SUGAR AND ACID METABOLISM IN CITRUS FRUIT

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Two important horticultural questions in this area are:
1. What affects sugar levels in citrus fruit?
2. What affects acid levels in citrus fruit?

Sugar Levels - Photosynthetic activity in nearby leaves has long been thought to influence levels of soluble solids in fruit, and these solids are predominantly sugars. Classic work by Sites and Reitz (Fig. 1) showed highest solids were in fruit picked from the outside of the tree on the southeast, south, and west exposures; positions where light intensity and photosynthetic activity would likely have been greatest.

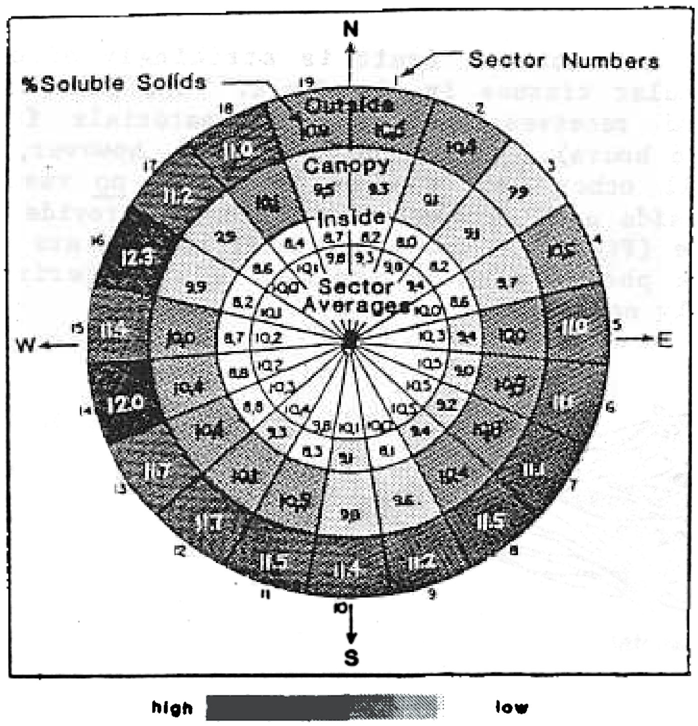

Fig. 1. Effect of direction of sunlight exposure and shading on total soluble solids (%) of 'Valencia' oranges harvested from portions of the tree shown here in cross section. (redone from Sites and Reitz, 1949)

A still closer tie has recently been found between photosynthesis in single leaves near fruit, and sugars translocated into fruit sections vertically aligned with them. The fruit quarter positioned as shown in Figure 2 usually receives over 90% of the photosynthetic material exported from the nearby leaf. Further examination of individual juice segments has shown that most of these photosynthates from a single leaf move into only one or two of the segments. Similar patterns of sugar distribution occur from an individual leaf even if it is farther away from the fruit or if all other nearby leaves are removed.

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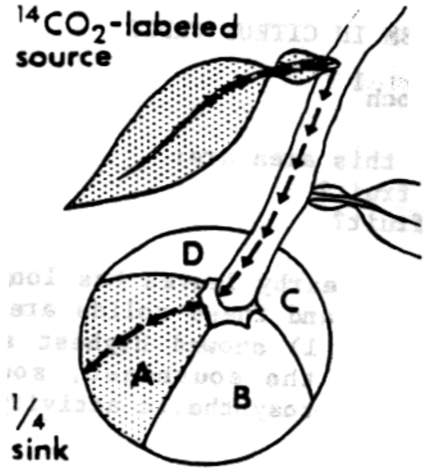


Fig. 2. Labeled products of photosynthesis move from leaves near fruit into sections vertically aligned with them. Greater than 90% of photosynthates from a given leaf will typically be found in the 1/4 fruit labeled A in this figure. Transport into individual juice sections is still more specific. (from Koch, 1984a)

Sugar movement into citrus fruit is strikingly affected by the unusual distribution of vascular tissues in the fruit. The peel has a dense network of vascular bundles and receives photosynthetic materials from leaves relatively rapidly (about 3 to 6 hours). Citrus juice tissues, however, differ from the juice tissue of almost all other crop species in having no vascular strands. Three vascular bundles outside each segment must therefore provide all the solids to the juice vesicles inside (Fig. 3). Dorsal vascular bundles are the main path of sugar movement, with some photosynthetic products also entering by septal bundles. Central strands supply only seeds.

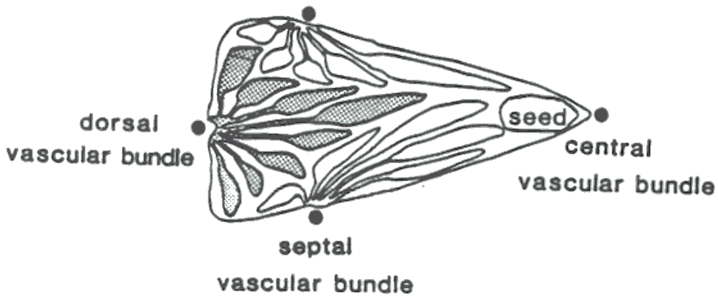


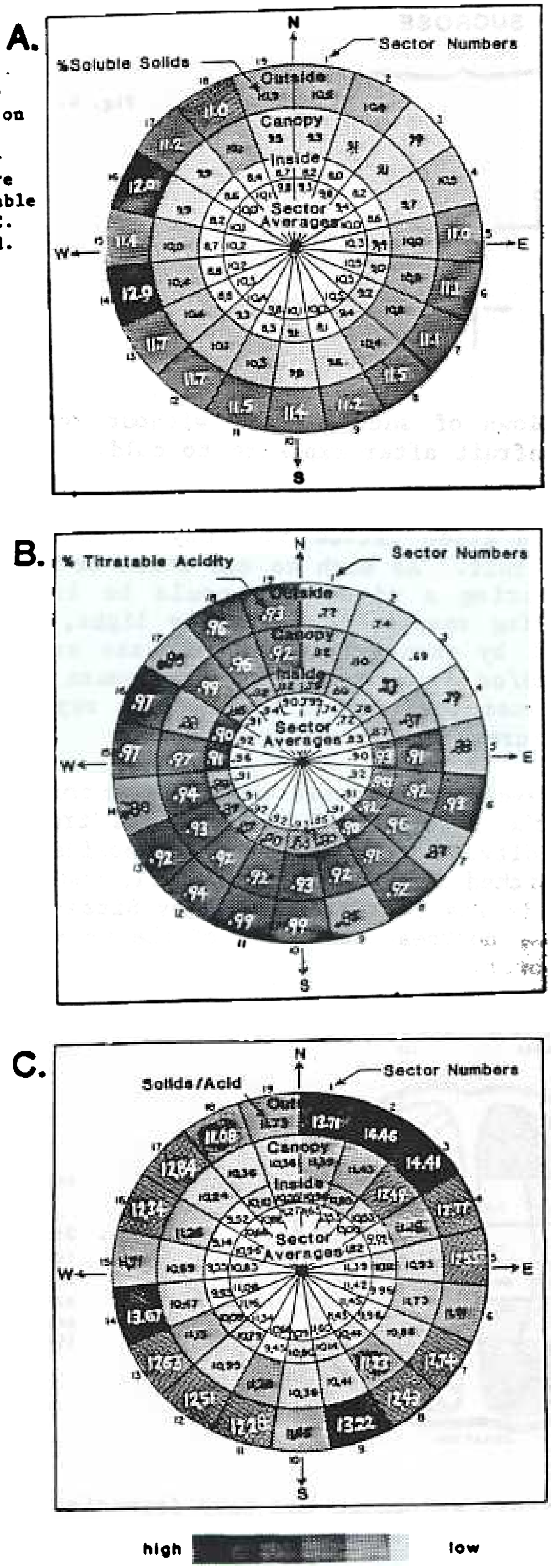
Fig. 3. Three vascular bundles supply photosynthetic products (primarily sugars) to all juice tissues inside a given segment. Citrus fruit differ from all other agronomic crops in having such extensive nonvascular areas. Each juice vesicle is joined to the segment epidermis at a site near a vascular bundle by a hair-like vesicle stalk.

Figure 3 also shows that each juice vesicle is attached to a point on the inside of the segment epidermis just opposite one of the three vascular bundles. The base of most juice vesicles is a minute, hair-like strand up to 2 cm long (about 3/4 inch). Sugar movement through this zone is apparently not facilitated by any vascular tissues or other specialized structures. Photosynthetic materials from leaves move through these vesicle stalks and segment epidermis so slowly, that complete transfer may take 3 to 5 days. The sugars appear to reach the fruit within less than 1 day, but redistribution into juice tissues requires an extended time.

The primary sugar transported from leaves to fruits of citrus trees is sucrose (common table sugar), which can be broken down into two other smaller sugars, glucose and fructose (Fig. 4). Even though sucrose is also the main sugar in citrus juice, it is apparently broken down and resynthesized as it moves into the fruit. A possible reason for this could be to maintain a "down-hill" concentration gradient from leaves to points where sugars are "unloaded" from the vascular tissues in the fruit. Sucrose could then continue to move into the fruit even though very high levels are accumulating in the juice vesicles.

Fig. 5.

Effect of direction of sunlight exposure and shading on fruit quality of 'Valencia' oranges harvested from portions of the tree shown here in cross section. A. Soluble solids, B. Acid (%), and C. Ratio of soluble solid/acid.



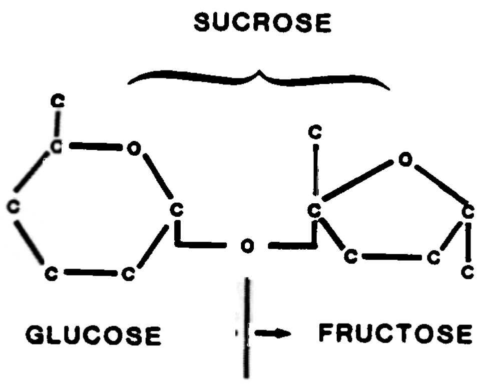


Fig. 4. Sucrose (table sugar) is the primary sugar transported in citrus trees and stored in fruit, but can be broken down into glucose and fructose.

A similar breakdown of sucrose (but without resynthesis) has been found to occur in peel of grapefruit after exposure to cold. A resistance to later chilling injury then develops.

Photosynthesis in green citrus peel may be important in reducing losses of respiratory CO_2 from fruit. As much as one third or more of the sugars moving from leaves into fruit during a given day could be lost to the atmosphere after conversion to CO_2 during respiration. In the light, however, some of this CO_2 is "trapped" in the peel by photosynthetic processes and recycled back to the fruit interior as sugars and/or organic acids. The amount of recycling will vary during fruit development because respiration occurs very rapidly during early growth, and peel photosynthesis decreases with color change.

Acid Levels - Levels of organic acids in citrus juice (mostly citric acid) differ depending on the position of fruit on the tree. Figure 5 (previous page) shows that total acidity, like total soluble solids is highest in fruit on the outside of the tree picked from southeast, south, and west exposures. The ratio of soluble solids to acids was therefore found by Sites and Reitz (also shown in Fig. 5) to be highest in the northeast quadrant of the tree, even though the total solids in these fruit were lower.

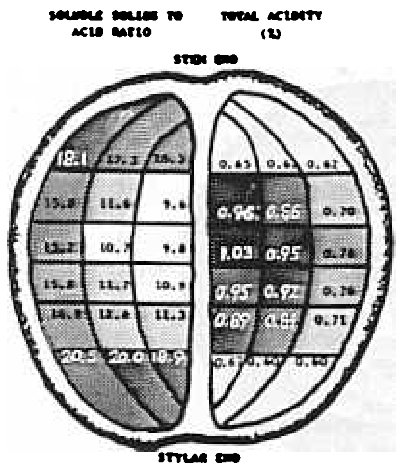


Fig. 6. Distribution of total acidity (on right) and ratio of soluble solids/acids (on left) in edible portion of 'Valencia' orange. (redone from Ting, 1969)

Total acidity within an orange can vary dramatically from one part of the juice tissues to another, and the right side of Figure 6 shows the most acid part of Valencia orange pulp is in its center. The resulting soluble solids/acid ratio (left side of Figure 6) is also lowest in the middle of the fruit.

Levels of organic acids have long been known to be reduced in grapefruit (and other citrus) by application of arsenic-based compounds. Results are often evident as early as August and the change in soluble solids/acid ratio is due specifically to effects on acidity.

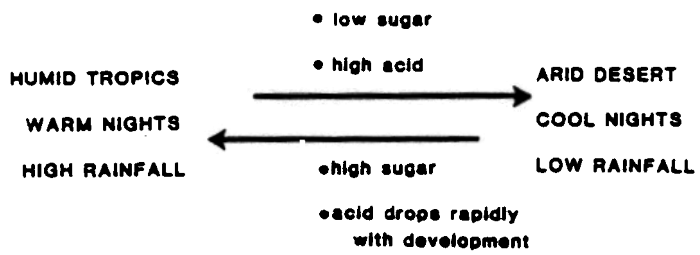


Fig. 7. Long-term climatic effects on sugar and acid in citrus fruit.

Long-term climatic effects on sugar and acid levels are shown in Figure 7. Additional information has begun to appear regarding short-term effects of environmental conditions, but reports are conflicting.

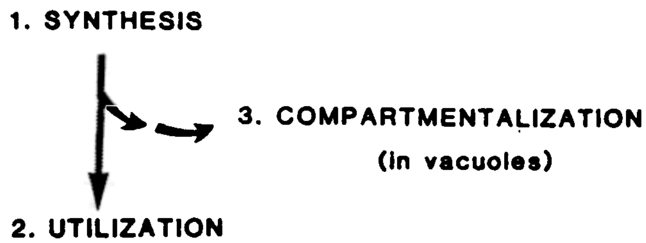


Fig. 8. Three processes which can influence the extent of acid accumulation in citrus fruit.

All three of the processes shown in Figure 8 must be considered; synthesis utilization, and compartmentalization.

Evidence suggests that at least some of the organic acids in citrus juice may be synthesized A) in leaves and translocated to fruit, B) in peel and moved inward to pulp, and C) inside juice vesicles. Organic acids from leaves were initially discounted as a major source of citrus fruit acidity years ago after an experiment showed that fruit of sweet and sour lemon were still "sweet" or "sour" if grafted and grown on leafy branches of the opposite type. Still, somewhat less dramatic effects of leaves on fruit acidity may still be important. In grapes, for example, at least one of the major types of organic acids in the fruit (tartaric acid) has been found to be synthesized in leaves and transported to fruit. Acid levels in citrus leaves are also extremely high, even more so than the fruit.

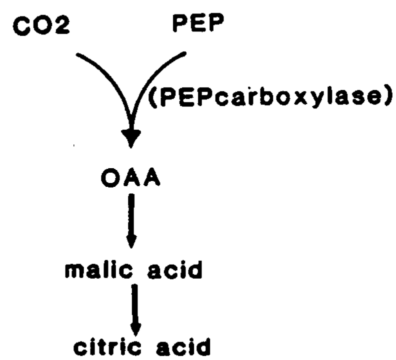


Fig. 9. The enzyme PEP carboxylase begins a series of reactions leading to formation of organic acids from CO_2.

The possibility of organic acid transport from peel to pulp is also suggested by several observations. The first of these is that the arsenic treatments noted above affect juice acidity without the arsenic ever reaching the pulp. Only leaves and peel retain levels of this compound that can be readily measured. Known effects of arsenate on metabolic pathways may therefore be occurring only in peel and leaves. In addition, transport of labeled materials from peel to pulp has been measured, and high levels of organic acids occur in peel. Lastly, an enzyme known to synthesize organic acids (PEP carboxylase) is present in peel tissues (see Fig. 9).

Juice vesicles may produce their own organic acids, either by metabolizing sugars, or through activity of the enzyme shown in Figure 9. Greater activity of this enzyme occcurs in peel, but juice vesicles have an extensive capacity to take up CO_2 (presumably as shown in Fig. 9).

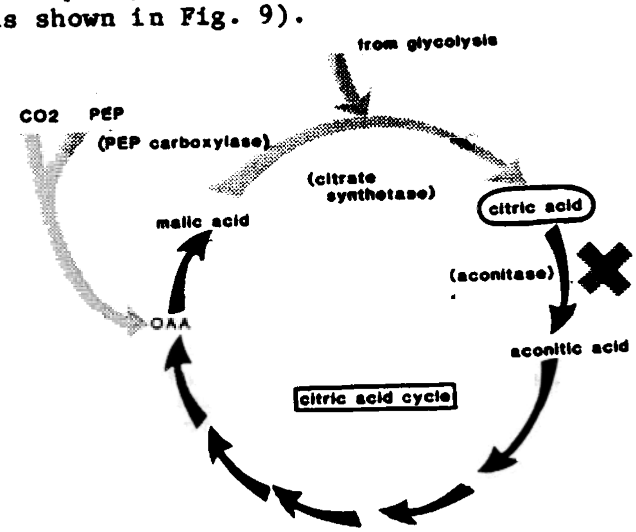


Fig. 10. The first step in citric acid utilization is the enzyme aconitase shown here with an X. Activity of this enzyme appears to influence levels of citric acid where examined thus far.

Rates of citric acid utilization could ultimately affect levels of this acid which accumulate, and the enzyme aconitase is primarily responsible for its direct breakdown of citrate in most tissues (Fig. 10 on previous page). Research in Japan on sweet and sour mandarins and in Florida on low-acid grapefruit mutants (developed by C. J. Hearn, U.S.D.A. Orlando) has indicated that activity of this enzyme of the citric acid cycle may be low in fruit where the most acid accumulates.

Compartmentalization of organic acids can prevent their utilization. This "storage" occurs when acids are transported across a membrane into the central vacuole of a cell. Vacuoles are known to be the site of acid storage and occupy over 90% of the volume in most cells. Investigations into properties of the vacuolar membrane in citrus are just beginning, but may clarify part of the basis for fruit acidity.

The ultimate goal of current research at the University of Florida on sugar/acid levels in citrus fruit is to provide alternative means of controlling this ratio.

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