

DOCIS: A MODEL TO SIMULATE CARBOHYDRATE BALANCE AND DEVELOPMENT OF INFLORESCENCE DURING VASE LIFE

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Abstract

The concept of a dynamic and deterministic model (DOCIS) was developed to simulate post harvest development of an inflorescence during vase life based on carbohydrate content at harvest. The model was partly parameterized using lily 'Enchantment'. The inflorescence as a system was defined by the state variables: the carbohydrate pool, structural biomass and development stage of each floret in the inflorescence and the carbohydrate pool in the stem. An additional auxiliary state variable was used to describe whether a floret is alive or dead due to shortage of carbohydrate supply. The model is temperature driven. It is assumed that the available carbohydrates are distributed among the floret(bud)s proportional to their total sink strengths. An osmotic pool of the petal cells is included which is treated as an independent sink. By priority, carbohydrates imported by a floret are used for maintenance respiration. Distribution of available carbohydrates among the osmotic and the non-osmotic (substrate available for structural biomass production) pool was assumed to be proportional to the sink strengths of both pools. Sink strength was defined as the capacity to accumulate carbohydrates under conditions of non-limiting carbohydrate supply. Available carbohydrates did not influence osmotic potential of petal juice (vacuolar solution) at a certain development stage. The resulting concept of constant osmotic potential makes it possible to predict floret fresh weight (size), an important aspect of decorative value.

1. Introduction

As regards carbohydrates cut flowers relies on their presence at harvest due to the low light intensities during storage, transport and at the consumer. In many studies (Berkholst, 1989; Berholst and Gonzales, 1989; Van Doorn *et al.*, 1991) the role of starch, stored in the petals of roses, has been emphasized and is supposed to determine successful flower opening. However, the starch levels measured in rose petals at the cutting stage are at most sufficient to meet the demands of the petals for the first 48 h (Kuiper *et al.*, 1995). The beneficial effect of supplying sugars to cut flowers is well known, although the mechanism of action of sucrose in extending vase life is poorly understood. Besides petals, also leaves and stems of cut roses are important sources from which carbohydrates are transported to the flowers (Marissen and La Brijn, 1995; Ichimura *et al.*, 1999). Decreasing the stem length of cut freesia inflorescence greatly reduced the increase in dry weight and in total carbohydrates of the flower buds (Van Meeteren *et al.*, 1995), confirming the role of the stem as store of carbohydrates.

Leaves, stem and petals are not only sources of carbohydrates. To maintain normal functioning of the tissue, they will use carbohydrates by respiration to counteract the continuous degradation of proteins and ion concentrations (Thornley, 1976; De Wit, 1978). This 'maintenance respiration' is assumed to be related to the amount of tissue present, especially amounts of proteins and minerals. As a consequence larger or more developed

flower(bud)s will have a higher maintenance respiration compared to small or less developed flower(bud)s. However, small buds will use more carbohydrates by growth, due to synthesis of new structural biomass and to achieve the osmotically derived turgor pressure essential for expansion of the cells. This need for growth is coupled to growth rate and will diminish when flowers reach their final size.

The various florets within an inflorescence will compete for the available carbohydrates. Their actual need for carbohydrates will be different, because they vary in size and in their development stage. Shortage of carbohydrates will result in different effects in florets of different development stages. It can lead to smaller florets, to premature dead of the floret, or probably to enhanced senescence (Eason *et al.*, 1997). All mentioned effects result in a decrease of sink strength of the floret involved, which will influence the actual distribution of carbohydrates among the florets. Also petals within a flower differ in size and development stage, and compete for available carbohydrates (Marissen, 1991).

As result of the before-mentioned processes, the carbohydrate balance of a cut flower behaves very dynamic. The final result will depend on amount of carbohydrates present at severance from the intact plant, number of florets or petals present and their individual development stages, number of leaves and stem length. As maintenance respiration and development rates are influenced by temperature, temperature after harvest will also effect the final result. Simulation models are powerful tools to understand dynamic systems. If a mechanistic simulation model can be developed, which predict the changes in carbohydrate balance in relation to development during vase life based on measurable characteristics at harvest, quality of the cut flower can be (partly) quantified using these characteristics. Therefore we developed a conceptual model about carbohydrate balance related to development of an inflorescence during vase life. The model was partly parameterized using lily and called DOCIS (Development and Ornamental value of Cut Inflorescence Simulator).

2. Material and methods

2.1. Experimental part

To obtain preliminary data some experiments are done with lily (*Lilium* L.) mid century hybrid 'Enchantment' flowers. Bulbs (circumference 12 cm) were planted in boxes (20 bulbs/box of 1m x 1m) in climate rooms at 20°C, 70% RH and 16h light (219 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, HPI + SON/T). To investigate the effect of competition between individual florets on dry weight accumulation in the floret(bud)s, available amounts of carbohydrates during growth were influenced. Therefore two different experiments were carried out: a One bud at different positions within the inflorescence was left attached to the plant, while all other buds were removed when they reached a length of about 1 cm. Buds left at the plant were at position 1, 4, 5, 6 or 7; position 1 is the most basal (oldest) position. b By shading, plants were grown at 100% or 50% of the available irradiance in the climate room. From all treatments dry weight of flowers at position 1, 4, 5, 6 and 7 was determined at anthesis.

To obtain data about osmotic potentials in vacuoles of petals under various supplies of carbohydrates, cut flowers were placed in solutions of 1, 1.5 and 2% sucrose (+ 50 $\text{mg} \cdot \text{l}^{-1}$ DICA). All flower buds except one were removed at the start of vase life; at start of the experiment the flower buds left had development stage 0.3 (see 2.2.4). During vase life buds were regular harvested and frozen (-20°C); three buds per treatment per date. After thawing, sap was pressed out and osmotic potential measured by cryoscopy.

2.2. Concept of the model

The model is dynamic and deterministic, and temperature driven. The inflorescence as a system is defined by the following state variables: the carbohydrate

pool in the stem and the carbohydrate pool, structural biomass and development stage of each floret in the inflorescence. Besides the development stage as result of the genetic program of the floret, an additional auxiliary state variable is introduced to describe whether a floret is alive or dead due to shortage of carbohydrate supply. It is assumed that there is no shortage of water, nitrogen or other nutrients except carbohydrates.

2.2.1. Distribution of carbohydrates among florets

In principal three different strategies of distribution control for carbohydrates can be considered: i) First all the needs for carbohydrates of one floret(bud) will be fulfilled, probably the most basal oldest bud; the remaining carbohydrates are available for the next floret(bud) and so on, ii) The available carbohydrates are distributed among the florets(buds) proportional to their sink strengths, iii) All florets(buds) are supplied with carbohydrates to fulfil their maintenance needs; thereafter, remaining carbohydrates can be used for growth and storage of the various florets(buds). In most crop growth models, the last strategy is applied.

In case of the first control mechanism, a constant limiting carbohydrate supply will result in a clear difference between the weights and sizes of the individual florets within an inflorescence. The weight of the floret will be largely depended on its position within the inflorescence. Experimental results showed that there was no difference in final dry weight between florets(buds) at different positions when the amount of available carbohydrates was varied during the growth of lily flower buds attached to the plant, either by varying the number of sinks by removing floret buds (Fig. 1A), or by varying assimilation rate by different light intensities (Fig. 1B). Therefore, the first strategy was rejected.

At this moment there is no experimental proof for either of the two other partitioning mechanisms. In DOCIS, it is assumed that carbohydrates are distributed proportional to the total sink strengths of the florets.

2.2.2. Sink strength of a floret

The sink strength of a floret was defined as the potential demand for assimilates, consequently as the sum of maintenance respiration and potential growth rate. Potential growth rate is the maximum growth rate (without any limitation) related to the development stage of the floret. Growth comprises as well increase in structural biomass as increase in osmotic substances to facilitate cell enlargement. From anthesis of the floret its sink strength is assumed to decrease to zero, in spite of its maintenance respiration. Of course, florets also loose their sink strength when they prematurely die due to a shortage of carbohydrates.

2.2.3. Carbohydrate flow in a floret

The flow of carbohydrates in an individual floret is represented by the diagram in Fig. 2. The carbohydrates available for an individual floret are used for maintenance respiration, for increase in structural dry mass and to maintain an osmotic pool in the petal cells of the floret.

It is assumed that all carbohydrates imported by a floret can be used to provide for the need of maintenance respiration. Maintenance respiration is made proportional to structural biomass and to a function of temperature. The remaining carbohydrates are partitioned among a hypothetical short-term substrate pool used for the formation of new structural biomass and an 'osmotic pool', which is believed to play an important role as driving force for cell elongation, hence affecting the size of the floret. Flowers accumulate sugars in their petals in accordance to their development stage, even under limited supply of carbohydrates (Van Meeteren *et al.*, 1995). So, this accumulation is not the result of a surplus in the supply of carbohydrates. Therefore, an osmotic pool of the

petal cells is included in the model, which is treated as an independent sink. The maximum amount of the osmotic pool is reached around anthesis of the floret. The total dry weight of a floret is the sum of the structural biomass and the osmotic pool.

Distribution of carbohydrates among the osmotic and the non-osmotic (substrate) pool is proportional to the sink strengths of both pools. Sink strength is defined as the capacity to accumulate carbohydrates and is quantified by the rate of increase under conditions of non-limiting carbohydrate supply.

The carbohydrates of the osmotic pool are not available for the formation of structural biomass. However, when imported carbohydrates cannot fulfil the need for maintenance respiration, carbohydrates stored in the osmotic pool will be used for maintenance.

The growth rate (rate of increase of structural biomass) is assumed to be proportional to the amount of the short term 'non-osmotic substrate pool', with a maximum rate related to the development stage of the floret (potential growth rate). Growth rate is assumed to be independent of temperature. Cumulative potential structural biomass (DW_{st}) could be described by

$$DW_{st} = a + \frac{b + c \cdot DV}{1 + d \cdot DV + e \cdot DV^2}$$

where DV is development stage. Growth respiration is a constant fraction of the rate of growth.

Florets are assumed to die when the available carbohydrates for maintenance (so the sum of available carbohydrates imported from the stem and the osmotic pool present) cannot fulfil the need for maintenance. By definition, florets will also die when they have reached their maximal development stage.

2.2.4 Development stage

In the model, flower development is described as an index ranging from zero to unity where zero corresponds to a green bud with a length of 2 cm and unity is anthesis. Intermediate stages of development have values within the unit range and can be calculated by

$$DV = \frac{d_{tot} - d_{act}}{d_{tot}}$$

where DV is development stage, d_{tot} is the number of days needed from stage zero (2 cm green bud) to anthesis and d_{act} is the number of days needed from the actual stage to anthesis. With the lily plants used, d_{tot} was 23 days at 20°C; the flowers had a full grown, orange colored bud at stage 0.8.

Development rate is a function of temperature.

2.2.5. Osmotic potential

Measuring osmotic potential from petal juice showed that this potential is rather constant at specific development stages (Fig. 3), although the offered amount of sugar was different. Measurements showed that the amount of sugars in the buds was affected by the treatments (data not shown). Concentration of sugars in the sap could explain only a small part of the osmotic potential.

3. Some preliminary outcomes and discussion

Until now, the model was only partly parameterized and validated. As a consequence of the assumed disappearance of sink strength at anthesis combined with maintenance respiration, floret dry weight decreases after anthesis by using the osmotic pool. This is in accordance with experimental data.

In general, there is reasonable consensus concerning the simulation of growth respiration, but the simulation of maintenance respiration is still an area of great uncertainty. The contribution of maintenance respiration to the carbohydrate balance is very pronounced during vase life of cut flowers. Progress in understanding the underlying principles and validation of maintenance respiration will be of great importance for a satisfactory accuracy of models simulating the carbohydrate balance of cut flowers.

Some preliminary scenario studies showed that the carbohydrate amount in the stem at harvest affected largely the number of buds that will develop into full bloom. However, the final result depended largely on the level of carbohydrates. At low amounts an increase enhanced mostly the live and development of the oldest buds; when a critical level was passed, a small increase in carbohydrate amount had a tremendous effect on the young buds. Probably this explains the sometimes conflicting reports about the relation between carbohydrates present at harvest and vase life.

A constant supply of a low amount of sugar to the vase water of the cut flower especially enhanced the development of the young buds. The effect was mainly the result of preventing premature death of the young buds, by which they could grow as soon as the oldest florets were senesced and lost their sink strength. The result interacted strongly with the initial amount of carbohydrates in the stem.

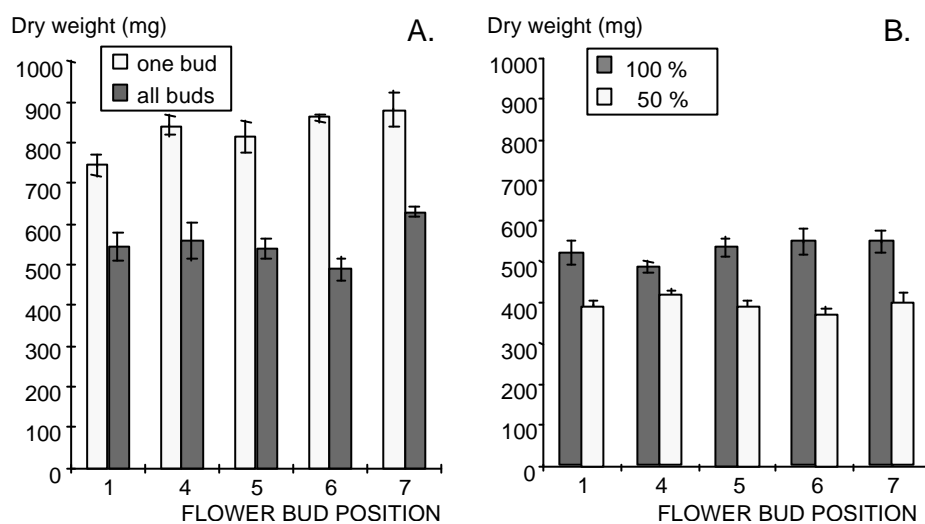
Sugars in the petal juice explained only a part of the osmotic potential. The same was found for freesia florets (Van Meeteren *et al.*, 1995) and for rose petals (Evans and Reid, 1988). It can be assumed that the main part is due to organic acids. For biosynthesis of organic acids carbon atoms are needed. Interesting is the nearly constant osmotic potential at certain development stages, although the available carbohydrates fluctuated. Osmotic values will be important for functioning of cells (functioning of enzymes, permeability of membranes, etc.); when available carbohydrates are limiting other molecules will be used. In leaves mostly nitrate is used as osmotic substance; we measured only minimal amounts of nitrate in lily and freesia petal juice (not published). Another possibility to maintain osmotic potential is uptake of less water resulting in smaller flower petals and less fresh weights. Smaller sized flowers is a common experience when flowers are cut at a young development stage or have a large number of florets within an inflorescence, especially when they are put in a vase without additional sugar. More knowledge about the regulation of osmotic potential and the substances involved, will make it possible to predict floret weight (size), besides number of living florets, an important aspect of ornamental value.

References

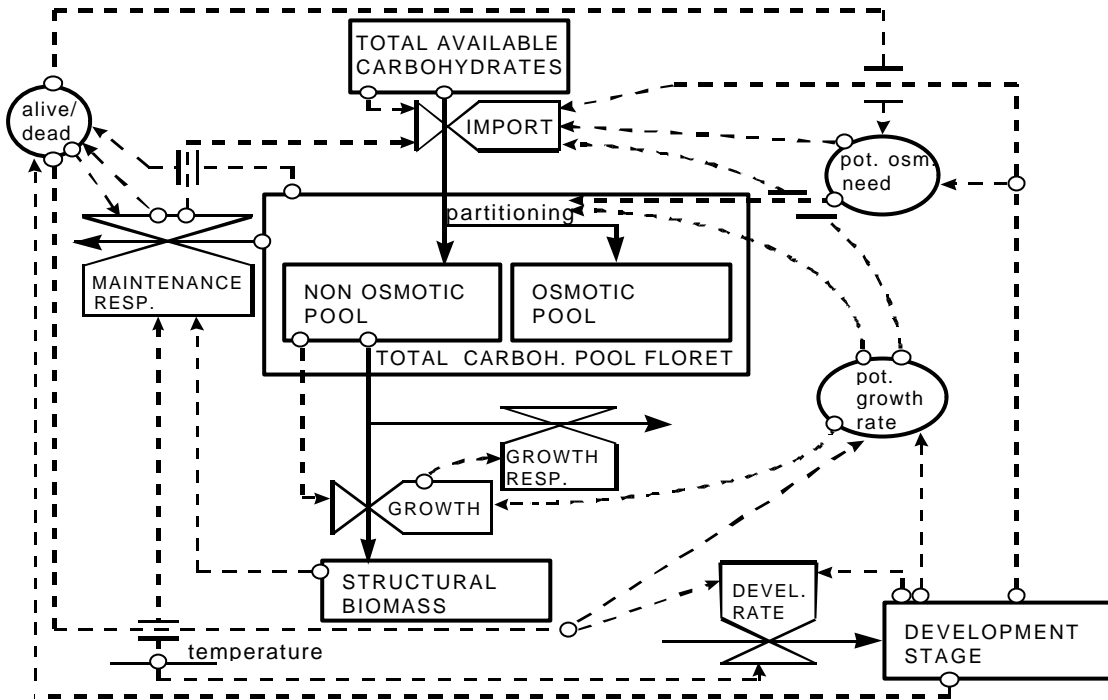
- Berkholst, C.E.M., 1989. High starch content in 'Sonia' rose corollas at picking may add quality to vase life. *Gartenbauwissenschaft* 54, 9-10.
- Berkholst, C.E.M. and Gonzales, M.N., 1989. A simple test for starch in rose petals. *Adv. Hortic.Sci.*, 3, 24-28.
- De Wit, C.T., 1978. Simulation of assimilation, respiration and transpiration of crops. PUDOC, Wageningen The Netherlands, 141 p.
- Eason, J.R., De Vré, L.A., Somerfield, S.D. and Heyes, J.A., 1997. Physiological changes associated with *Sandersonia aurantiaca* flower senescence in response to sugar. *Posth. Biol. Techn.* 12, 43-50.
- Evans, R.Y. and Reid, M.S., 1988. Changes in carbohydrates and osmotic potential during rhythmic expansion of rose petals. *J.Amer.Soc.Hort.Sci.* 113, 884-888.
- Ichimura, K., Mukasa, Y., Fujiwara, T., Kohata, K., Goto, R. and Suto, K. Possible roles of methyl glucoside and myo-inositol in the opening of cut rose flowers. *Ann. Bot.* 83, 551-557.
- Kuiper, D., Ribot, S., Van Reenen, H.S. and Marissen, N., 1995. The effect of sucrose on the flower bud opening of 'Madelon' cut roses. *Scientia Hort.* 60, 325-336.
- Marissen, N., 1991. Osmotic potential and carbohydrate contents in the corolla of the rose cv. Madelon. *Acta Hort.* 298, 145-152.

- Marissen, N. and La Brijn. L., 1995. Source-sink relations in cut roses during vase life. *Acta Hort.* 405, 81-88.
- Thornley, J.H.M., 1976. *Mathematical models in plant physiology.* Academic Press, London, 318 p.
- Van Doorn, W.G., Groenewegen, G., Van de Pol, P.A. and Berkholst, C.E.M., 1991. Effects of carbohydrate and water status on flower opening of cut Madelon roses. *Posth. Biol. Techn.* 1, 47-57.
- Van Meeteren, U., Van Gelder, H. and Van de Peppel, A.C., 1995. Aspects of carbohydrate balance during floret opening in freesia. *Acta Hort.* 405, 117-122.

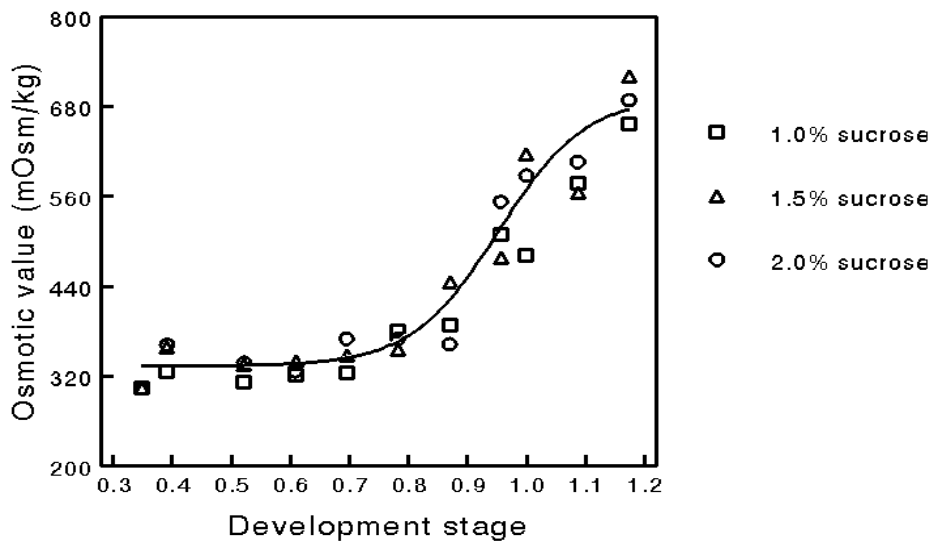
Figures



1. Dry weight at anthesis of intact lily florets at different positions within the inflorescence (position 1 is the most basal position). Available amount of assimilates during growth of the inflorescence was influenced by: A. either removing buds at the moment they reached a length of 1 cm except the bud at the investigated bud position or no bud removal; B. growing plants at two different light intensities (100% or 50% of the irradiance). Plants grown in a climate room at 20 °C, irradiance 219 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for 16h day⁻¹.



2. Diagram illustrating a conceptual model about the carbohydrate balance and development of a floret during vase life of a cut inflorescence. Full lines are fluxes of carbon; dotted lines are fluxes of information.



3. Osmotic value of petal juice at various flower bud development stages. Petals obtained from cut lily flowers placed in 1%, 1.5% or 2% sucrose solution from development stage 0.3.