

# Sink Strength of Fruits of Two Tomato Genotypes Differing in Total Fruit Solids Content<sup>1</sup>

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**Abstract.** Mobilization of carbohydrates to fruits of 2 genotypes of tomato (*Lycopersicon esculentum* Mill.) differing in total fruit solids content, LA 1563 (1563) and 'VF145B-7879' ('7879'), was investigated. On the basis of 2 separate studies, fruits of 1563, the higher solids genotype, appeared to be stronger sinks for assimilates than fruits of '7879'. LA 1563 partitioned a significantly larger percentage of <sup>14</sup>C to the fruits than '7879'. Fruits of 1563 took up more <sup>14</sup>C-sucrose from agar medium than '7879' fruits, both on the basis of total uptake and specific activity. Starch was found at higher levels in fruits of 1563 than in those of '7879' from 10–30 days after anthesis. No starch was detectable in either genotype 50 days after anthesis. Fruit sucrose levels tended to be lower in 1563 than in '7879' throughout fruit development. The possible physiological relationships between carbon metabolism and the rate of import of assimilates by fruits are discussed.

A high leaf area/fruit ratio is 1 explanation for genotypic differences in solids content of tomato fruits (1, 3). However, a large leaf area does not insure high fruit solids and large leaf area may create problems for mechanical harvesting (3). Other factors which may also influence the solids content of tomato fruits include the rate of assimilate export from leaves, rate of import of assimilates by fruits, and fruit carbon metabolism.

The rate of export of assimilates from a leaf depends upon plant age, leaf age and position, and the rate of carbon fixation (4, 5, 6, 11). Genotypic variation in the rate of export of assimilates from leaves has been observed in soybean (8) and in tomato as a response to high temperature (Dinar and Rudich, unpublished). The rate of transport of assimilates to a fruit depends upon the fruit's developmental stage. Recent work has demonstrated that fruits exert a controlling influence on the rate of import of assimilates (4). The metabolism of carbon, particularly sucrose, has been implicated as having a controlling function in the capacity to mobilize carbon (12, 13).

Previous work (3) has shown LA 1563 (1563) (10) to have significantly higher fruit solids than VF145B-7879 ('7879') from as early as 10 days after anthesis through maturity. LA 1563 and '7879' had 7.08% and 6.51% total solids, respectively, 50 days after anthesis. In this report, these genotypes were studied in an attempt to determine whether there is an association between the rate of import of assimilates by fruit, carbon metabolism, and fruit solids content.

## Materials and Methods

<sup>14</sup>C-translocation to attached fruits. LA 1563 and 'VF145B-7879' were seeded in 8-liter pots containing sterilized potting soil in the fall of 1978 and grown under high intensity metal halide lights (500 μE m<sup>-2</sup> sec<sup>-1</sup> at the top of the plants) in a greenhouse. Axial buds were pruned as they appeared, except for the shoot immediately below the first truss, which was permitted to grow and become the new leader. Trusses were tagged at anthesis of the first flower, and the first and second trusses

were trimmed to 3 fruits; other trusses had not yet set fruit. Several days prior to the experiment, 7 plants of each genotype with fruits of similar ages were selected. The oldest fruit on each plant was 25 days old.

Labelling of leaves with <sup>14</sup>CO<sub>2</sub> was performed by a method similar to that of Hale and Weaver (2). A KAPAK bag was placed around the leaf opposite the first truss and Tygon tubing was inserted through the bag's opening before securing to the leaf. The other end of the tubing was connected to the reaction flask (a 50-ml Erlenmeyer flask) in which 0.15 ml of NaH<sup>14</sup>CO<sub>3</sub> (100 μc/ml) had been placed. The flask was sealed with a rubber septum. A 2-way bulb was connected by Tygon tubing to the reaction flask. At the time of labelling, 1 ml of 0.5 N H<sub>2</sub>SO<sub>4</sub> was injected into the reaction flask, releasing <sup>14</sup>CO<sub>2</sub>, which was pumped into the collapsed bag with the 2-way bulb. The bag was left in place for 1 hr, after which any <sup>14</sup>CO<sub>2</sub> remaining in the bag was removed. This was accomplished by alternately pumping the air inside the bag into a solution of NaOH and refilling the bag with air. After pumping all excess <sup>14</sup>CO<sub>2</sub> into the NaOH solution, the bag was removed from the source leaf. Twenty-four hours after labelling, plants were divided into: fruits on trusses 1 and 2; peduncles of trusses 1 and 2; source leaf; other leaves; stem tissue; trusses above truss 2; and axial branch. These samples were frozen at -20°C, freeze-dried, and dry weights of each component determined. The tissue was ground with a Wiley mill using a 40-mesh screen. Samples (about 100 mg) of each component were weighed, oxidized using a Packard Tri-Carb sample oxidizer, and <sup>14</sup>C was measured using a Beckman model LS 7000 scintillation counter. The scintillation fluid consisted of 5 ml of Carbo-Sorb II and 13 ml of Permafluor V, automatically dispensed by the oxidizer.

The distributions of <sup>14</sup>C from the source leaves to the fruits and other plant parts in the 2 lines were compared in 2 ways. First, the amounts of <sup>14</sup>C in each plant part were calculated as percentages of the total <sup>14</sup>C exported from the source leaf. These values were averaged and genotype means for each plant part were compared. Second, the sink activities of 1563 and '7879' fruits were compared relative to other parts of their respective plants according to the formula

$$\text{Relative fruit specific activity} = \frac{\text{cpm/g dry weight (fruit)}}{\text{cpm/g dry weight (plant)}}$$

where the plant is considered to be the above-ground portion of the plant minus the source leaf and fruits.

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<sup>14</sup>C-Sucrose uptake by detached fruits. LA 1563 and '7879' were seeded on beds in a greenhouse in the winter of 1980 and grown under natural lighting. Axial buds were pruned as in the <sup>14</sup>C-translocation experiment. Individual flowers were tagged at anthesis, and fruits were not pruned. Three experiments were performed, and except for one modification, the procedure used was essentially the same in each. Fruits were selected for age or size and detached from the plants at the joints in the pedicels. The pedicels of the fruits were placed on 2-ml paper cups containing 2 µC of <sup>14</sup>C-sucrose and 1% sucrose dissolved in agar. Fruits were placed in a tray containing moist blotter paper and the tray was covered with Parafilm to retain moisture. The tray was placed in the dark at 25°C. After 24 hr, the fruits were removed and pedicels were detached from the fruits. In the third experiment, fruits were divided into pedicel and blossom halves prior to freezing. Fruits were subsequently freeze-dried, weighed, and ground and 50 mg samples were taken. Ethanol-soluble components were extracted in boiling 80% ethanol (repeated 3 times for one-half hour each). Samples from a known volume were added to scintillation fluid (PCS Amersham) and counted as in the <sup>14</sup>C-translocation experiment.

*Analysis of glucose, fructose, and sucrose in developing fruits.* Sugars were extracted by heating 100 mg (10 days following anthesis samples) or 200 mg (13, 16, 30, and 50 days following anthesis samples) of dry tissue in 10 ml of H<sub>2</sub>O for 90 min in boiling water. Following heating, samples were centrifuged, the supernatant removed and concentrated by evaporation to about 4 ml. Ribose (0.1 ml of a 10 mg ml<sup>-1</sup> solution) was added as an internal standard, and the samples were brought to 10 ml with 80% ethanol.

Samples of 1 ml were removed, evaporated to dryness, and derivatized with 0.5 ml Tri-Sil Z (Pierce Chemical Co.) by heating for 20 min at 75°C. About 1 µl samples were injected into a Hewlett-Packard gas chromatograph, model 5710A, outfitted with a F.I.D. and a 3.2-mm diameter S.S. column, 30 cm long, packed with 3% OV-3 on chromosorb GH.P. Column flow rate was 60 ml N<sub>2</sub> min<sup>-1</sup>. Flow rates for H<sub>2</sub> and air were 30 ml min<sup>-1</sup> and 240 ml min<sup>-1</sup>, respectively. The column oven was programmed from 80 to 250° at 8° min<sup>-1</sup>.

*Analysis of starch in developing fruits.* Starch was analyzed according to the method of MacRae (9) with modifications. Samples of 25 mg of dried tissue were weighed into test tubes with screw caps. To each tube, 10 ml of 80% ethanol was added and samples were heated in a boiling water bath for 30 min. The ethanol was removed and discarded. The ethanol extraction was repeated twice to be certain all free sugars were removed. After the third extraction, residual ethanol was evaporated by heating. Three ml of distilled H<sub>2</sub>O was added to each sample and the tubes were sealed. The samples were incubated at 100°C for 24 hr.

After allowing the samples to cool, 3 ml of amyloglucosidase (Sigma Chemical Co.) in 0.2 M acetate buffer, pH 4.5 (20 mg amyloglucosidase per 3 ml buffer) was added to each sample. The samples were incubated overnight at 40°C.

After allowing the solid material to settle, 1 ml of solution was removed from each tube, vortexed with 5 ml H<sub>2</sub>O, 2 ml 0.3 M NaOH and 2 ml 5% ZnSO<sub>4</sub> and filtered. Aliquots of 1 ml were removed and 2 ml of glucose oxidase reagent (7) was added. The solutions were incubated for 1 hr at 40°C. Reactions were stopped upon addition of 2 ml of 18 N H<sub>2</sub>SO<sub>4</sub> to each sample. The samples were mixed and absorbance read at 540 nm on a Beckman, model DB spectrophotometer.

*Translocation and partitioning of <sup>14</sup>C within the plant.* When the 2 lines were pruned to similar leaf/fruit ratios, the amounts of <sup>14</sup>C exported from the source leaves in 24 hr were not significantly different. LA 1563 and '7879' source leaves exported 41.8 ± 1.3% and 42.9 ± 3.1%, respectively, of their assimilated <sup>14</sup>C. The predominate sink for exported <sup>14</sup>C was the fruit in both lines (Table 1), but a significantly larger percentage of exported <sup>14</sup>C was found in the fruits of 1563 than in those of '7879'. In contrast, the stem tissue of '7879' contained a significantly larger percentage of <sup>14</sup>C than the stem of 1563. Amounts of <sup>14</sup>C located in the leaf, peduncle, flower, and axial branch tissues were small and no significant differences between lines were observed.

The higher percentage of <sup>14</sup>C found in the fruits of 1563 indicated their greater sink strength. Sink strength, however, is a function of both sink activity and sink size. To determine which of these factors was the primary cause of the greater sink strength of 1563 fruits, relative fruit specific activities (RFSAs) and mean fruit dry weights were calculated for each genotype. LA 1563 had a significantly higher mean RFSAs (11.91 ± 0.73 SE) than '7879' (7.44 ± 0.72 SE). The mean dry weights of 1563 and '7879' fruits were not significantly different (15.8 g and 14.3 g, respectively) suggesting that the greater sink strength of 1563 fruits was due mainly to higher sink activity.

*<sup>14</sup>C-Sucrose uptake.* Uptake of <sup>14</sup>C-sucrose by different-sized fruits of both genotypes is expressed as a function of fruit dry weight in Fig. 1. Clearly, 1563 fruits took up greater amounts of <sup>14</sup>C than '7879' fruits of comparable sizes. However, in a separate experiment, in which uptake of <sup>14</sup>C was examined as a function of fruit age (Fig. 2), no differences were observed between the genotypes in fruit sink strength. Uptake of <sup>14</sup>C was observed to peak rather than level-off (Fig. 2), suggesting that sink strength of the fruits reached a maximum level, followed by a decrease. When fruits were fed <sup>14</sup>C-sucrose and subsequently divided into their pedicel and blossom halves, both halves of 1563 fruits contained more <sup>14</sup>C than those of '7879' (Fig. 3).

*Fruit components.* In both 1563 and '7879' fruits, starch as a percentage of the dry weight increased from 10 to 16 days following anthesis and declined from days 16 to 50 (Fig. 4). From the data, it was not possible to determine when the maximum starch levels were reached, except that it was at some point between days 16 and 30. On days 10, 13, 16, and 30, 1563 fruits had significantly higher levels of starch than '7879'. On day 50, neither genotype had any detectable starch.

Table 1. Mean distribution of <sup>14</sup>C to fruit, stem, leaf, peduncle, other truss, and axial branch tissue (% to each part) ± SE in LA 1563 and 'VF145B-7879' plants.

Plant part	Distribution of <sup>14</sup> C (%) <sup>z</sup>		
	LA 1563	'VF145B-7879'	<i>t</i>
Fruit	87.71 ± 1.03	79.61 ± 2.04	3.537**
Stem	7.08 ± 1.58	14.68 ± 2.01	2.969*
Leaves	1.66 ± 0.47	3.26 ± 1.39	1.088 NS
Peduncle	2.30 ± 0.30	1.73 ± 0.27	1.390 NS
Other trusses	0.06 ± 0.04	0.10 ± 0.05	0.729 NS
Axial Branch	1.20 ± 0.76	0.62 ± 0.16	0.753 NS

<sup>z</sup>Values are means of 7 plants.

NS, \*, \*\*Genotypic means nonsignificant (NS) or significantly different at 5% (\*) or 1% (\*\*) levels.

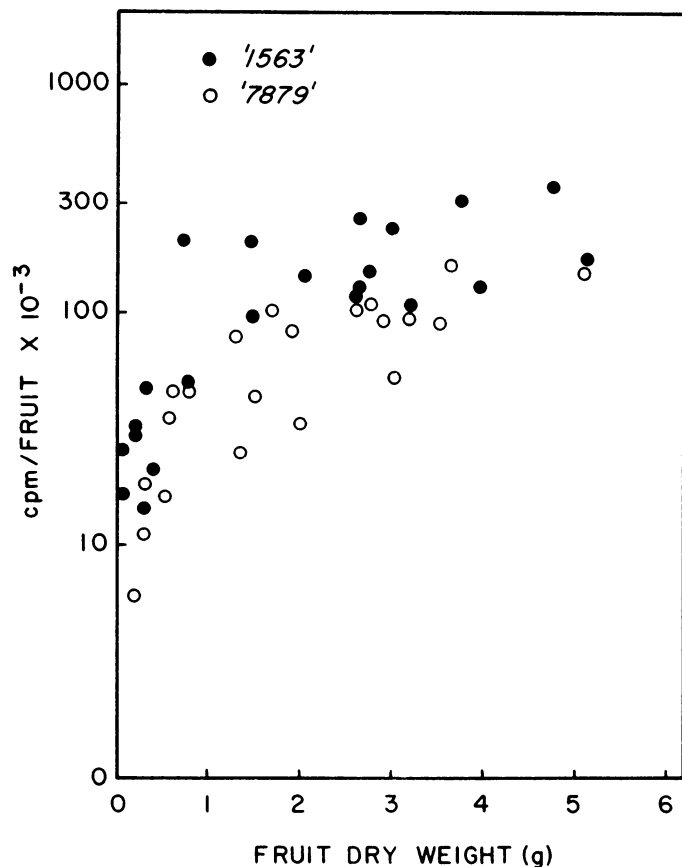


Fig. 1. Uptake of  $^{14}\text{C}$ -sucrose by fruits of different weights of LA 1563 (1563) and 'VF145B-7879' ('7879'). Each circle represents 1 fruit.

Levels of fructose and glucose increased as fruits developed in both genotypes (Fig. 4). At 10, 13, and 16 days following anthesis, '7879' fruits tended to have higher levels of glucose and fructose than 1563. The only differences which were statistically significant, however, were the levels of glucose on day 13 and fructose on days 10 and 13. At 30 and 50 days after anthesis, 1563 fruits tended to have higher levels of glucose and fructose than '7879', although none of these differences were statistically significant.

At all 5 ages, 1563 fruits tended to have lower levels of sucrose than '7879' (Fig. 4). This difference was significant on days 13, 30, and 50 following anthesis. The concentration of sucrose as a percentage of the dry weight tended to decline in both genotypes from 10 to 50 days.

### Discussion

This study suggests that the higher fruit solids of 1563, as compared to '7879' are due not only to large leaf area (3), but also to greater fruit sink strength. Furthermore, carbon metabolism appears to be related to the rate of assimilate import, supporting the conclusions of Walker and Ho (12, 13).

The concept of sink strength used in this study is based on that developed by Warren-Wilson (17) and Wareing and Patrick (16), where sink strength is the product of sink size and sink activity. In the present study, 2 separate approaches were used to compare the sink strengths of 1563 and '7879' fruits,  $^{14}\text{CO}_2$  and  $^{14}\text{C}$ -sucrose feeding.

The distribution of  $^{14}\text{C}$  to different plant parts is a good measure of the sink strength of portions of the plant, because the

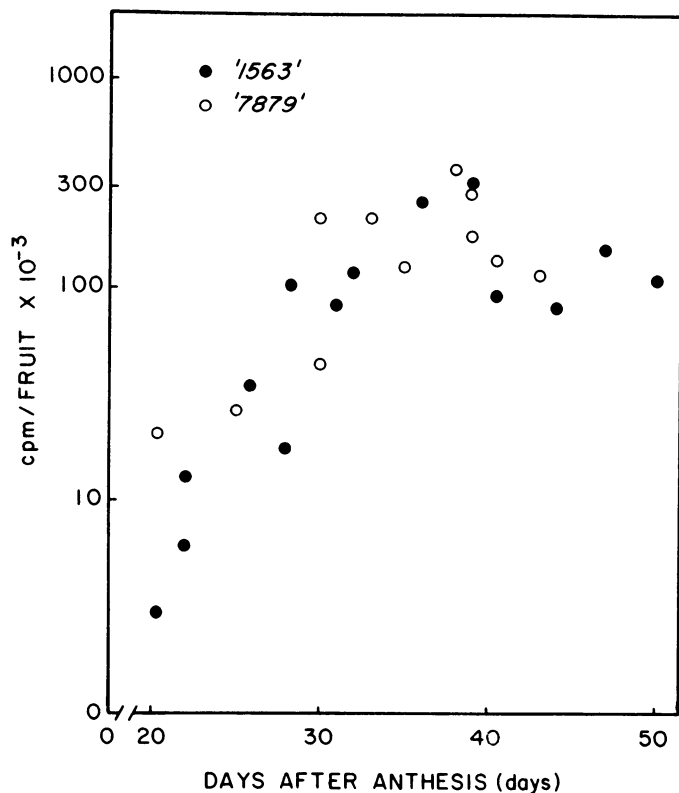


Fig. 2. Uptake of  $^{14}\text{C}$ -sucrose by fruits of several ages of LA 1563 (1563) and ('VF145B-7879' '7879'). Each circle represents one fruit.

allocation is a function of both the capacity of the plant part to attract assimilates (sink activity) and of the size of the part. In the  $^{14}\text{CO}_2$ -feeding study, the percentage of  $^{14}\text{C}$  located in 1563 fruits was significantly higher than in those of '7879'. This could have been a result of either 1563 fruits being stronger sinks than those of '7879' and/or the other parts of 1563 plants being poorer competitors for assimilates. There was no difference between the lines in the percentage of assimilated  $^{14}\text{C}$  exported from their source leaves, indicating that the greater ability of 1563 fruits to mobilize assimilates relative to '7879' fruits affects only the partitioning of assimilates and not the amount exported from leaves.

The  $^{14}\text{C}$ -sucrose studies with detached fruits indicated that the high sink strength of attached 1563 fruits was due, at least partially, to their own capacity to mobilize sucrose. This greater ability to take up sucrose was a function of higher sink activity, since at any given size (dry weight) 1563 fruits took up more sucrose (Fig. 1). Thus, differences between genotypes for sink strength seemed to be determined primarily by sink activity and less so by sink size, which is consistent with Walker and Ho's conclusion (12). The lower specific activity in the blossom-half of the fruits (Fig. 3.) may have resulted from an insufficient time for label to move from the pedicel-half. The trend for the blossom-end of 1563 fruits to have higher specific activities than '7879' fruits may have been a function of more uptake and/or greater mobilization of carbon within the fruits.

According to Walker et al. (15), the rate of assimilate import by a tomato fruit is controlled by carbon metabolism and/or enzyme activity within the fruit. Walker and Ho (13) found that the rate of import of carbon by tomato fruits was inversely related to their sucrose content. They concluded that transport of sucrose into tomato fruits may be controlled by a sucrose gradient. Al-

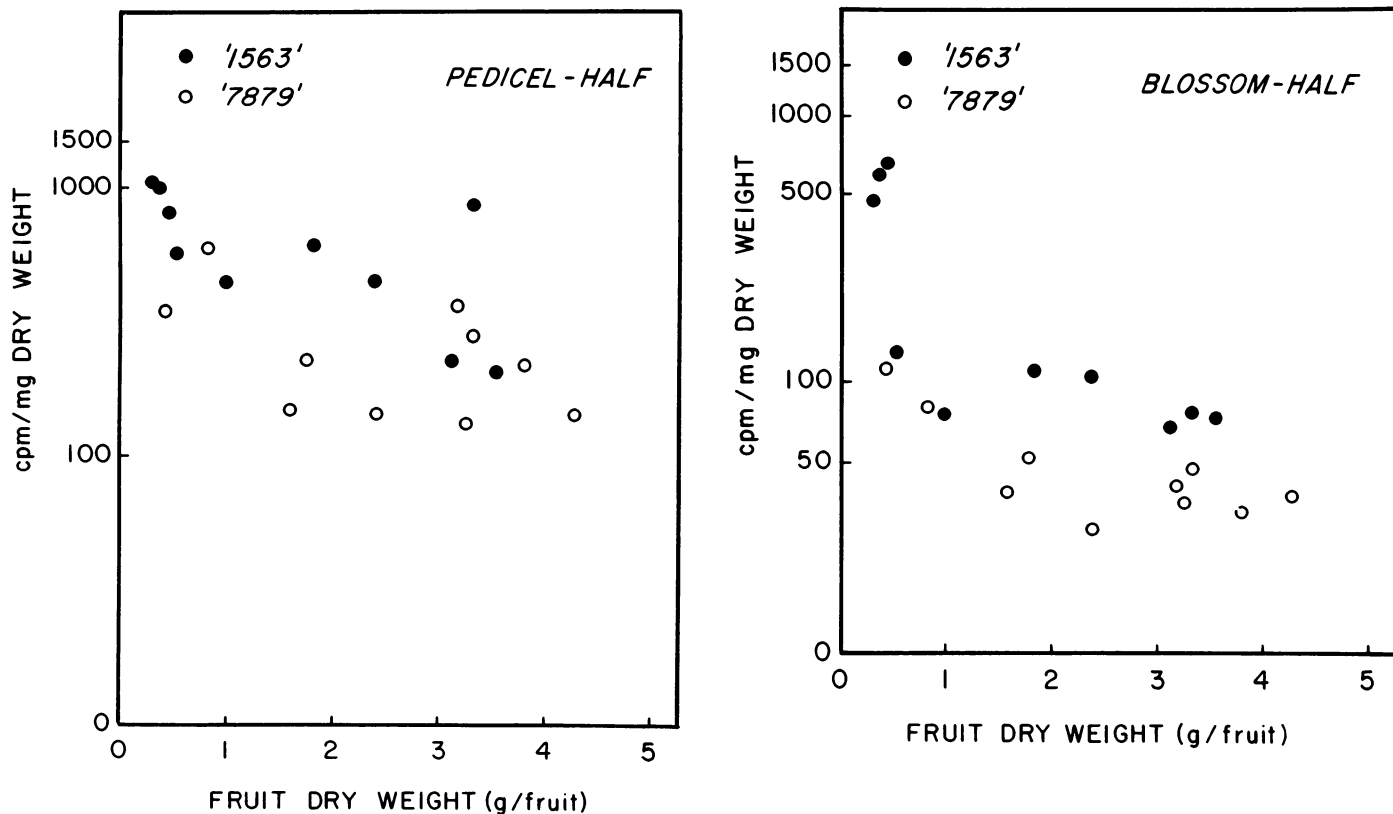


Fig. 3.  $^{14}\text{C}$  content of pedicel-half (left) and blossom-half (right) of fruits of different weights of LA 1563 (1563) and 'VF145B-7879' ('7879'). Each circle represents one-half fruit.

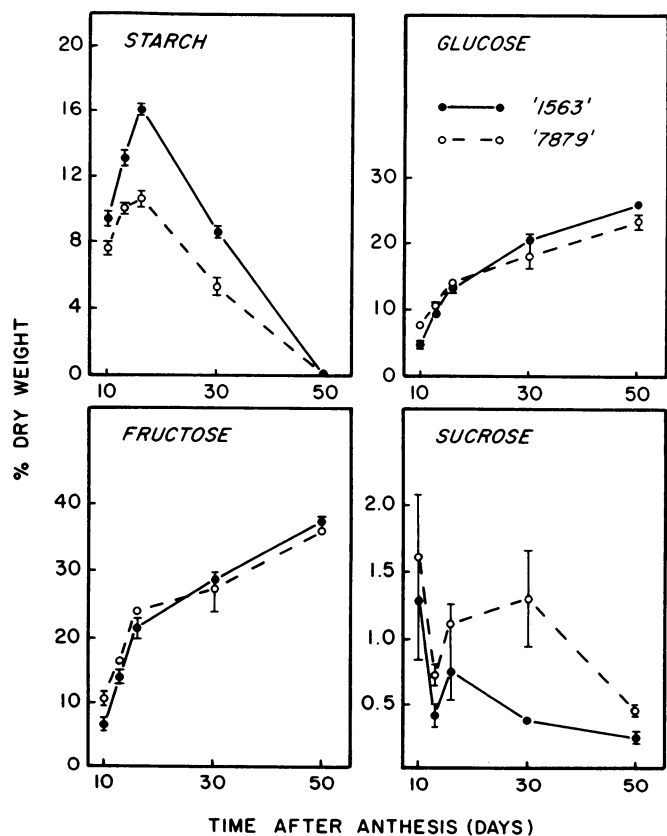


Fig. 4. Carbohydrate composition of fruits of different ages of LA 1563 (1563) and 'VF145B-7879' ('7879'). Each point represents a minimum of three fruits. Plotted values are genotype means  $\pm$  SE.

though no sucrose gradient has been demonstrated in tomato, the existence of one cannot be ruled out. Since the levels of sucrose in the 2 genotypes were shown to be different, incubating fruits of the 2 genotypes on agar with a known concentration of sucrose created a different gradient for each. The greater uptake of  $^{14}\text{C}$ -sucrose was associated with the steeper sucrose gradient, i.e., in 1563. Further work is needed, however, to determine whether there is an actual sucrose gradient between the loading and unloading points of the phloem in tomato. This work suggests that sucrose hydrolysis is occurring at a faster rate in fruits of 1563 than in '7879', since the uptake of  $^{14}\text{C}$  was greater by the former, but the level of sucrose was lower. The association between carbon partitioning and sucrose uptake found here supports the conclusion that the import rate of carbon by tomato fruits is determined largely by fruit metabolism.

It is not clear whether starch accumulation exerts control over the rate of carbon import into tomato fruits. Walker and Ho (13) found no correlation between the carbon import rate and the rate of starch accumulation in tomato fruits at  $35^\circ\text{C}$ . They concluded, therefore, that there was no dependence of carbon import rate on starch accumulation. Walker and Thornley (14), however, found that the relative growth rate and starch level of tomato fruits were positively related. The starch content of 1563 fruits was higher than that of '7879' fruits from 10 to 30 days after anthesis. It may be that there is a causal relationship between high starch accumulation early in fruit development and high carbon import rate, but at present no physiological basis for this relationship, should it exist, is apparent.

Data presented here indicate that the difference in solids between 1563 and '7879' fruits may be due to different rates of translocation of assimilates. In addition, genotypic differences in partitioning of carbon into various metabolic forms may play a significant role in determining solids content.

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# Relationship of Number of Long Nights to Meristem Development and Flowering in *Kalanchoe*<sup>1</sup>

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**Abstract.** Cultivars of *Kalanchoe blossfeldiana* Poelln. varied in number of long nights required for complete flower initiation and development. 'Montezuma' and 'Texas Sunset' required 14 long nights, while 'Pixie', 'Nugget', 'Cactus Candy', 'Goddess', 'Tobasco', 'Osage Orange', 'Toltec', 'Adobe Rose' and 'Rotkappchen' required 15 to 28 nights. Height of apical meristems increased in 'Montezuma' after 7 long nights, but changes were not evident in 'Pixie' until 9 long nights. Scanning electron microscopic analysis showed first evidence of sepal primordia in 'Pixie' after 28 long nights—6 nights later than 'Montezuma'. Differences in the number of long nights required for flower induction were related to delayed floral initiation rather than organogenesis or maturation.

With the development of new cultivars which vary in flower colors and time from floral induction to anthesis, kalanchoes are an important floricultural crop (6). Kalanchoes are short-day plants with the number of long nights required for plants to reach

marketable flowering varying with cultivar (2, 7, 8, 14) and temperature (6, 8, 10, 14).

The number of long nights required for flower induction has been related to histochemical changes in meristems (12), hormonal translocation (12), and exogenous growth regulator application (3, 9). Early meristem dimensional changes have been reported to occur 8 to 10 days after photoinduction (5, 13). However, the developmental stage necessary for further development and anthesis to occur if plants are shifted to short nights has not been identified.

This study was initiated to relate the effects of longer sequences of long nights to floral induction, initiation, and development in these new cultivars; and via meristematic examination, to determine the earliest induction, initiation, or development stage at which anthesis occurs with the minimum number of long nights.

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