- - *glucose*; —▽— *fructose*; —△— starch; arrows indicate time of anthesis; vertical bars represent SE of the mean.

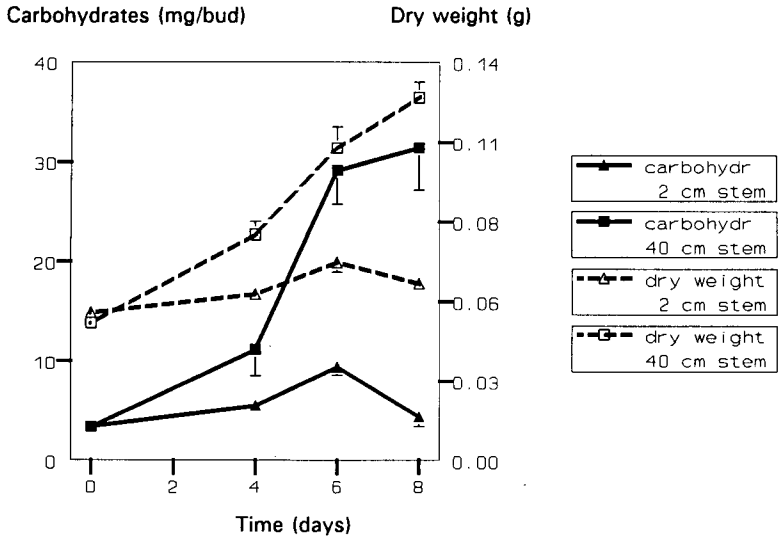

Figure 2. Time course of dry weight (broken lines, right axes) and total carbohydrate content (solid lines, left axes) of florets during vase life of cut inflorescences with different stem length. Inflorescences picked when bud at position 3 was green and for about 50% enclosed by its bracts. Stems were trimmed at 2 cm (triangles) or 40 cm (squares) length; at the start of vase life all florets except bud 3 were removed. Time from start of vase life.

Table 1. Effect of stem length on the number of florets/inflorescence that reached anthesis. Total number of florets in each inflorescence was 9-10. Inflorescences were harvested at commercial cutting stage (exp.'s A, B) or when the oldest bud was green and for about 50% enclosed by its bracts (exp. C). Mean values (SE in brackets) from 10-17 inflorescences.

	# florets that reached anthesis	
	stem length 2 cm	stem length 40 cm
Experiment A	3.9 (0.2)	3.9 (0.2)
Experiment B	3.9 (0.1)	3.6 (0.1)
Experiment C	2.4 (0.2)	2.8 (0.1)