

ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

A Review on Sugar and Organic Profiles on the Postharvest Quality of Fruits

Nur Hidayatul Fatihah Johari, Noer Hartini Dolhaji*, Shampazuraini Shamsuri and Phatimah Abdol Latif

¹Faculty of Plantation and Agrotechnology, University Technology MARA Cawangan Melaka Kampus Jasin, 77300, Merlimau, Malaysia

Corresponding author: noer_hartini@uitm.edu.my

Accepted: 1 April 2023; Published: 21 June 2023

ABSTRACT

Sugar and organic acids are abundant constituents of ripe fruits. They are responsible for the sweetness and sourness of fruit; hence they contribute towards the postharvest quality, especially the physical characteristics and flavors. Sugars play a key role in fruit quality, as they directly influence taste and determine consumer acceptance. The most abundant sugars in many fruits are sucrose, glucose, and fructose, while organic acids are malic and citric acids. This review aims to provide information about sugar metabolism after postharvest. Metabolic changes in mature or senescent fruits during postharvest storage cause a general degradation in qualitative characteristics, including diminishing flavors and forming offaroma compounds. Sucrose is created and transported from photosynthetically active leaves (sources) to non-photosynthetic tissues (sinks), such as developing seeds, fruits, and tubers. Secondly, to analyze the relationship between organic acid content and sugar content that affect the postharvest quality of fruits. The metabolic mechanisms employed in fruit synthesis, sugar metabolism, and malic and citric acid dissimilation are discussed. The activities of malic and citric acids in fruit flesh are also deliberated. In this review, citric acid was found to be predominated in acidic fruits, while malic acid surpassed it in acidic ones. Fructose substituted citric acid in acidless fruit and could be produced directly from citric acid or indirectly from glucose.

Keywords: Sugar profiles, organic acid, quality, postharvest, maturity



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

INTRODUCTION

Sugar provides sweetness, the most significant criterion for the quality of fruit. Several horticultural studies have examined the association between sugar concentrations and fruit yields [1 - 3]. Sugars are also vital in the production of turgor pressure, which promotes fruit cell growth, and as signal molecules, sugars control the development and metabolism of fruits. Sugars are closely linked to fruit yield and quality since they play a significant role in fruit set, growth, ripening, and composition. Glucose and fructose were the most common sugars in early fruit growth. Sucrose began to accumulate in fruit six weeks before harvesting at a faster rate than in the winter fruit tissue [2]. Research has been conducted on various species during fruit development. The total soluble sugars in a fruit typically increase with growth, peaking at maturity or ripening. Sugar builds patterns and concentrations, but they differ between species. Glucose and fructose account for most soluble sugars in most fruits [3].

Organic acids are abundant in nature as they are widely found in animal, plant, and microbial sources. They have one or more carboxylic acid groups that can be covalently linked to form amides, esters, and peptides [4]. Organic acids and their derivatives in fruit flesh have crucial physiological implications, affect the taste and quality of the fruit and, in some circumstances, determine the suitability of the fruit to be processed into various fruit products. The acidity of a fruit is an essential factor in the organoleptic quality of the fruit. Fruit acidity is indicated by the presence of organic acids produced within the fruit, with significant variations in production during various stages of development [5]. Organic acids are also critical in fruit pH maintenance and sensorial quality changes. Fruit maturity is determined by the sugar-to-acid ratio and the cultivar's quality. Good-quality fruits are obtained when harvesting is carried out at the appropriate stage of maturity. Crops harvested over their maturity stage will have a shorter postharvest life and deteriorate more quickly. In contrast, fruits harvested before their optimum maturity may not ripen sufficiently or develop good flavors [6].

SUGAR METABOLISM IN SINK CELL

Carbohydrates are the most important direct organic products of photosynthesis in most green plants, as previously indicated. The chemical equation that describes glucose production, a simple carbohydrate, is as follows.

 $\begin{array}{cccc} & & & \text{light} \\ 6\text{CO}_2 \ + \ 12\text{H}_2\text{O} & & & \text{green plants} \\ & & & \text{green plants} \end{array} \xrightarrow{} \text{C}_6\text{H}_{12}\text{O}_6 \ + \ 6\text{O}_2 \ + \ 6\text{H}_2\text{O}. \\ & & \text{carbon} & & \text{water} \\ & & & & \text{glucose} & & \text{oxygen} & \text{water} \\ & & & & \text{dioxide} \end{array}$

Equation 1

Plants transform light energy into chemical energy during photosynthesis. Glucose is stored in plants as starch, which can be broken down again into glucose via cellular respiration to supply ATP. ATP is referred to as adenosine triphosphate, where the source of energy for cellular use and storage. Glucose molecules can be mixed with and transformed into different forms of sugars as part of plant chemical



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

processes [7]. In tree crops, growth and development are linked processes in which the metabolic needs of non-photosynthetic "sink" tissues are balanced by the primary absorption of photosynthetically active "source" tissues. Typically, glucose units are connected to make starch or coupled with another sugar, fructose, to form sucrose [8].

Sugars are essential in fruit quality because they impact taste and customer acceptance. Research, which includes metabolomics-driven techniques, has documented sugar content performance during fruit growth and ripening. Sucrose and fructose, essential for plant development signaling control, are created when sucrose is broken down [9]. Sucrose is the most common fixed carbon carbohydrate (C) for long-distance transport through the phloem from leaves to non-photosynthetic sink organs such as ripening fruits [10].

Photosynthesis in Sink Cells

Photosynthesis is a process by which plants and several other organisms create carbohydrates. Figure 1 shows the entire process of photosynthesis, which influences the metabolic process of sugar in fruits [11]. Photosynthesis in leaves generates photoassimilate, but they rely on sugars translocated on the leaves. The sink strength is the force that attracts translocation sugars in fruit. If the sink strength of the fruit is weak, the fruit cannot grow adequately, growth is slow, or the fruit shrinks due to sugar starvation. Sucrose is typically produced in leaves by sucrose phosphate synthase (SPS). SPS significantly contributes to the division of carbons between sucrose and starch in photosynthetic and non-photosynthetic tissues, which impacts the development and growth of the plant. SPS oversees converting starch into sucrose and other soluble sugars in ripening fruits.

During metabolic conversion, sugars released into fruits through the cytoplasmic or apoplastic pathway are transformed into various compounds. High sugar accumulation in the vacuoles results in a high osmotic pressure, which drives cellular growth. Sugars that have been translocated in fruit tissues are carried out by phloem tissues. If enough photoassimilate is available, some regulation steps for modulating fruit sink strength, which include unloading, membrane transfer, metabolic conversion, and compartmentation, are required. During this metabolic conversion, the invertase and sucrose synthase initially metabolize sucrose, then sorbitol dehydrogenase metabolizes sorbitol, and finally, sucrose phosphate synthase synthesizes sucrose. Among these four primary processes, the role of enzymes in metabolic conversion appears to be the most significant in creating fruit sink strength since this step is closely related to sugar unloading and compartmentation [11].

Yamaki et al. stated that in the sugar metabolism of seeded and seedless fruits, the sucrose content in seeded fruits was higher than in seedless fruits due to the increased activity of SPS in seeded fruits [11]. This sucrose build-up was caused by increased sucrose synthase (SuSy) activity during fruit development, while the SPS activity did not increase [11]. A large amount of sugar accumulates in vacuoles, resulting in high turgor pressure. Much sugar accumulates in vacuoles, resulting in high osmotic pressure, and it needs sugar transporters to transport sugar into vacuoles.



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

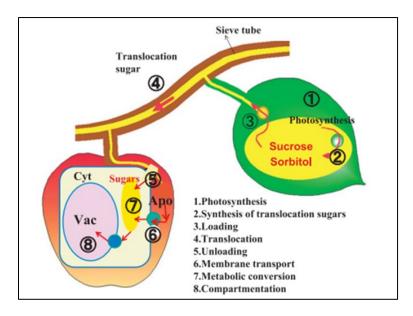


Figure 1: Photosynthesis that relates to sugar storage [11]

Sugar Transporter

Early fruit development stages are critical for determining quality crop yields [12]. Sugar transport is tightly controlled, with several transporters involved in sucrose export from photosynthetic cells and phloem loading and unloading. Once in the fruits, a portion of the sucrose-derived hexose pool is transported to the vacuole to maintain the sink strength. Only a small proportion of the sugars generated in plants, which usually are highly soluble and chemically inert, are transported across long distances through the phloem. Sucrose, less reactive than reducing sugars such as glucose and fructose, is the predominant type of carbon in the phloem; however, some other sugars, such as sorbitol, are translocated in the phloem [8].

There are different types of sugar transporters in plants, including sucrose uptake transporters (SUTs symporters), hexose transporters (hexose/H+ symporters), and SWEETs (sucrose facilitator), which is also known as Sugars Will Eventually be Exported Transporters. Sugar transporters and cell wall invertase (CWIN) are essential in carbon allocation and plant development. Carbon sinks such as ovaries and young fruits depend on sugar transporters from the source leaves. Sucrose can also be unloaded into sink cells via cytoplasmic or apoplastic or both simultaneously in these sink cells. When sucrose efflux from the phloem and hexose uptake by parenchyma cells are in high demand, some specific sugars will eventually be exported transporters (SWEETs), and hexose transporters (HTs) respond to increase CWIN activity, which is more to promote rapid fruit expansion [12].



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

Sucrose Cycle

Sucrose is the primary sugar carried in the phloem of most plants and is the product of photosynthesis. Sucrose synthase (SuSy) is a glycosyl transferase enzyme found primarily in sink tissues and is involved in sugar metabolism. SuSy catalyzes the reversible conversion of sucrose to fructose and uridine diphosphate glucose (UDP-G) or adenosine diphosphate glucose (ADP-G) [13]. Once it enters the tissues of sink cells, sucrose can enter the sink by various mechanisms [14]. Sucrose transporters can carry sucrose from the phloem to the apoplast. Sucrose transporters can then transport it into sink cells, or it can be hydrolyzed by cell-wall invertase (celNV) to produce glucose (Glc) and fructose (Fru), which hexose transporters can then transport them into sink cells [13].

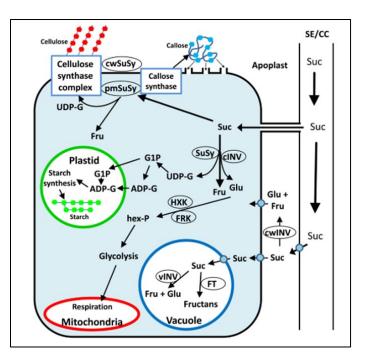


Figure 2: Sugar metabolism in tissue sinking to cellulose, callose, and starch synthesis [13]

Figure 2 shows that cell wall invertase (cwINV) can dig into sucrose in the apoplast to produce glucose and fructose, which a monosaccharide transporter can then transport into the cell. Sucrose can also move through plasmodesmata from the phloem to sink cells. Sucrose can be hydrolyzed in the cytosol by cytosolic INV to produce glucose and fructose, or it can be cleaved in the cytoplasm by cytoplasmic SuSy to produce fructose and UDP-G. The phosphorylation of hexoses forms hexose phosphates (hex-P) and can be used for starch formation in the plastid, glycolysis, mitochondrial respiration, or other metabolic pathways. SuSy can create UDP-G when connected to the plasma membrane, which is required to synthesize cellulose for the cell walls and callose for plugging of plasmodesmata (pmSuSy) [13].



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

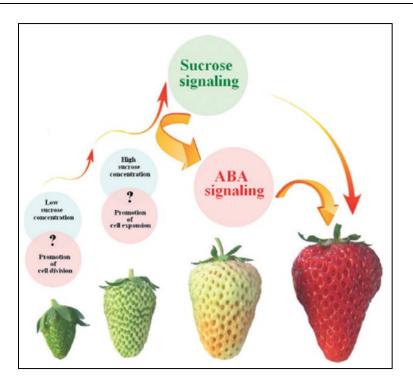


Figure 3: Sucrose signaling in strawberry fruit [15]

The sucrose signaling role in the development and ripening of strawberry fruit is depicted in Figure 3. In the early phases of fruit development, sucrose content is lower than glucose content. As the fruit matures, the sugar level rises substantially. The substantial increase in the sucrose-to-glucose ratio could be due to the conversion of cell division to cell growth. When the sucrose concentration reaches a certain level, it stimulates the formation of abscisic acid (ABA) and the following ABA signaling cascade in conjunction with the independent sucrose signaling route, which triggers fruit ripening. Fruit ripening is slowed by sucrose but not fructose, implying that sucrose-accelerated ripening is not due to sucrose metabolism [15]. From the early stages of development, strawberry has low sucrose concentration because all the enzymes in the fruit are focused on promoting cell division. It has a high sucrose concentration in the following stages to promote cell expansion and accumulate sugar. At the final stages of ripening, the fruit has reached maturity and has a high sugar content, and will produce the best fruit quality.

CONCENTRATION OF SOLUBLE SUGAR

Different fruits will have different stages of development until they reach maturity. At the early stage of fruit development, the total soluble sugar content of a fruit that consists of sucrose, fructose, and glucose is low compared to that of a fruit that has achieved maturity. This part of the review focused on four examples of fruits and their soluble sugar concentrations during fruit development.



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

Watermelon

Watermelon (*Citrullus vulgaris*) is a species of Cucurbitaceae that provides a dense source of vitamins and minerals [16]. The soluble sugar content is a significant determinant of the quality of watermelon. The firmness of watermelon is the main quality that contributes to commercial fruit values along with storage, transportability, and shelf life. Through research, watermelon contained various sugars like fructose, glucose, and sucrose. They were detected by mapping via quantitative trait loci (QTL) experiment. For the organic acids, malic and citric acids were found to be the main content in ripe watermelon.

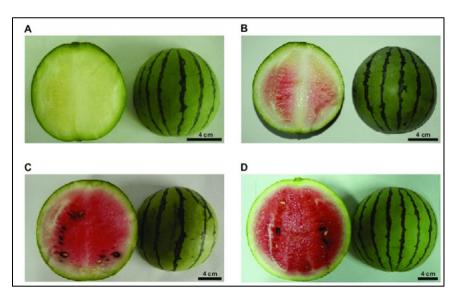


Figure 4: Different stages of watermelon cultivar 97103 Immature white - 10 DAP (A), white-pink flesh - 18 DAP (B), red flesh - 26 DAP (C), and over-ripe - 34 DAP (D). (DAP stands for days after pollination) [17].

Figure 4 describes the four different stages of ripening of watermelon cultivar 97103. Stage A shows the condition of the fruit ten days after pollination. It is still in its immature white stage, and at this stage, it contains a low quantity of soluble sugar content (SSC). The fruit continues to expand without much increase in SSC at the white-pink flesh stage, as shown in stage B, but the fruit flesh begins to turn pink and loses its firmness as in stage C. Stage D shows that the fruit is fully mature when it reaches the red flesh stage, and its flesh turns light red, crispier, and sweeter. A rapid increase in soluble sugar content (SSC) is also linked to changes in texture and taste. The fruit has become overripe, and the flesh has turned bright red due to the accumulation of volatile compounds that give watermelon its distinct aroma and flavor [17]. Comparing all stages, the fruit at stage C will have the highest customer demand because of its quality. The soluble sugar content (SSC) in the fruit will influence the taste and quality of the watermelon.



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

Pineapple

The pineapple (*Ananas comosus*) core extract has the highest concentrations of fructose, glucose, and sucrose than the other part of the fruit. According to Figure 5, in index 3, the amount of sugar in the pineapple core extract was higher than in indices 1 and 2. In the pineapple core extract for index 2, glucose and fructose levels were higher than in indices 1 and 3. The primary sugar in the pineapple core and peel extracts is sucrose [18].

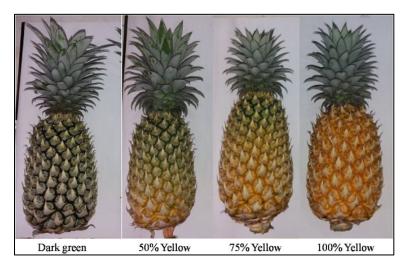


Figure 5: Different maturity stages of Mauritius pineapple (Queen type) [19]

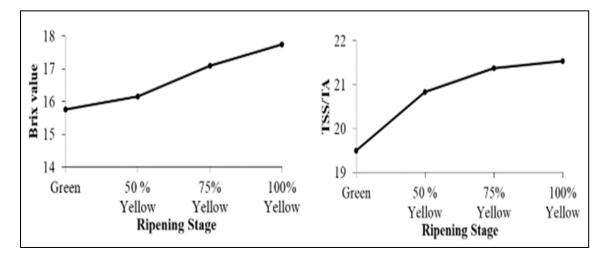


Figure 6: Brix value (TSS) and total soluble solid/titratable acidity (TSS/TA) in different ripening stages of Mauritius pineapple (Queen type) [19]



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

According to Figure 6, there are differences among the pineapple fruits in terms of color, firmness, total soluble sugar content, and titratable acidity. The pineapple's total soluble solid (TSS) content in the dark green stage differed significantly from those in the 75% and 100% yellow color stages. In comparison, the pineapple in the 50% yellow color stage differed significantly from that of the 100% yellow color stage. TSS increased steadily as the fruit ripened, reaching a peak of 12.69% in the 100% yellow stage compared to the dark green stage. During ripening, ADP-glucose pyrophosphorylase, amylases, and sucrose phosphate synthase convert starch to sugars such as glucose, sucrose, and fructose, increasing the TSS value of pineapples [19]. It is shown that the pineapple in the 100% yellow color stage will produce the best quality fruits in terms of their taste.

Tomato

Tomatoes (*Solanum lycopersicum*) are an important horticultural crop, with the biggest global production volume (t) and economic value e (Ministry of Agriculture, Forestry, a Fisheries) of all fruits and vegetables [1]. Tomatoes are medium-sized fruit with a delicate sweetness and a slightly harsh and acidic flavor. Brix9-2-5, a cell wall invertase (LIN5) functional amino acid polymorphism, is found to influence tomato fruit sugar levels. This has an enormous impact on the strength of the fruit sink because it changes the kinetics, which affects the sugar content. Tomatoes have a moderate sweetness complemented by a somewhat bitter and acidic flavor. Fruit sugar content and yield are thought to compete. While the sugar content of tomato fruit increases as the sucrose-to-hexose ratio increases, the size of the fruit decreases as the expression of the vacuolar invertase gene decreases [1].

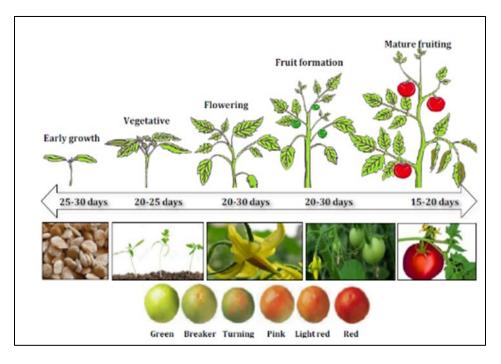


Figure 7: Different stages of tomato growth and ripening [20]



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

The research discovered that tomatoes' soluble sugar started accumulating within 15-20 days of maturing. Figure 7 implies that the sugar content is very low from the early growth of the fruit. The green-colored fruit has a lower taste and quality than the red-colored, which has a higher sugar content. Tomatoes that reach high maturity will have a higher sugar content and produce the best quality fruit in terms of taste [20].

ACTIVITIES OF KEY ENZYMES IN SUGAR METABOLISM

Sucrose synthases, glucosyl transferase enzymes, play a crucial role in sugar metabolizing by breaking down sucrose into fructose and glucose in the sink cells. This helps to keep the sink strong. Sucrose synthases have a role in synthesizing carbohydrate polymers such as starch and cellulose and in generating energy for manufacturing several compounds that aid fruit growth and seed dissemination [21]. Based on their subcellular location, invertases are classified as cytoplasmic invertases (CIN), vacuolar invertases (VIN), and cell wall invertases (CWIN) [22]. VIN and CWIN have been related to biotic and abiotic reactions, linking sucrose and hexose signaling to stress adaptation. Invertases regulate plant growth and development, and VIN and CWIN have been associated with biotic and abiotic responses, linking sucrose and hexose signaling to stress adaptation. CWIN activity increases, possibly to aid phloem unloading and transmit a glucose signal that promotes cell proliferation [23].

Although there is less investigation in this field than in sugar-metabolizing enzymes, genetic alteration of sugar sensors and signaling and sugar-metabolizing enzymes could effectively increase sugar accumulation and modify sugar composition [1]. A group of such systems, namely hexokinase (HXK), boosts signaling directly. In contrast, another group, such as sucrose-non-fermentation-related protein kinase 1 (SnRK1), modifies signaling proteins indirectly via sugar-derived bioenergetic molecules and metabolites. HXK, a well-known sugar sensor, mediates photosynthesis-related gene expression suppression. In hexose phosphorylation and glucose sensing, it fulfills two separate functions. HXK regulates transcription by building a complex with vacuole H+-ATPase B1 (VHA-B1) and the 19S regulatory particle of the proteasome subunit and binding to the promoter region of genes in the nucleus (RPT5B). The sensor and signaling systems of the two metabolic sugars, sucrose, and fructose, on the other hand, are virtually intact [24].

Because fructose is sweeter than sucrose and glucose, metabolic engineering has raised fructose concentration at two locations along the sugar metabolic pathway. When sucrose is unloaded into fruit cells, and fructose and hexose are produced, the fructokinase (FRK) enzyme is required for fructose metabolism. Plants have numerous FRK genes, which have different roles in phosphorylating fructose to fructose-6-phosphate, used in starch production. In order to increase the fructose content in fruits, such as tomatoes, the FRK gene expression has been suppressed. The alteration of the sugar to produce a higher ratio of "sweeter" fructose to glucose without increasing the total sugar content appears to be a potential technique for generating sweet fruits, as this may be easier than increasing the total sugar content [1].



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

ORGANIC ACID

All fruits have many organic acids in their fleshy parts, but most are in small amounts, as summarized in Table 1. Fruits contain a variety of organic acids, but most fruits are primarily composed of one or two primary organic acids, which are malic acid and citric acid. The remaining types of organic acids, such as quinic acid, isocitric acid, galacturonic acid, and oxalic acid, are the minor ones in most fruits. Different types of fruits contain different levels of organic acids [25]. The various organic acids found in fruits are involved in a variety of metabolic processes, including acting as intermediates in various metabolic pathways, precursors for amino acid synthesis, and many plant hormones such as auxins, gibberellins, fatty acids, a wide variety of secondary metabolites, and specific components of the cell wall [26]. J.B Gurtler and T.L Mai [27] reported the different types of organic acids detected in various fruits in their research article titled *Traditional Preservatives – Organic Acids* (Table 1). Fruit acid levels vary greatly depending on how ripe the fruits are. Fruits that are not fully ripe have a higher acid content but less sugar [27]. There are three metabolomic groups of organic acids. The first group consists of malic, citric, and isocitric acids. The second is ascorbic and tartaric acids, while the third is quinic acid.

Fruit	pH range	Major acids	Other acids
Apple	2.9-4.5	Citric, malic	Quinic, tartaric, caffeic ferulic, benzoic
Blueberries	2.8-3.2	Quinic, citric	Malic, ellagic, chlorogenic, salycilic
Cherry	3.7-4.4	Ascorbic, citric	Malic, tartaric, quinic, shikimik
Grape	2.9-3.9	Malic, tartaric	Quinic, ellagic, citric
Guava	3.2-4.2	Citric, malic	Ellagic, salycilic
Kiwifruit	3.1-4.0	Quinic, citric	Malic, oxalid, ascorbic
Lemon	2.0-2.6	Citric, quinic	Malic, tartaric, oxalid, succinic, ascorbic
Lime	1.6-3.2	Citric, malic	Benzoic, salycilic, lactic
Mango	4.3-6.0	Citric, tartaric	Anacardic, gallic, dehydroascorbic, ascorbic, malic
Orange	2.6-4.3	Citric, quinic	Malic, tartaric, oxalic, succinic, ascorbic, ferulic, dehydroascorbic
Papaya	5.2-5.7	Citric, malic	Dehydroascorbic, ascorbic, oxalic, tartaric, quinic, succinic, fumaric
Pear	3.0-4.5	Malic, citric	Caffeic, quinic, tartaric, fumaric, shikimik, lactic, succinic, oxalic, acetic
Pineapple	3.1-4.0	Citric, malic	Quinic, tartaric, chlorogenic, ferulic, oxalic
Strawberry	3.0-3.5	Citric, ascorbic	Malic, tartaric, hydroxybenzoic, ellagic, gallic, chlorogenic
Tomato	4.1-4.7	Citric, ascorbic	Oxalic, salycilic, ascorbic, malic, glutamic, aspartic

Table 1: The range of primary organic acids in fruits at the normal ripeness stage [27]



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

Citric Acid

Citric acid is the primary organic acid in fruits and is most abundant in citrus fruit. It rises during fruit growth and drops during ripening and postharvest [28]. The reduction of citric acid is primarily due to its usage as a respiratory substrate or in amino acid synthesis. Various enzymes, including aconitase (ACO), phosphoenolpyruvate carboxykinase (PEPCK), and isocitrate dehydrogenase (IDH), catalyze citric acid breakdown [29]. The production and breakdown activity of citric acid determines the organic acid levels in most citrus fruits. The primary enzyme producing citric acid in fruits is citrate synthase (CS), expressed similarly in regular and granulated juice sacs. The tricarboxylic acid (TCA) cycle, which allows citric acid to be used as a respiration substrate, is one of the most important mechanisms for citric acid degradation [30]. Aconitase (ACO) catalyzes the conversion of citrate to isocitrate in the citric acid breakdown pathway.

Malic Acid

Malic acid is a C4 dicarboxylic acid that could be a key platform chemical in the post-fossil fuel era. Malic acid is a naturally occurring intermediate in the tricarboxylic acid cycle (TCA) that various microorganisms and plants can accumulate. The taste of malic acid is said to develop more slowly than that of citric acid and last longer, making it ideal for masking the aftertaste of artificial sweeteners [31]. The chiral product is produced synthetically, but there appears to be no difference in taste quality or sour intensity. In Japan, chiral malic acid has been approved as a food additive. It has a slightly stimulating and continuous sour taste that is almost as sour as citric acid [32].

Other Types of Organic Acids

Tartaric acid has a relatively strong, more sharp flavor than citric acid. Although it is mainly found in grapes, it can also be found in apples, cherries, papaya, peach, pear, pineapple, strawberries, mangos, and citrus fruits [27]. Isocitric acid, a product of the tricarboxylic acid cycle, is the primary acid found in blackberries but can also be found in other fruits in lower concentrations. Isocitric acid is a minor organic acid found in most fruit juices, particularly blackberries, youngberries, and vegetables, especially carrots. The determination of d-isocitric acid has become necessary in the analysis of fruit juices for the detection of illegal additives (adulteration).

D-Galacturonic acid is the main ingredient of pectin, a compound found naturally. When sugar is extracted from sugar beets, or juice is extracted from citrus fruits, pectin-rich residues accumulate. Another type of organic acid in fruits is quinic acid. The accumulation of quinic acid occurred primarily in the early stages of fruit development around 60 days after anthesis (DAA). For example, in kiwifruit, separate quinate dehydrogenase (QDH) and shikimate dehydrogenase (SDH) activities were discovered, most likely representing different proteins. In plants, oxalic acid serves various functions that depend on the plant species and tissue or cell type. The skin of kiwifruit contains more calcium oxalate crystals than the flesh, which could serve as a deterrent to animal attack. Oxalate oxidase breaks down oxalate, producing carbon dioxide (CO2) and peroxide, and this peroxide may play a role in the oxidation of phenols in the extracellular matrix. Oxalic acid is found in a wide range of fruits and is probably present in them, but it is not abundant in most. Research has found that oxalic acid content is often determined by the genotype or cultivar of a particular fruit [26].



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

Ascorbic acid, or the other name for vitamin C, is a water-soluble vitamin found in various biological systems and foods such as fresh vegetables and fruits, namely citrus. Ascorbic acid is involved in wound healing, osteogenesis, collagen biosynthesis, iron absorption, and immune response activation [33]. Fruits are the primary sources of ascorbic acid.

Citric Acid Cycle

Most organic acids found in fruit flesh are not imported but rather synthesized in the flesh from imported sugars. There are several outcomes if these acids are metabolized during ripening. The main ones are the citric acid cycle (respiration), gluconeogenesis, fermentation to ethanol, synthesis or interconversion of amino acids, and as a substrate for synthesizing secondary metabolites such as pigments [34]. In this part of the review, a citric acid cycle, the primary process of producing organic acids in fruits, is focused. Malic and citric acid are the most common citric cycle acids in fruits. Most citric cycle acids found in fruits are believed to be synthesized from imported sugars within the fruit [26].

Types of fruit	Organic acid concentration (malate/citrate)	Duration
Grape	Increase	Beginning of ripening
	Decrease	Ripening
Cherry	Increase	Beginning of ripening
	Decrease	Ripening
Mango	Decrease	Ripening
	Increase	Commercial harvest
Strawberry	Decrease	Ripening
	Increase	Commercial harvest
Plum	Decrease	Ripening
Banana	Increase	Ripening
Lemon	Increase	Ripening

 Table 2: Organic acid concentration that accumulates during the citric acid cycle in fruits [34]

Based on the review by Franco Famiani *et al.* [34], the anions of citric, isocitric, and malic acids, which are namely citrate, isocitrate, and malate, are citric acid cycle intermediates, and one or more of them, usually citric or malic acids, accounts for a large proportion of the organic acid content of the flesh of all fruits studied. However, large amounts of acids of the citric acid cycle accumulate in the vacuole of many fruits, and these acids serve other purposes. For example, they are likely to contribute to the fruit's quality until the seeds have developed in many fruits. The fruit begins to ripen as the seed matures, and its



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

citric cycle acids concentration (mg⁻¹ FW) decreases. These acids can be used as metabolic substrates if net dissimilation occurs during ripening. The stage of development of the fruit and the specific part of the fruit also determines this abundance. Fruits protect and aid in the dispersion of seeds, so the accumulation of some organic acids in fruits could be related to these functions.

QUALITY, SUGAR, AND ORGANIC ACID

Color, appearance, texture, and flavor are the three essential aspects that determine fruit quality. Although suppliers are frequently reimbursed based on the physical features of their fruit, such as color, size, lack of flaws, and texture, it is critical to assess the fruit's flavor, as it is the primary driver of consumers' repeat purchases. Each fruit has its sugar profile, some sweet and others sour. This is determined by the substances found in each fruit. The amount of sugar, fructose, acid, vitamins, proteins, cellulose, and starch in each fruit species varies, giving it a distinct sweet or sour flavor. Most people evaluate fruit quality primarily on its flavor. Fruits are available in various flavors, including sweet, sour, and other variations [35].

The type of sugar in a fruit determines its sweetness. The sweetness of the fruit increases as the sugar level increases. Furthermore, the sweetness of the fruit is affected by different types of sugar, with sucrose, fructose, and glucose being the most prevalent sugars found in fruits. Each of these sugars is sweet to a different degree. Fructose is 1.7 times sweeter than glucose and sorbitol, although they are only 0.8 and 0.6 times, respectively, sweeter than sucrose. If one type of apple contains more fructose and another contains more glucose, the former will be sweeter [35].

Organic acid levels are frequently inversely related to sugar levels during fruit development. As a result, sugar levels rise during maturity and ripening because of either sugar import or starch decomposition, while organic acids stored in early fruits degrade quickly [36]. Many fruits, including peach, lemon, pineapple, apple, and strawberry, have shown changes that genetically regulate variations among organic acids during development. Citrus is one of the most popular fruits in the world. It has a delicious flavor and is high in vitamins. Granulation, also known as section drying or crystallization, is a significant physiological condition that affects a wide range of citrus species during late harvest and storage. Sugars and organic acids regulate the sweetness and acidity of citrus fruits. Sugar levels rise throughout fruit development and ripening, then decrease or drop during the postharvest period [30]. The balance of sugar breakdown and biosynthesis, carried out by numerous essential enzymes such as sucrose synthase (SUS), sucrose phosphate synthase (SPS), and invertase, determines the sugar content in the postharvest fruit.

CONCLUSION

In this review, plants convert carbon dioxide and water into sugar via light energy in photosynthesis. This process creates a variety of energy-rich compounds that are the building blocks of all life on Earth. A recent study by some researchers discovered that unidentified signaling pathways might be involved in sugar metabolism. The researchers used the model plant Arabidopsis to study mutants that lack the Squamosa promoter binding protein-like 7 (SPL7) protein. These mutants' poor sugar metabolism caused sugars to build up in their tissues. According to the study, SPL7 does more than activate the copper deficiency response, and it also regulates plant energy metabolism. This newly discovered regulatory link illustrates



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

the importance of protein activities in energy metabolism, such as respiration and land plants' photosynthesis, and it is copper independent. The best-studied plant sugar signaling pathways were discovered to function generally in the SPL7 mutants, suggesting the involvement of an additional, as-yet-unidentified pathway [39].

ACKNOWLEDGMENTS

The authors would like to acknowledge the support of Universiti Teknologi Mara (UiTM), Cawangan Negeri Sembilan, Kampus Kuala Pilah and Faculty of Applied Sciences, Universiti Teknologi MARA, Shah Alam, Selangor, Malaysia, for providing the facilities and financial support on this research.

AUTHOR'S CONTRIBUTION

All authors were equally contributed to the writing of the article.

CONFLICT OF INTEREST STATEMENT

The authors agree that this research was conducted without any self-benefits or commercial or financial conflicts and declare the absence of conflicting interests with the funders.

REFERENCES

- [1] Kanayama, Y. (2017). Sugar metabolism and fruit development in the tomato. *Horticulture Journal*, 86(4), 417–425. https://doi.org/10.2503/hortj.OKD-IR01
- [2] Chen, C. C., & Paull, R. E. (2000). Sugar metabolism and pineapple flesh translucency. *Journal of the American Society for Horticultural Science*, *125*(5), 558–562. https://doi.org/10.21273/jashs.125.5.558
- [3] Desnoues, E., Gibon, Y., Baldazzi, V., Signoret, V., Génard, M., & Quilot-Turion, B. (2014). Profiling sugar metabolism during fruit development in a peach progeny with different fructose-toglucose ratios. *BMC Plant Biology*, *14*(1), 12–14. https://doi.org/10.1186/s12870-014-0336-x
- Papagianni, M. (2011). Organic Acids. In *Comprehensive Biotechnology, Second Edition* (Second Edit, Vol. 1). Elsevier BV https://doi.org/10.1016/B978-0-08-088504-9.00011-8
- [5] Mu, X., Wang, P., Du, J., Gao, Y. G., & Zhang, J. (2018). Comparison of fruit organic acids and metabolism-related gene expression between cerasus humilis (Bge.) Sok and cerasus glandulosa (Thunb.) Lois. *PLoS ONE*, 13(4), 1–14. https://doi.org/10.1371/journal.pone.0196537
- [6] Umer, M. J., Bin Safdar, L., Gebremeskel, H., Zhao, S., Yuan, P., Zhu, H., Kaseb, M. O., Anees, M., Lu, X., He, N., Gong, C., & Liu, W. (2020). Identification of key gene networks controlling organic acid and sugar metabolism during watermelon fruit development by integrating metabolic phenotypes and gene expression profiles. *Horticulture Research*, 7(1).



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

https://doi.org/10.1038/s41438-020-00416-8

- [7] Lemoine, R., La Camera, S., Atanassova, R., Dédaldéchamp, F., Allario, T., Pourtau, N., Bonnemain, J. L., Laloi, M., Coutos-Thévenot, P., Maurousset, L., Faucher, M., Girousse, C., Lemonnier, P., Parrilla, J., & Durand, M. (2013). Source-to-sink transport of sugar and regulation by environmental factors. *Frontiers in Plant Science*, 4(JUL), 1–21. https://doi.org/10.3389/fpls.2013.00272
- [8] Falchi, R., Bonghi, C., Drincovich, M. F., Famiani, F., Lara, M. V., Walker, R. P., & Vizzotto, G. (2020). Sugar Metabolism in Stone Fruit: Source-Sink Relationships and Environmental and Agronomical Effects. *Frontiers in Plant Science*, 11(November). https://doi.org/10.3389/fpls.2020.573982
- [9] Durán-Soria, S., Pott, D. M., Osorio, S., & Vallarino, J. G. (2020). Sugar Signaling During Fruit Ripening. *Frontiers in Plant Science*, *11*(August), 1–18. https://doi.org/10.3389/fpls.2020.564917
- [10] Julius, B. T., Leach, K. A., Tran, T. M., Mertz, R. A., & Braun, D. M. (2017). Sugar transporters in plants: New insights and discoveries. *Plant and Cell Physiology*, 58(9), 1442–1460. https://doi.org/10.1093/pcp/pcx090
- [11] Yamaki, S. (2010). Metabolism and accumulation of sugars translocated to fruit and their regulation. Journal of the Japanese Society for Horticultural Science, 79(1), 1–15. https://doi.org/10.2503/jjshs1.79.1
- [12] Ru, L., He, Y., Zhu, Z., Patrick, J. W., & Ruan, Y. L. (2020). Integrating Sugar Metabolism With Transport: Elevation of Endogenous Cell Wall Invertase Activity Up-Regulates SIHT2 and SISWEET12c Expression for Early Fruit Development in Tomato. *Frontiers in Genetics*, 11(October). https://doi.org/10.3389/fgene.2020.592596
- [13] Stein, O., & Granot, D. (2019a). An overview of sucrose synthases in plants. Frontiers in Plant Science, 10(February), 1–14. https://doi.org/10.3389/fpls.2019.00095
- [14] Ma, S., Li, Y., Li, X., Sui, X., & Zhang, Z. (2019). Phloem Unloading Strategies and Mechanisms in Crop Fruits. *Journal of Plant Growth Regulation*, 38(2), 494–500. https://doi.org/10.1007/s00344-018-9864-1
- [15] Jia, H., Wang, Y., Sun, M., Li, B., Han, Y., Zhao, Y., Li, X., Ding, N., Li, C., Ji, W., & Jia, W. (2013). Sucrose functions as a signal involved in the regulation of strawberry fruit development and ripening. *New Phytologist*, 198(2), 453–465. https://doi.org/10.1111/nph.12176
- [16] Amin, M., Ullah, S., Rehman, S., Ullah, Z., & Amir, M. (2014). Comparison of Different Types of Water Melon for Their Important Nutrients. *Journal of Biology, Agriculture and Healthcare*, 4(14), 59–66.
- [17] Guo, S., Sun, H., Zhang, H., Liu, J., Ren, Y., Gong, G., Jiao, C., Zheng, Y., Yang, W., Fei, Z., & Xu, Y. (2015). Comparative transcriptome analysis of cultivated and wild watermelon during fruit development. *PLoS ONE*, 10(6), 1–21. https://doi.org/10.1371/journal.pone.0130267
- [18] Siti, A. M., Zainal, S., Noriham, A., & Nadzirah, K. Z. (2013). Determination of sugar content in pineapple waste variety N36. *International Food Research Journal*, 20(4), 1941–1943.
- [19] Kumara, B. A. M. S., & Hettige, K. D. T. (2020). Ripening stage Affects the Quality of Fresh and Dehydrated Pineapples (*Ananas comosus* (L.) Merr.) cv. Mauritius in Sri Lanka. Sustainable Food Production, 8(October 2020), 29–37. https://doi.org/10.18052/www.scipress.com/sfp.8.29
- [20] Janssen, B. J., Thodey, K., Schaffer, R. J., Alba, R., Balakrishnan, L., Bishop, R., Bowen, J. H., Crowhurst, R. N., Gleave, A. P., Ledger, S., McArtney, S., Pichler, F. B., Snowden, K. C., & Ward, S. (2008). Global gene expression analysis of apple fruit development from the floral bud to ripe fruit. *BMC Plant Biology*, 8, 1–29. https://doi.org/10.1186/1471-2229-8-16
- [21] Braun, D. M., Wang, L., & Ruan, Y. L. (2014). Understanding and manipulating sucrose phloem loading, unloading, metabolism, and signaling to enhance crop yield and food security. *Journal of*



Experimental Botany, 65(7), 1713–1735. https://doi.org/10.1093/jxb/ert416

- [22] Li, M., Feng, F., & Cheng, L. (2012). Expression patterns of genes involved in sugar metabolism and accumulation during apple fruit development. *PLoS ONE*, 7(3). https://doi.org/10.1371/journal.pone.0033055
- [23] Palmer, W. M., Ru, L., Jin, Y., Patrick, J. W., & Ruan, Y. L. (2015). Tomato ovary-to-fruit transition is characterized by a spatial shift of mRNAs for cell wall invertase and its inhibitor with the encoded proteins localized to sieve elements. *Molecular Plant*, 8(2), 315–328. https://doi.org/10.1016/j.molp.2014.12.019
- [24] Li, M., Li, P., Ma, F., Dandekar, A. M., & Cheng, L. (2018). Sugar metabolism and accumulation in the fruit of transgenic apple trees with decreased sorbitol synthesis. *Horticulture Research*, 5(1). https://doi.org/10.1038/s41438-018-0064-8
- [25] Jiang, Z., Huang, Q., Jia, D., Zhong, M., Tao, J., Liao, G., Huang, C., & Xu, X. (2020). Characterization of organic acid metabolism and expression of related genes during fruit development of Actinidia eriantha 'game 6.' *Plants*, 9(3). https://doi.org/10.3390/plants9030332
- [26] Walker, R. P., Chen, Z. H., & Famiani, F. (2021). Gluconeogenesis in Plants: A Key Interface between Organic Acid/Amino Acid/Lipid and Sugar Metabolism. *Molecules*, 26(17), 1–18. https://doi.org/10.3390/molecules26175129
- [27] Gurtler, J. B., & Mai, T. L. (2014). Preservatives: Traditional Preservatives Organic Acids. In Encyclopedia of Food Microbiology: Second Edition (Second Edi, Vol. 3). Elsevier. https://doi.org/10.1016/B978-0-12-384730-0.00260-3
- [28] Ding, Y., Chang, J., Ma, Q., Chen, L., Liu, S., Jin, S., Han, J., Xu, R., Zhu, A., Guo, J., Luo, Y., Xu, J., Xu, Q., Zeng, Y., Deng, X., & Cheng, Y. (2015). Network analysis of postharvest senescence process in citrus fruits revealed by transcriptomic and metabolomic profiling. *Plant Physiology*, 168(1), 357–376. https://doi.org/10.1104/pp.114.255711
- [29] Sheng, L., Shen, D., Yang, W., Zhang, M., Zeng, Y., Xu, J., Deng, X., & Cheng, Y. (2017). GABA Pathway Rate-Limit Citrate Degradation in Postharvest Citrus Fruit Evidence from HB Pumelo (Citrus grandis) × Fairchild (Citrus reticulata) Hybrid Population. *Journal of Agricultural and Food Chemistry*, 65(8), 1669–1676. https://doi.org/10.1021/acs.jafc.6b05237
- [30] Wu, B. H., Zhao, J. B., Chen, J., Xi, H. F., Jiang, Q., & Li, S. H. (2012). Maternal inheritance of sugars and acids in peach (P. persica (L.) Batsch) fruit. *Euphytica*, 188(3), 333–345. https://doi.org/10.1007/s10681-012-0668-2
- [31] Kövilein, A., Kubisch, C., Cai, L., & Ochsenreither, K. (2020). Malic acid production from renewables: a review. *Journal of Chemical Technology and Biotechnology*, 95(3), 513–526. https://doi.org/10.1002/jctb.6269
- [32] Izawa, K., Amino, Y., Kohmura, M., Ueda, Y., & Kuroda, M. (2010). Human-environment interactions taste. *Comprehensive Natural Products II: Chemistry and Biology*, *4*, 631–671. https://doi.org/10.1016/b978-008045382-8.00108-8
- [33] Danet, A. F., Pisoschi, A. M., & Kalinowski, S. (2008). Ascorbic acid determination in commercial fruit juice samples by cyclic voltammetry. *Journal of Automated Methods and Management in Chemistry*, 2008(Ii). https://doi.org/10.1155/2008/937651
- [34] Famiani, F., Battistelli, A., Moscatello, S., Cruz-Castillo, J. G., & Walker, R. P. (2015). Ácidos orgánicos acumulados en la pulpa de los frutos: Ocurrencia, metabolismo y factores que afectan sus contenidos- una revisión. *Revista Chapingo, Serie Horticultura*, 21(2), 97–128. https://doi.org/10.5154/r.rchsh.2015.01.004
- [35] Macarena. (2020). Fruit Quality How Do Fruit Get Their Flavor? What Factors Affect Flavor?
- [36] Batista-Silva, W., Nascimento, V. L., Medeiros, D. B., Nunes-Nesi, A., Ribeiro, D. M., Zsögön, A.,



ISSN: 1675-7785 eISSN: 2682-8626 Copyright© 2023 UiTM Press. DOI:

& Araújo, W. L. (2018). Modifications in organic acid profiles during fruit development and ripening: Correlation or causation? *Frontiers in Plant Science*, 871(November), 1–20. https://doi.org/10.3389/fpls.2018.01689

- [37] Guo, S., Liu, J., Zheng, Y., Huang, M., Zhang, H., Gong, G., He, H., Ren, Y., Zhong, S., Fei, Z., & Xu, Y. (2011). Characterization of transcriptome dynamics during watermelon fruit development: Sequencing, assembly, annotation, and gene expression profiles. *BMC Genomics*, 12(1), 454. https://doi.org/10.1186/1471-2164-12-454
- [38] Stein, O., & Granot, D. (2019b). An overview of sucrose synthases in plants. In *Frontiers in Plant Science* (Vol. 10). https://doi.org/10.3389/fpls.2019.00095
- [39] Julia Weller. (2022). How do plants regulate their sugar metabolism? Retrieved November 23, 2022, from News.rub.de website: https://news.rub.de/english/press-releases/2022-08-04-biology-how-do-plants-regulate-their-sugar-metabolism