

## DEVELOPMENTAL CHANGES OF CARBOHYDRATES IN CAPE GOOSEBERRY (*Physalis peruviana* L.) FRUITS IN RELATION TO THE CALYX AND THE LEAVES\*

### Cambio de los carbohidratos en el fruto de la uchuva (*Physalis peruviana* L.) durante su desarrollo en relación al cáliz y las hojas

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#### SUMMARY

Glucose, fructose, sucrose and starch were analyzed in fruits, calyx and the two next leaves during fruit development of cape gooseberry under glasshouse conditions in Berlin-Germany. Calyx was eliminated completely or half-sided vertically 5, 25 and 45 days past fruit set (PFS). Fruits growing completely without calyx slowed down their growth rates significantly from 10-15 days PFS on. Fruits with half-sided calyx or with a complete removal of the calyx after 25 and 45 days grew unaffectedly.

Higher increment rates of all carbohydrates were measured during the first 10-20 days of fruit development in fruits and calyx. Both organs showed higher sucrose concentrations as compared to the other carbohydrates and sucrose rose sharply from 20-30 days PFS in fruits and from 40-50 days in calyx. Glucose and fructose content rose in a lower scale than sucrose and both had very similar increase patterns in the fruit. Starch decreased in fruit and calyx from 10-20 days PFS until harvest (60 days) continuously. Leaf starch content was highest of the measured

carbohydrates and followed a Gauss curve pattern type during fruit growth. Leaf sucrose decreased after 40 days PFS, probably due to an increased translocation to the fruit. 47.2 % of total dry matter in mature fruits were carbohydrates, whereas in calyx and leaves the percentages were 5.7 and 7.4 % respectively. Fruits with detached calyx 5 days PFS presented lower monosaccharide concentration during the initial fruit growth and lower sucrose during the midseason of fruit development. From the analyzed carbohydrates starch was highest during all stages of fruit development in fruits growing completely without husk.

It is supposed that the calyx plays a dominant role in both built up and translocation of carbohydrates, mainly sucrose. With its removal fruit development is delayed indicated by the increased starch contents during all development stages. Thus, calyx has not only a protective function but is also an important source for assimilates especially in the early growth stage of the fruit. The decrease in sucrose content of leaves from the midseason on of fruit development might be due to an increased translocation from the leaf to the fruit.

**Key words:** Glucose, fructose, sucrose, starch, translocation, calyx separation

#### RESUMEN

Glucosa, fructosa, sacarosa y almidón se analizaron en frutos, cáliz y las dos hojas más cercanas al fruto durante el desarrollo

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de la uchuva bajo condiciones de invernadero de vidrio en Berlín-Alemania. El cáliz se eliminó totalmente o, verticalmente la mitad, a los 5; 25 y 45 días después del cuajamiento del fruto (DCF). Los frutos que se desarrollaron completamente sin cáliz redujeron sus tasas de crecimiento significativamente a partir de 10-15 días DCF. Los frutos con medio cáliz o aquellos con un cáliz separado a los 25 o los 45 días no fueron afectados en su crecimiento.

En frutos y cálices, las tasas más altas de incremento de todos los carbohidratos se midieron durante los primeros 10 a 20 días de su desarrollo. En ambos órganos, la sacarosa tuvo las concentraciones más altas y aumentó considerablemente a partir de 20 a 30 días DCF en frutos y, a partir de 40 a 50 días, en cáliz. Los contenidos de la glucosa y fructosa se incrementaron en un nivel más bajo que la sacarosa y ambos mostraron un comportamiento muy similar en el fruto. El almidón disminuyó en forma constante en el fruto y en el cáliz a partir de los 10 a 20 días DCF y hasta la cosecha (60 días). En las hojas, el contenido más alto de los carbohidratos lo presentó el almidón siguiéndose una curva de Gauss durante el crecimiento del fruto. La sacarosa disminuyó en las hojas después de 40 días DCF, debido, probablemente, a un aumento de la translocación al fruto. En la madurez, los frutos secos tuvieron 47,2 % de carbohidratos y los cálices y las hojas, 5,7 y 7,4 %, respectivamente. Los frutos con cáliz separado a los cinco días DCF presentaron una menor concentración en los monosacáridos durante el crecimiento inicial y un menor contenido de sacarosa durante la mitad de su desarrollo. De los carbohidratos analizados, el almidón fue el más alto durante todas las etapas del desarrollo de los frutos que crecieron completamente sin el cáliz.

Se supone que el cáliz juega un papel dominante en la producción y en la translocación de carbohidratos, principalmente de la sacarosa. Con su eliminación, el desarrollo del fruto es más demorado, lo cual se indica por los contenidos mayores de almidón. Así, el cáliz tiene, no solamente, una función protectora, sino que también, es una

fuente importante para los asimilados, especialmente en la etapa temprana del crecimiento del fruto. La disminución en el contenido de sacarosa en las hojas a partir de la mitad del desarrollo del fruto podría ser debida a una mayor translocación desde la hoja al fruto.

**Palabras claves:** Glucosa, fructosa, sacarosa, almidón, translocación, separación cáliz.

## INTRODUCCION

*Physalis peruviana* L. belongs to the family Solanaceae, in which the genus *Physalis* includes close to 100 species which form their fruit in an inflated calyx (Legge, 1974). Plants grow wild in many parts of the Andes, particularly in the Colombian highlands above 2.200 m above sea level (m a.s.l.). Recently the cape gooseberry has developed commercial potential especially for the Colombian fresh fruit export.

Physiological studies of the cape gooseberry in order to understand and improve development and production of this plant are very scarce (Fischer, 1989). There exists any physiological information about the calyx (husk), which surrounds and protects the fruit during its whole development. Therefore, in this study an attempt was made to clarify the importance of the calyx investigating the carbohydrate metabolism of the fruit in relation to the calyx and the two nearest leaves.

In *Physalis* the five sepals grow together forming the so-called calyx (Raven et al., 1985). The sepals, as a sterile part of the flower, are essentially leaf-like in form and anatomy, but are generally simpler in detailed structure than a foliage leaf (Esau, 1977). In cape gooseberry, sepals are upright and most chloroplasts are on the abaxial side. Also the stomates are located on the abaxial side while fruits have stomata only in the epidermic basal zone (Valencia, 1985). Investigating the role of *Physalis*-sepals in fruit development, Bose (1972) found that sepals stimulate the growth of ovaries (*in-vitro*) in the case of unpollinated flowers. He also stated that the

function of calyx is not nutritional, as the ovaries with sepals from pollinated flowers show satisfactory growth in the same culture media.

The cape gooseberry fruits are nearly round glossy yellow berries with many flat seeds (150-300/fruit) measuring 1.25-2.50 cm in diameter and weighing about 4-10 g. Sugiyama et al. (1991) reported that the sugar components of ripe cape gooseberry fruits are sucrose, glucose and fructose. The content of these three sugars is highly dependent on the fruit maturity stage and varies according to variety, leaf-fruit relation and growing conditions (Friedrich et al., 1986). Carbohydrates in *Physalis* fruit development were measured only in *Physalis ixocarpa*. In that species sucrose increased with fruit growth (Ostrzycka et al., 1988), whereas monosaccharides remained constant (Cantwell et al., 1992). In another solanaceous fruit, tomato, the soluble carbohydrates are mainly reducing sugars (Varga and Bruinsma, 1986). These sugars increased progressively throughout development and to maturation and ripening (Ho et al., 1982/83). Similar to tomato, *Passiflora edulis* has a higher reducing sugars (fructose and glucose) content than sucrose (Arjona et al., 1991) and also in apples 'Anna' the highest sugar content was glucose with constant increment rates during its development (Saucedo and Corrales, 1987).

Assimilates are supplied to the fruit generally by leaf photosynthesis and plant carbohydrate reserves (Pavel and DeJong, 1993). Even though photosynthetic assimilation of the fruit itself may account for a relatively small percentage of the total stored material the compounds formed in fixation of carbon dioxide might have a strong effect on the quality of the fruit (Bean and Todd, 1960). Fruits contain, as do leaves of many species, C<sub>3</sub> sun-type chloroplasts for photosynthesis (Blanke, 1990).

When a plant develops a heavy fruit load, the fruits seem to have priority for the photosynthate from most leaves. In plants having many fruits dispersed on the main stem or branches, the photosynthates from the

leaves go primarily to the nearest developing fruit (Brown, 1984; Hansen, 1969). The principal use of carbohydrates in fruits is for dry matter accumulation, so Pavel and DeJong (1993) calculated in 'Cal Red'-peaches 78% of the total carbohydrate requirement for dry matter accumulation and 22% for respiration use.

## MATERIAL AND METHODS

The trial was carried out in the glasshouse of the Department of Fruit Science in the Technical University of Berlin (now Humboldt University of Berlin). The seed propagated ecotype Colombia was used which is originated from native plants in the Boyacá region (2.000-2.800 m a.s.l.) of Colombia. This ecotype has the highest growth habit with smaller leaves as compared with other types from Africa (Kenia or Southafrica). The fruits are small but intensive orange in color and a sweeter taste than the African ecotypes.

One month after sowing in intermittent mist chambers, vigorous plants were transplanted in 9-10 cm diameter pots, and 6 weeks later in 2.5 l black plastic containers. The substrate used in propagation and culture was washed quartz sand (0.7-1.2 mm). Plants were triple irrigated daily by a Wuxal solution, whose composición was 8: 8: 6 (N: P: K), 300-500 ml/pot, depending on their development and climate conditions. Calcium and magnesium were taken from tap water.

Plants were kept on cement tables and trained in the following way:

- Pruned up to one main vegetative stem with two generative leaders.
- Lateral generative shoots were cut after the first node.
- Leaders were supported by threads connected to the glasshouse construction.

Mean minimum and maximum air temperature in the glasshouse in Berlin were 18°C and 26°C. Relative humidity was between 60 and 90%.

Calyxes were excised at different stages of fruit development a) 5, b) 25 and c) 45 days from the day of husk elongation. The removal was a) half-sided vertical (fig. 1), b) total and c) without removing (check). The treatments were arranged in a completely randomized design with a 3x3 factorial arrangement and 6 replications (single plants). Data was analyzed by using the SAS programm and mean separation was done by using the LSD test.

After five days, in the case of total separation, calyx was separated manually by pulling it out with two fingers. At 25 and 45 days a pair of small scissors were used in the case of half-sided and full calyx removal treatment. Fruit setting date was registered and at the end of the experiment fruit weight and carbohydrates were analyzed relating them to fruit age.

When 5 basal fruits per plant reached their maturity (60 days), so that the two fruiting shoots represented all development stages, plants were harvested. For carbohydrate analysis fruits, calyxes and the two next leaves to the fruit were shock frozen in liquid nitrogen immediately after excision from the plant (between 10 and 11 a.m.) in order to completely stop metabolic processes. After freeze drying, samples were finely ground in an agate mill. Samples were submitted to extraction 5 times with 80% ethanol at 60°C, the extractions were combined and the pellet separately prepared for starch analysis. Glucose, fructose, sucrose, and starch were determined enzymatically (Bergmeyer, 1977; Boehringer AG, 1989) using a spectro photometer.

## RESULTS

At the experiments end the two generative shoots had reached an average length of 1.80 m each and formed about 100 leaves and 50 fruits. There were no differences between the check (growing with the complete husk) and the treatments in which calyx was removed at 25 and 45 days and the half-sided calyx separation treatments so that in the following results only the treatments in

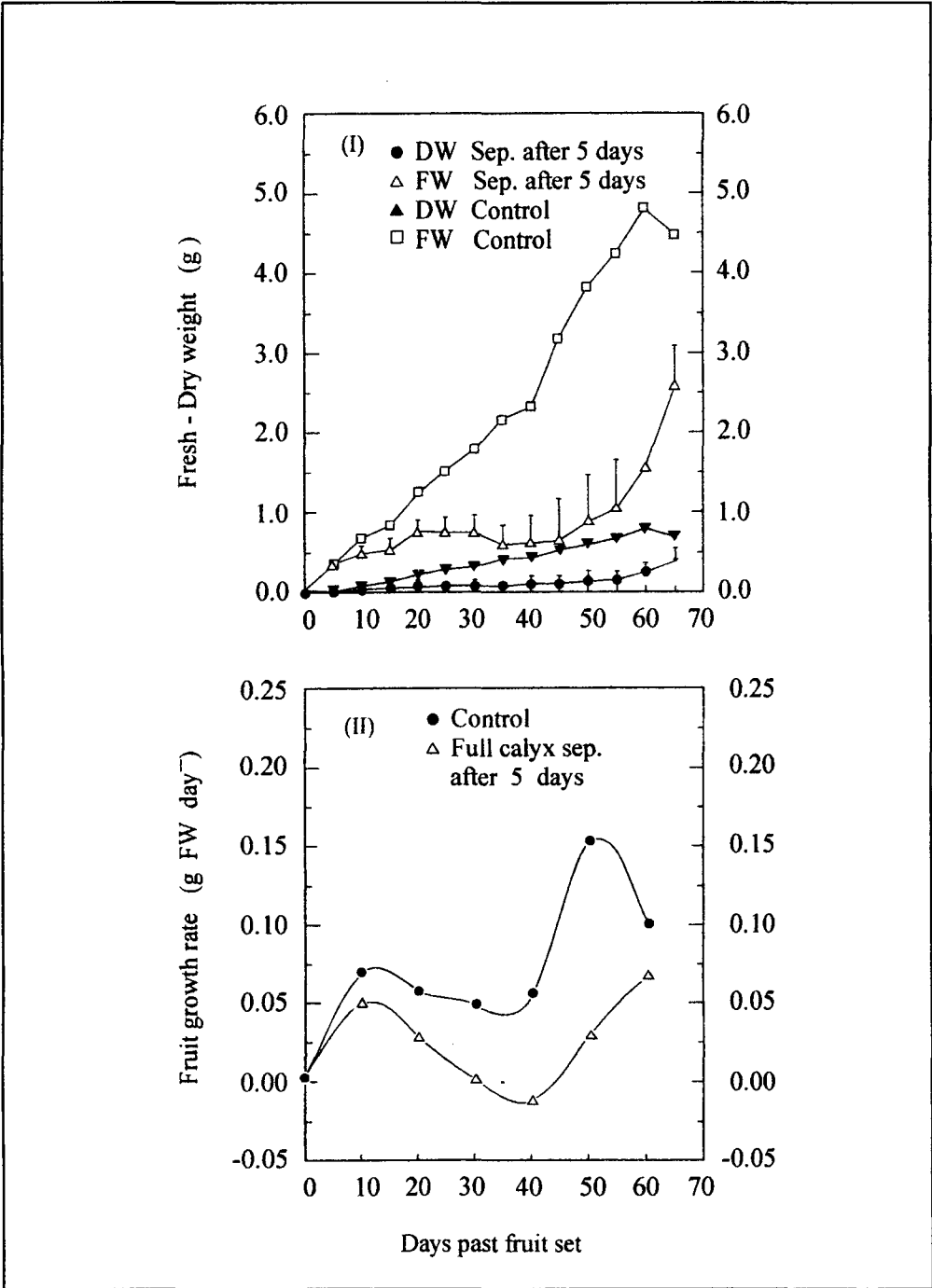
which the whole calyx was removed and the check are presented. Detailed information about all treatments with regard to fruit development are described in Fischer et al (1997).

### Fruit weight

Complete calyx separation 5 days past fruit set (PFS) noticeably affected fruit fresh and dry weights. Whereas cape gooseberry fruits with calyx (control) grew continuously from fruit set until 60 days those without husk showed a marked reduction in their **fresh weight** since from 10 days on (at this stage significantly 28% lower than the control fruits) (fig. 1-1). Without calyx, after a slow increase of fresh weight until 20 days PFS, it remained constant from the 20<sup>th</sup> to the 30<sup>th</sup> day of fruit development, then decreased slightly and from the 40<sup>th</sup> day on weight increased steadily up to 55 days when enhancement became over-proportional. In general, fresh weight increase of fruits of control plants was proportional in a nearly linear pattern for 60 days (up to 4.8 g), but then over-ripen decreased weight in the same proportion (fig. 1-l).

With regard to the **dry weight** development (fig. 2-l) in control plants the same pattern followed as compared to the fresh weight, naturally on a much lower scale (17.7 % dry weight portion of fresh weight of 60 days old fruits). Dry weight of fruits without calyx increased up to 0.08 g after 20 days of fruit development, then remained steady for 15 days and after a slight increase followed the highest increment rates from 55 to 65 days PFS.

Fig. 1-II indicates that after 10 days PFS **fruit growth rates** slowed down until 40 days of development, not only in calyx separated fruits but also in control plants. The former remain in positive rates, whereas calyx-removed fruits fell to zero at 30 days and to -0.014 at 40 days because of their fresh weight decrease at this stage of development. Very evident is the declining growth rate of control plants at the late stage of fruit development when ripening occurs, whereas husk separated fruits continue their growth rate increment phase (fig. 1-II).



**Figure 1.** Influence of calyx separation 5 days past fruit set on developmental changes of fresh and dry weight (I) and of growth rate (II) of cape gooseberry fruits. Vertical bars indicate significant differences (LSD) at  $P < 0.05$ .

### Fruit, calyx and leaf carbohydrates

Changes in carbohydrate components in fruits, calyx and nearest leaves occurred in relation to developmental stage.

In **fruits** monosaccharides as glucose and fructose had very similar curves during fruit development (fig. 3-I). Fructose increased rapidly, somewhat higher than glucose, at early stage of development and, during a slight decrease up to 30-40 days PFS fructose content increased especially and simultaneously with glucose from 40-50 days onwards. In comparison, starch content increased more sharply than monosaccharides during the first 10-20 days PFS but then decreased steadily as the fruits developed and ripened. In contrast, sucrose had nearly opposite behaviour as remaining carbohydrates in fruits. Sucrose concentration increased moderately until 20-30 days PFS and then increased over-proportional as the fruits ripened to a 2.5 fold higher content than monosaccharides at 60 days (fig. 2-I).

Developmental changes of carbohydrates in the **calyx** followed a similar pattern as in fruits (fig. 2-II). However, in calyx, starch content was at a lower level than glucose and sucrose increased sharply at the early developmental stage, compared to its behaviour in fruits. Also different was the steady content of sucrose during 10 to 50 days of fruit development with a sharp rise at the late stage, similar to the early stage increase (fig. 2-II).

In **leaves**, all carbohydrates incremented in a similar way at the initial fruit growth (fig. 2-III). In contrast, starch concentration continued an over-proportional increase up to 20-30 days and then, with a decreased increment until nearly 4 % DM (dry matter), from 30-40 days onwards the curve declined constantly up to fruit ripening. In general, leaf starch content was much higher than in fruits and in the calyx at the late fruit development stage, nearly at the same level as fructose concentration. Also, contrary to fruit and calyx, leaf fructose content increased constantly, at least up to 50-60 days PFS, and passed glucose value at the 30-40 days stage (fig. 2-III).

Comparing the developmental changes of total **carbohydrates** in **fruits**, **calyx** and **leaves** differences between these organs become more evident (fig. 2-IV). In general, carbohydrates are found in a much higher level in fruits (at 60 days 47.2 % DM) than in calyx (5.7%) and in the two nearest leaves (7.4%). Fruit carbohydrates showed a steep curve of increase, interrupted only by the decrease after the initial growth stage. However, in calyx the nearly uniform steady level during the 10 to 50 day stage, with an increase at the late developmental stage, is apparent. Leaf carbohydrate concentration increased until the 30-40 days stage of development in order to decrease as the fruit ripened (fig. 2-IV).

With regard to the influence of the **calyx separation** at the **5 day stage** of fruit development differences in the developmental changes of fruit carbohydrates are evident.

Concentration of monosaccharides **glucose** and **fructose** of fruits growing without calyx tended to be higher at the initial developmental stage, especially by glucose, compared to the control fruits and those with half calyx (fig. 3-I y II). Monosaccharid values of fruits with fully separated calyx decreased then until 30-40 days PFS followed by a moderate content increase, which was more accentuated by fructose, at the late developmental stage. Glucose content of full calyx separated fruits was significantly lower at the 50-60 day stage and fructose content at the 40-50 and at the 50-60 days stage compared to fruits with complete or half-vertical calyx.

**Sucrose** content of fruits was characterized through different increase patterns depending on the calyx treatment (fig. 3-III). After the steep sucrose increment from the 20-30 day stage, fruits without calyx remained clearly behind at the 30-40 and 40-50 day stage of the other treatments. However, at the late developmental stage sucrose concentration was equal in all treatments (fig. 3-III).

Nearly opposite to sucrose was the behaviour of **starch** in fruits (fig. 4-IV). Already at the sharp increase at early stage of

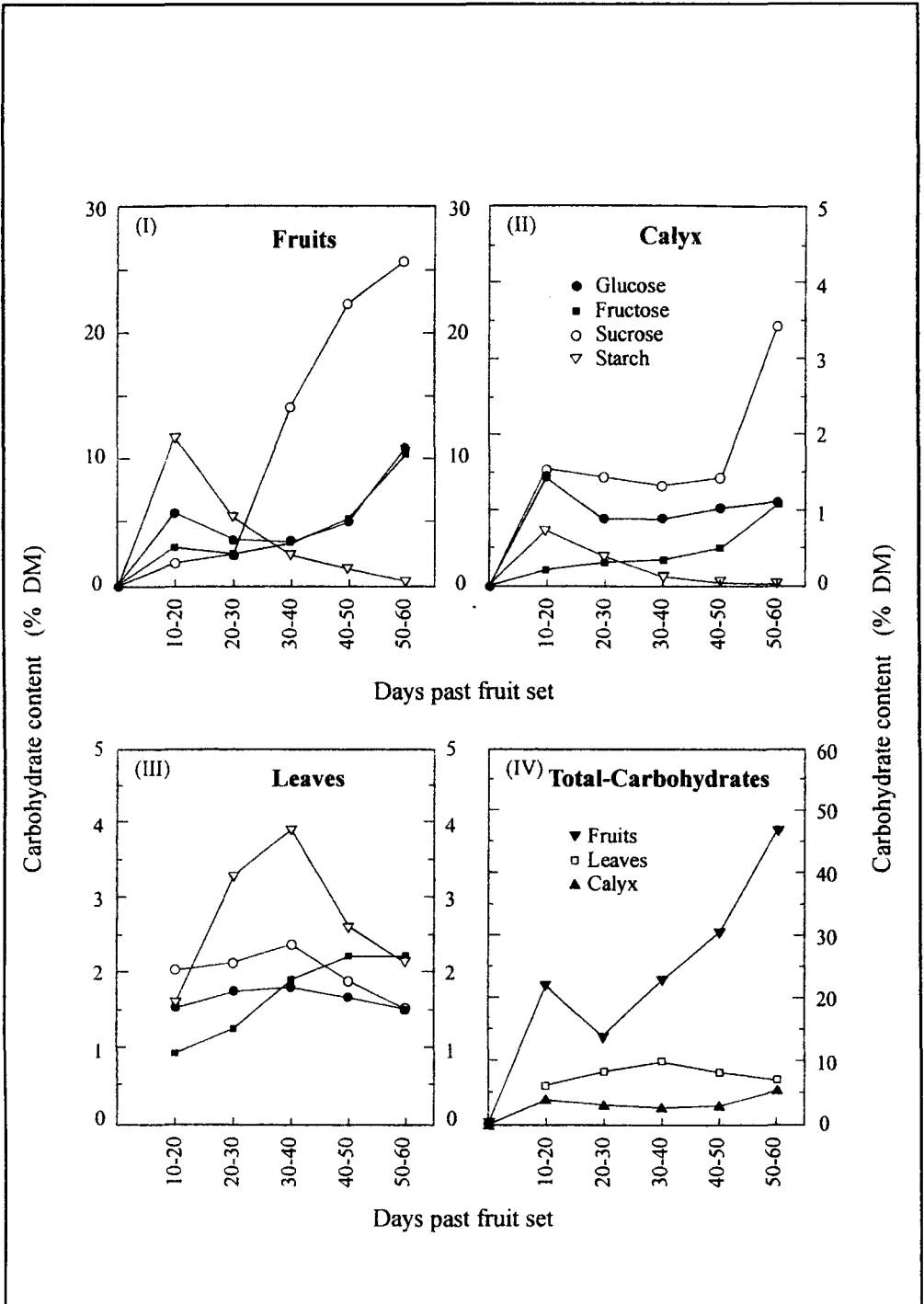


Figure 2. Developmental changes of carbohydrate components in fruits (I), calyx (II) and two leaves next to fruit (III) and fruit total carbohydrate content (IV) of cape gooseberry.

development starch concentration of fruits without calyx was markedly higher as compared to the other treatments. This higher level remained steady until fruit picking at 60 days. Fruits with complete and with half vertical calyx contained almost same starch levels (fig. 3-IV).

## DISCUSSION

With a view to the **carbohydrate** distribution in **fruits**, leaves and calyxes, it seems very evident that sink strength of ripening fruits have affected severely carbohydrate translocation to this organ (Ho, 1988).

Sucrose content increases sharply from 20-30 days PFS on with some reduced increment rates during the last 20 days of fruit development. Genard and Souty (1996) observed, in peaches, that the most influential parameter on sucrose concentration was the date of maximal absolute growth rate. In our study this strong relation was missing because during the highest sucrose rates between day 20 and 40 of the fruit development fruit growth rates remain constant.

Generally, sucrose rise with fruit development are in close agreement with results obtained by Ostrzycka et al. (1988) who worked with *Physalis ixocarpa*. They suggested that sucrose increase resulted through a conversion of simple sugars into sucrose (Whiting, 1970), because these decreased at the same time. The rapid increase of sucrose in the later stages of fruit development also is common in fruit species which have normally a low sucrose content like pears and apricots (Bollard, 1970). The ability to retain so much carbohydrate in soluble form is characteristic of mature fruit tissues.

Sucrose as the major sugar component of cape gooseberry fruits is in agreement with fruits like mango, pineapple, melon, orange (Sugiyama et al., 1991), peach and apricot (Friedrich et al., 1986), but in opposite to other tropical and subtropical fruits like papaya, fig, carambola, kiwi (Sugiyama et al., 1991) and tomatoes (Varga and Bruinsma, 1986; Dalal et al., 1965).

With reference to the monosaccharides detected Cantwell et al. (1992) in *Physalis ixocarpa* constantly remaining levels during fruit growth which did not agree with our findings. In *Physalis peruviana* glucose and fructose content initially rised and declined slightly between 20 and 30-40 days PFS and increased then steadily. Similarly are the findings of Dalal et al. (1965) in tomatoes where free reducing sugar content increased nearly in a straight line during fruit ripening. In contrast to these results Ostrzycka et al. (1988) recorded clearly decreased contents of hexose sugars with inceasing fruit maturity. Absolutely in opposite to our findings, Genard and Souty (1996) observed in peaches that the proportion of sucrose converted every day in glucose and fructose decreased during the growing period to almost cero at harvest.

In accordance with the behaviour in tomato fruits (Ho et al., 1982/83) starch content increased until 10-20 days PFS to more than 10% of dry weight, and then decreased progressively with fruit age to 0.3%. Starch is the first carbohydrate component which is used for energy build up through respiration, and starch hydrolisis is carried out by  $\alpha$ - and  $\beta$ -amylase to glucose (Friedrich et al., 1986).

**Carbohydrate** distribution in the **calyx** followed nearly the same pattern as in the fruits, but with reference to its content level this was more related to the leaf. Although calyx is leaf-like in form and anatomy (Esau, 1977) its physiological importance is more linked to the fruit than to the leaf. The increasing sucrose content at the late fruit ripening stage in calyx seems to indicate that sink effect of the «connected» fruit is very high (Schumacher, 1989) and great amounts of sucrose are translocated through this organ. Once the calyx has turned papery and bladder-like (Everett, 1981) sucrose production seems not possible through photosynthesis at this stage.

Although there is evidence that carbohydrates could be translocated from distant leaves there is a marked tendency for leaves close to a given developing fruit to supply that fruit (Hansen, 1970). In cape gooseberry, total **carbohydrate** content in the



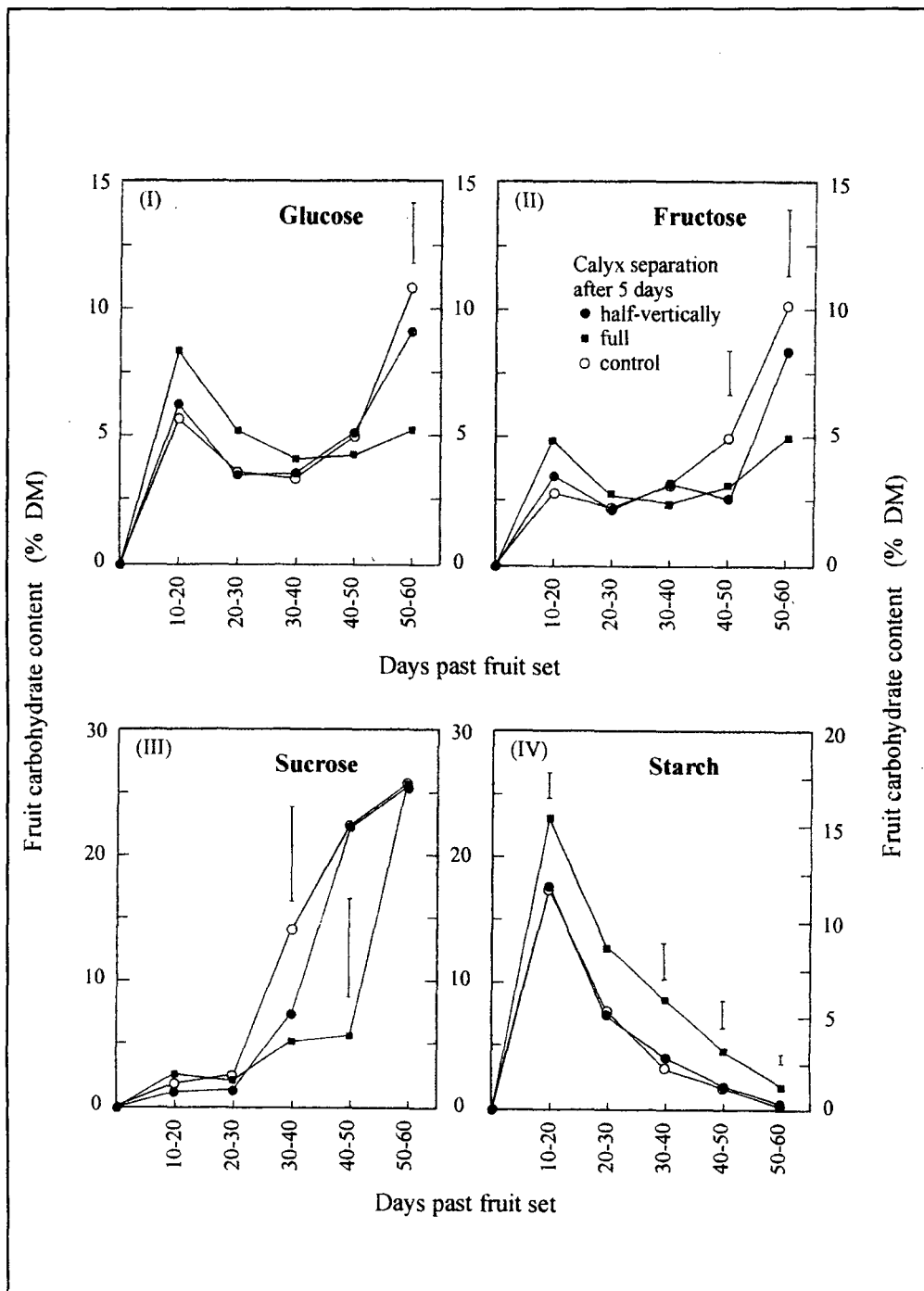


Figure 3. Developmental changes of glucose (I), fructose (II), sucrose (III) and starch content (IV) of cape gooseberry fruits with half-vertically and complete calyx separation 5 days past fruit set. Vertical bars indicate significant difference (LSD) at  $P < 5\%$ .

two *leaves* next to the fruit shows a Gauss curve. Similarly to our study, in apples, as much as 90% of labelled carbon, assimilated by the leaves, has been reported to be translocated to the fruits in the midseason of their development (Hansen, 1970). In general, carbohydrate content of the leaf is considerably lower than in the fruit (Bollard, 1970).

The high starch content between 30 and 40 days of fruit development which corresponds to a leaf age of about 50 to 60 days appears to indicate the high photosynthetic activity at this stage accumulating a high amount of primary starch in leaves (Barcelo et al., 1992). The pronounced decrease of starch and sucrose content in leaves at a fruit age of 40-50 days are probably caused by the increased physiological sink activity of fruits at this developmental stage (Bollard, 1970) showing at the same time the highest fruit growth rate. Coombe (1976) reported that when accumulation in the fruit is greatest also rates of photosynthesis in leaves increase to high levels. Compared to lychee fruit, concentrations of starch in small branches were already lower immediately after fruit set, suggesting that this starch is available for the new fruit growth (Menzel et al., 1995).

Changes of single *carbohydrate* components during fruit growth were explained before but with respect to *fruit* growth *without calyx* some further observations can be made. Under absence of the calyx fruits accumulated more starch and showed also a higher glucose and fructose content at the early development stage than fruits with complete or half-sided husk. As fruit growth rates, related to weight, decreased from 10 to 15 days PFS the increased starch content of fruits without calyx seem to point out that these remained behind the development, also with respect to the carbohydrate metabolism, from these fruits which are covered by the husk. Thus, hydrolysis of starch and decrease of glucose and fructose content during the mid-season of fruit development was retarded in fruits growing without calyx.

With regard to sucrose content, which is the most important carbohydrate in cape gooseberry fruits, values remained behind of control fruits between 30 and 50 days of development, however at the maturity stage content equaled between all treatments. It might be suggested that through the reduced and negative growth rates during the mid-phase of development fruits attracted less sucrose from leaves.

*Fruit weight* was affected detrimentally on fruits growing completely *without calyx*. Since there are reports that calyx has only protective functions against birds, insects and disease organisms (National Research Council, 1989) it is to be taken into account that there are great effects on biomass allocation which affect fruit weight during all development stages.

Negative effects begin after ten days when the calyx normally had the highest growth rate (Fischer et al, 1997). Westwood (1993) observed similar harmful effects on apples when calyx-cup was removed completely; fruit size was reduced and shape was altered to more flattened fruit forms. Fruit size already changed with a partial separation or chemical damage of calyx-cup in contrast to our observations in which half-sided removal did not exert any effect. In apples, calyx appears to have a great influence on the distal formation of fruit organs whereas in cape gooseberries fruit forms were not changed by husk separation.

The early calyx removal appears to affect fruit development detrimentally since cell division in numerous fruit species take place during initial stage of fruit growth (Coombe, 1976). According to the calculation of Westwood (1993) most species divide cells in 20% of time from bloom to harvest; this would correspond for cape gooseberries to the first 12 days of fruit development. The findings that fruits with a less cell number normally remain smaller (Faust, 1989) led to the suggestion that the calyx separation after five days could have influenced the cell division phase, so that a lower number of fruit cells were formed and therefore fruits remained

smaller. A later husk removal when fruit cells had finished cell division did not affect fruit development. It can be supposed that the smaller fruits without calyx had not only fewer cells but also less seeds as a longer developmental period from anthesis to ripeness was observed in tomatoes (Varga and Bruinsma, 1986). In general, fruit growth is strongly dependent on seed development only during the early phases of ovary enlargement (Dennis, 1984).

In the present experiment, calyx separation effect was detected only when husks were removed at the early stage of fruit growth (5 days past fruit set) and when it was fully separated. This indicates that calyx influence is a function of time and of the size of the remaining calyx part. Early calyx separation removes this source of assimilates to the fruit which in turn affects fruit growth.

Specially during first 10 days of fruit development when fruit growth rate is very high through cell division and cell elongation (Varga and Bruinsma, 1986) supply with assimilates is of great importance. Increased sucrose values in the calyx, observed as soon as 10 days PFS seem to indicate that certain amounts of sucrose was translocated to the fruit specially in this early stage when fruit sucrose contents were very low. Comparing the leaf sucrose content, there is no evidence about an increased sucrose translocation rate to the fruit at an early growth stage because sucrose content remained nearly unchanged during fruit development. However, unchanged leaf sucrose content during the first 20-30 days of fruit development seems to point out that fruit can hardly attract greater amounts of assimilates from leaves when the calyx did not exist, at least during the early stage of fruit growth.

At the initial stage of fruit growth a certain self supply of assimilates appears possible since cape gooseberries have stomata situated in the epidermal basal zone of the fruit (Valencia, 1985). Light intensities inside the calyx of 15.1 Klux (which corresponds to 22.4 % of light intensity outside the husk) were recorded after 35 days of fruit

development when calyx is still completely green, indicate that fruit photosynthesis in this shaded space is possible, even though the luxmeter measured spectral ranges which are not effective for photosynthesis.

In apples, at early stages of fruit growth chloroplasts are situated below the epidermis and in tissues which surrounds the vascular bundles next to the core, photosynthesis takes place using the about 600-6.000 stomata (2-20/mm<sup>2</sup>) for gas exchange (Blanke and Lenz, 1988). Although photosynthesis rate per unit area of fruit surface is generally less than one-tenth per unit area of leaf surface (Bollard, 1970), it can supply enough energy to replace that used in respiration at this early fruit growth stage. Our results can be compared with these from Pavel and DeJong (1993) who measured, on peach fruits, receiving 21% and 35% of full sunlight, photosynthesis which contributed to 8% and 9%, respectively, of the total growth and maintenance carbohydrate requirements during growing season.

Complete early calyx separation affects all evaluated growth components and effects were specially pronounced through declined growth rates between 30 to 45 days past fruit set. During this phase simple sugars are also at a minimum and sucrose content in treated fruits is lower than those in control plants. It can be hypothesized that fruits without calyx have exhibited a lower sink strength because of their smaller size (Marcelis, 1992) and with a possible reduced cell and seed number (Luckwill, 1953) and therefore sucrose content in these fruits were lower. Also, after an initial supply of assimilates through fruit photosynthesis, during this later stage, fruit stomata were transformed to lenticels (Blanke and Lenz, 1988; Valencia, 1985) and respiration losses were higher than translocating assimilates which would come normally from the husk. The relatively seldom phenomenon of shrinking of growing fruits between 30 and 45 days past fruit set might be due a great water loss during transpiration when leaves in this zone (middle of the fruit branch) are pulling water from the fruit (Westwood, 1993).

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