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Starch and sugars as determinants of postharvest shelf life and quality: some new and surprising roles

Jingwei Yu¹, Yute Tseng^{2,3}, Kien Pham^{2,3}, Margaret Liu^{2,3} and Diane M Beckles²



Starch and sugars account for most of the dry weight of horticultural crops and in many species, are known determinants of quality. However, we posit that these carbohydrates often have less-obvious roles in plant tissues with direct implications for the postharvest quality and produce shelf life. The latter has not been given as much attention, but with the recent interest in reducing the scale of postharvest waste and loss, we highlight how dynamic changes in the spatial-temporal accumulation of carbohydrates, can influence myriads of biological processes affecting postharvest attributes. Versatile roles, some surprising, that carbohydrates play in determining produce of high value to consumers, are highlighted, and gene targets for biotechnological improvement are specified.

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Introduction

Carbohydrates, mainly sugars and starch, are the major reserve, flavor, and textural components of many horticultural crops, and as such, determine their nutritional value, postharvest quality, and storage life [1] (see [Box 1](#)). However, even in seemingly ‘carbohydrate-irrelevant’ leafy greens and various produce [1], starch and

sugars may exert less obvious, yet we argue, critical roles in shaping postharvest quality.

Starch and sugars have diverse functions in cells depending on their relative concentration, mobilization, subcellular location, and interaction with proteins. They sustain growth and buffer cells from stress [2], and as signaling molecules, they regulate many pathways that determine nutrient allocation to the sinks, and their partitioning into different biomolecular pools [2].

Most knowledge of carbohydrate metabolism is derived from cereals and model plants. Here, we intend to build several theoretical frameworks to show that carbohydrates, especially starch, may have ‘surprising’ roles in determining horticultural postharvest quality. We show that (a) starch may be essential to, and intertwined with, climacteric ripening of fruits; (b) starch is a determinant of leafy-green shelf life; (c) sugars can influence the synthesis of specialized ‘sensory’ compounds; (d) carbohydrates have roles in biotic and abiotic stress response and in determining fruit size; and (e) that source tissue can determine sink quality. We then point to molecular targets that can alter the carbohydrate profile of produce to obtain desirable traits.

Starch is a sugar and energy reserve for maintaining postharvest life

Starch and sugars accumulate in many fruits, tubers, and leaves, but with different temporal patterns and consequences for postharvest shelf life and quality ([Figure 1](#)). The timeframe over which the flux between starch and sugars occurs determines the classification and the role of carbohydrates ([Figure 1](#)) [1].

Harvested produce is often stored in the dark and at low temperatures, where respiration of reserves sustains the hexose phosphate pool ([Figure 1a](#) panels 1–4). When reserves are exhausted, carbon starvation triggers senescence that manifests as spoilage [3]. In tissues that accumulate starch as a carbon and energy reserve ([Figure 1b](#)), granule degradation to sugar is surprisingly complex and multi-layered [1,4–6,70]. First, starch degradation occurs simultaneously with its biosynthesis at the granule surface even during the phase of net starch accumulation ([Figure 1a](#)) [6–8]. This permits a bidirectional flow of carbon from starch to sugars, and potentially, to other compounds via

Box 1 Postharvest definitions.

Waste:	Intentionally discarding edible produce because it does not meet expectations.
Loss:	Unintentional, incidental loss of produce before consumption, due to physical damage, rapid spoilage, microbial growth, and so on.
Quality:	Desirable attributes related to the appearance, texture, aroma and taste of produce.
Shelf life:	Timespan after crop harvest and before deterioration.

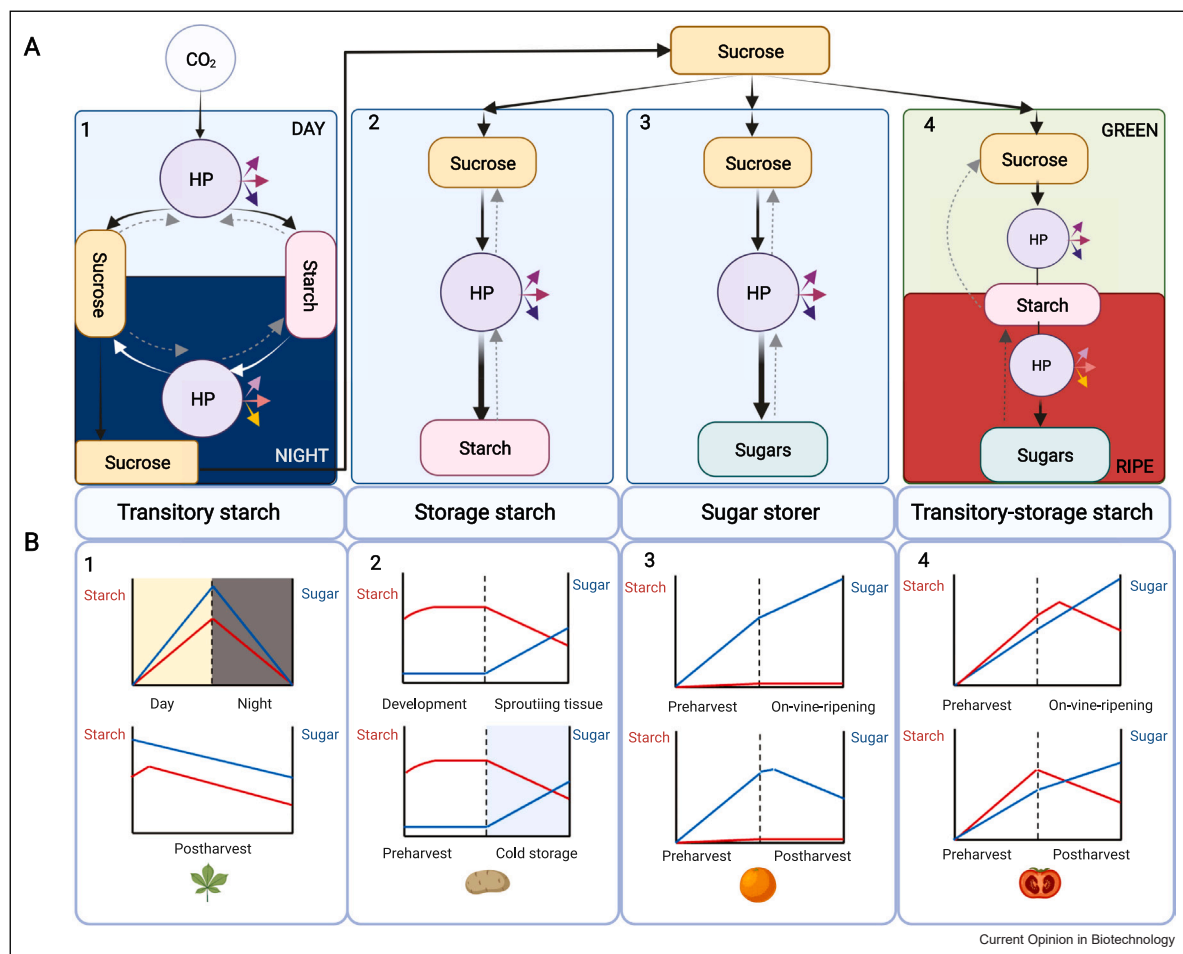
the hexose phosphate pool (Figure 1a). Second, in fruit, in addition to exocorrosion at the surface, there is evidence of some endocorrosion in the starch granule, during ripening and fruit cold storage [6,9]. Understanding the bidirectionality of flux between starch degradation and synthesis, and the physical organization of the starch granule-associated enzymes, may offer opportunities to adjust

reserve utilization during postharvest storage [10] (Figure 1a).

Starch as an underappreciated determinant of leafy- and microgreen shelf life and quality

The limited carbohydrate levels in leafy- and microgreens influence postharvest longevity [11] by buffering

Figure 1



The main pathways of starch and sugar metabolism in horticultural crops. **(a)** Carbon flux between starch, sugars, and the hexose phosphate (HP) pools in different horticultural species and tissues. A bidirectional carbon flow is indicated with black and gray dashed arrows. The three colored arrows indicate flux toward primary and secondary metabolism. Sucrose is shown as the assimilatory carbon, but polyols are prevalent in some species (Duran-Soria et al. [2]). **(b)** Changes in the accumulation of sugars (blue line) and starch (red line) in different tissue types, pre- and post harvest. **(1)** 'Transitory starch' — net biosynthesis and degradation is separated by the diurnal cycle (Zeeman et al., 2007). **(2)** 'Storage starch' — net synthesis and degradation is separated by the reproductive and the next generation. **(3)** 'Sugar-storers' — starch accumulation is low — < 2% and highly localized; sugars are accumulated at high levels. **(4)** 'Transitory-storage starch' — net synthesis and degradation of starch is separated by early and late organ development in some climacteric fruit (Luengwilai and Beckles [6]). The reference list for the citations in the figure legend is in the [supplementary materials](#).

against senescence [12]. Shelf life is extended when harvested leaf starch levels are high [11], such as at the end of the day or after an extended light period [11,13,14]. Starch content also positively correlates with desirable attributes such as sugar content, fresh weight, and texture (crunchiness) [15,16]. Identifying mechanisms that potentially coordinate photosynthesis, carbohydrate content, respiration, texture, and postharvest longevity in leafy greens is needed.

High starch accumulation is associated with species that undergo climacteric respiratory burst during ripening and fruit quality

Among fruits, the accumulation of high levels of starch (48% of the dry weight, Table S1) appears to be a unique feature of those with climacteric ripening [1,17] (Figure 1a.4; b.4). In tomato fruit, starch may provide ~40% of the carbon needed for fruit respiration [1,18]. Furthermore, some of the fruit's internal CO₂ from respiration is likely fixed by fruit chloroplasts, contributing to ~10–15% of ripe fruit carbohydrates [19,20].

Transitory-storage starch may represent an evolutionary strategy for reproductive fitness with unintended benefits for the postharvest industry [3]. First, its biosynthesis in climacteric species likely amplifies fruit sink strength, to undergird sink establishment and productivity [3]. A large difference in sucrose concentration between source and sink, which occurs when imported sugars are converted to starch, would enable higher carbon allocation to fruit. Further, carbon storage as starch rather than as sugars minimizes cells' osmotic disturbance [3]. Second, increased fruit starch biosynthesis may also enhance plant survival under stress [3,19] (see later sections). From a postharvest perspective, the starch in climacteric-ripening fruit may be a vital energy source for maintaining biological processes, and for the synthesis of 'quality-related' metabolites that would minimize loss and waste (PLW, Figure 2).

In contrast to the fruit described above, 'sugar-storers' are mainly nonclimacteric and accumulate comparatively little starch (Figure 1A.3; B.3; Table S1). Furthermore, the starch is deposited in the peripheral regions of the fruit, and unlike the climacteric fruit, its accumulation peaks and is degraded to sugars, early in fruit development [21–24]. However, starch in 'sugar-storers' may still contribute to fruit growth and quality by enabling a higher import of sugars into the developing fruit.

Starch content, structure, and composition can influence produce quality

Starch content and composition directly determine the functionality of starch in staple roots and tubers, but presumably, can also influence the biological processes

of fruits and vegetables, which do not accumulate high levels of starch, as shown below:

Produce firmness

The crystalline and insoluble nature of starch directly contributes to the firmness of fruit and the texture of leafy vegetables [15,25]. When the dense granule is degraded to soluble sugars, intercellular space increases [25], thus promoting tissue softening [26].

Tuber nutritional quality and textural attributes

The relative proportion of the amylose and amylopectin fraction of starch (Figure 2) is critical to tuber nutritional status and textural properties. Amylose is resistant to digestion and simulates fiber in the intestinal tract. Since amylose improves the nutritional value of starch-rich commodities, there have been many biotechnological efforts to increase its proportion relative to amylopectin in crops [27]. Furthermore, the molecular structure of amylose is such that if high-amylose potatoes, cassava, and so on, are fried, they should have a crisper texture that may be desirable to consumers. In contrast, amylopectin provides smooth and moist textures to cooked starches which may be suitable for other end-uses [27].

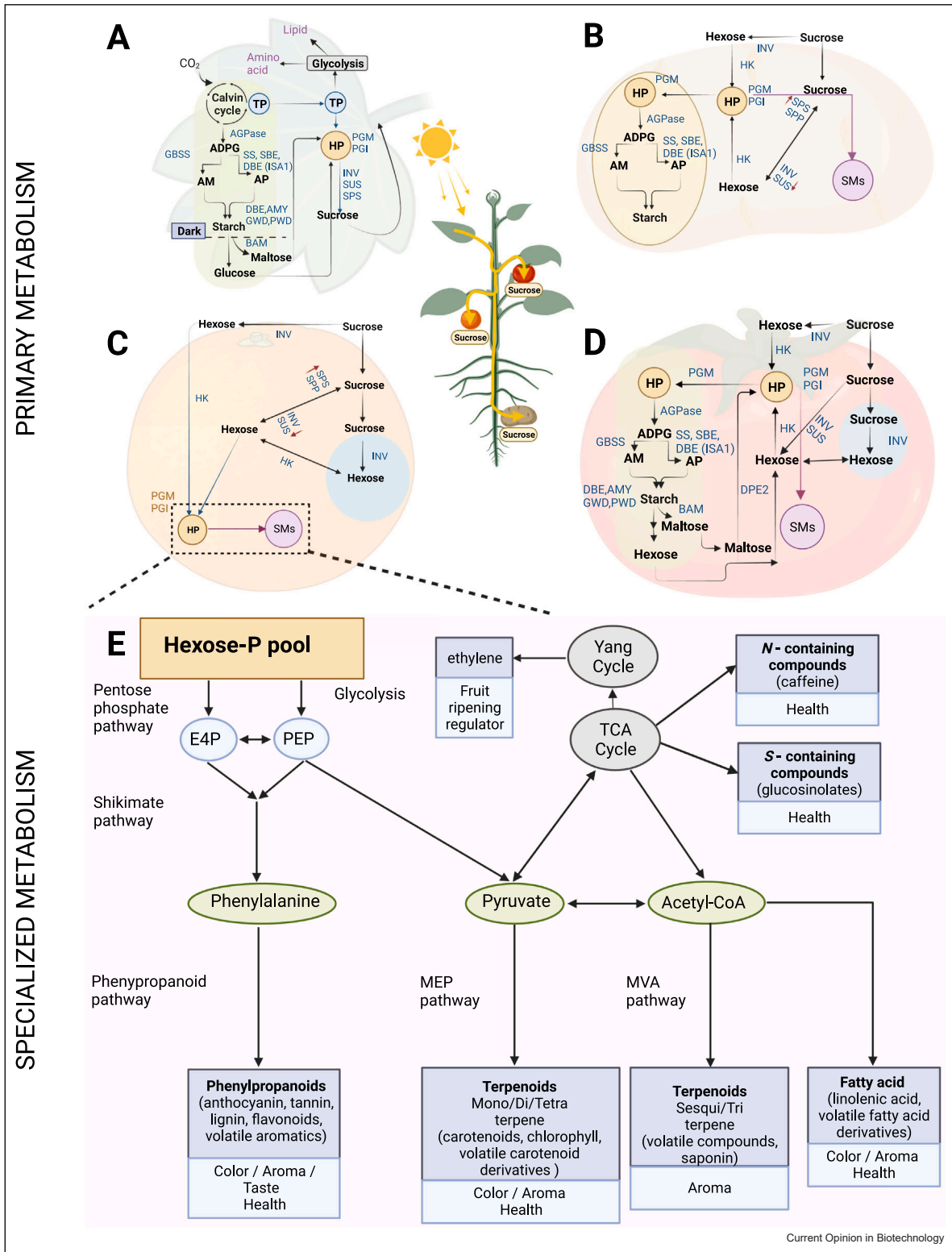
Sugar availability in fruit

Starch granule crystallinity, composition, morphology, and size collectively influence starch degradation to sugars, which in developing fruit could have consequences for fruit respiration, metabolism, and ripening [1,28]. We propose that the digestion of starch to sugars may be an inflection point for the rate of reserve use during ripening. Engineering starch with an optimal composition and crystalline structure to control the rate of release of sugars, may be valuable in regulating fruit metabolism, and hence quality

The relative proportion of fruit sugars affects sensory quality

The relative sweetness of sugars varies as such: fructose > sucrose > glucose > sorbitol, so if the sugar content is the same, different proportions of sugars will give the fruit distinct taste and flavor profiles [29] which are prime concerns for consumers. Modulating fructokinase activity [30] and the SISWEET sugar transporters [31] in tomato increased fructose content, silencing *A6PR* reduced sorbitol relative to glucose in apple [32], and modifying PuWRKY31, promoted sucrose accumulation in pear [33]. These changes should increase fruit sweetness, and, along with organic acids and aroma volatile compounds, should favorably influence fruit taste, flavor, and consumer likability [34].

Figure 2



Primary and secondary (specialized) metabolism in horticultural crops. Starch and sugar metabolism in different plant organs, is separated into four interconnected biological processes, sucrose synthesis, sucrose degradation, starch synthesis, and starch degradation, where hexoses, sucrose, and starch are the main carbohydrates. The inset images — (a) transitory starch – leaf; (b) transitory-storage starch – apple, tomato, kiwi, and banana fruit; (c) storage starch – tubers; (d) sugar-storers – grape, orange, and strawberry fruit. Pathways and compounds shown: triose phosphate (TP)

pool are the substrates for sucrose, the major assimilatory carbon in many model plant species, but in the Rosaceae, polyols dominate. Hexose phosphates (HP) are catalyzed by hexokinases (HK) and serve as the source of carbon for metabolism. Starch is made up of two polymers — 5–30% of starch is linear amylose (AM) and 70–95% is highly branched amylopectin (AP) (Yu et al. [1]), depending on the tissue. Key: Carbohydrates are in black; enzymes directly involved in starch metabolism are in blue; Metabolite abbreviations: SMs = secondary metabolites. Enzyme abbreviations: AGPase = ADP-glucose pyrophosphorylase; GBSS = granule-bound starch synthase; SS = starch synthase; SBE = starch-branching enzyme; DBE (ISA1) = debranching enzyme (isoamylase type1); INV = invertase; HK = hexose kinase; SPS = sucrose phosphate synthase; SPP = sucrose phosphate phosphatase; SUS = sucrose synthase; PGM = phosphoglucomutase; PGI = phosphoglucose isomerase. (e) Biosynthetic pathways for specific classes of SMs. Specialized metabolites define the aroma, taste, and mouthfeel of horticultural products, playing critical roles in consumer preference. HP are the intermediates of glycolysis, and the derived compounds, phosphoenolpyruvate, with erythrose-4-phosphates (E4P), are the initial precursors that enter into secondary metabolic pathways. The HP pool connects all pathways.

The carbohydrate profile of fruit tissues may indirectly influence fruit size

Sucrose and hexose have differential effects on fruit size [35], a trait determining consumer acceptance, shelf life, and nutritional characteristics [36]. A high hexose-to-sucrose ratio in early fruit development stimulates mitotic activity that increases cell number through hexokinase (HXK) signaling. Additionally, the higher osmotic potential of hexoses relative to sucrose will attract more water, increasing cell volume [2]. Genes influencing fruit size, mediated in part by changes in carbohydrates, include the SWEET phloem sugar transporters in tomato [37] and cucumber [38], the *CsSUS4* gene in cucumber [39], and the SICDF4 transcription factor (TF) [40] and its Arabidopsis homolog [78] in tomato. In apples, the sugar-to-acid ratio correlates with fruit size, which may have been selected through domestication [41]. Although the mechanisms underlying these phenomena may vary, they show that carbohydrates are key determinants of fruit/organ size.

Carbohydrates as important inputs and regulators of the synthesis of specialized 'sensory' compounds

Sugars both fuel and regulate the accumulation of specialized metabolites that are important to postharvest quality [2,42–45] (Figure 2b) [46]. Switches in the flux of carbon between primary and specialized metabolism were seen when sucrose was added exogenously to strawberry fruit, which inhibited the expression of many carbohydrate genes, but stimulated the MYB5 TF that regulates anthocyanin levels [47]. Changes in flux were also seen when ectopic expression of the AtMYB12 TF in tomato reprogrammed carbon away from primary metabolism and toward flavonoid biosynthesis via the shikimate and phenylalanine pathways (Figure 2b) [44]. There is a clear interrelation between primary and specialized metabolic pathways, but it remains relatively underinvestigated in horticultural crops. Identifying and modulating the TFs that regulate the fluxes between these pathways would enable the design of plants with a desirable combination of primary and secondary metabolites.

Starch metabolism acts as a protectant against postharvest abiotic stress

Changes in plant carbohydrates, including the starch-to-sugar conversion, are an important acclimatory response

to stress, often with consequences for produce quality [3]. For example, sugars maintain cells' osmotic potential, provide energy for stress defense, and act as membrane protectants and ROS scavengers [49], as shown below.

Cold-induced sweetening in potato

Storage at 4–8°C is desirable for extending potato shelf life, but cold-induced sweetening (CIS), that is, the degradation of starch to hexoses, occurs [48]. These sugars are protective [3], however, sugared tissues will form carcinogenic acrylamide under high-temperature processing, blacken, and become bitter, leading to PLW. Manipulating the pathways that influence hexose levels, that is, starch biosynthesis and degradation, sucrose hydrolysis to hexoses, and glycolysis, has provided some protection against tuber CIS [49], and thus has the potential to reduce PLW.

Postharvest chilling injury

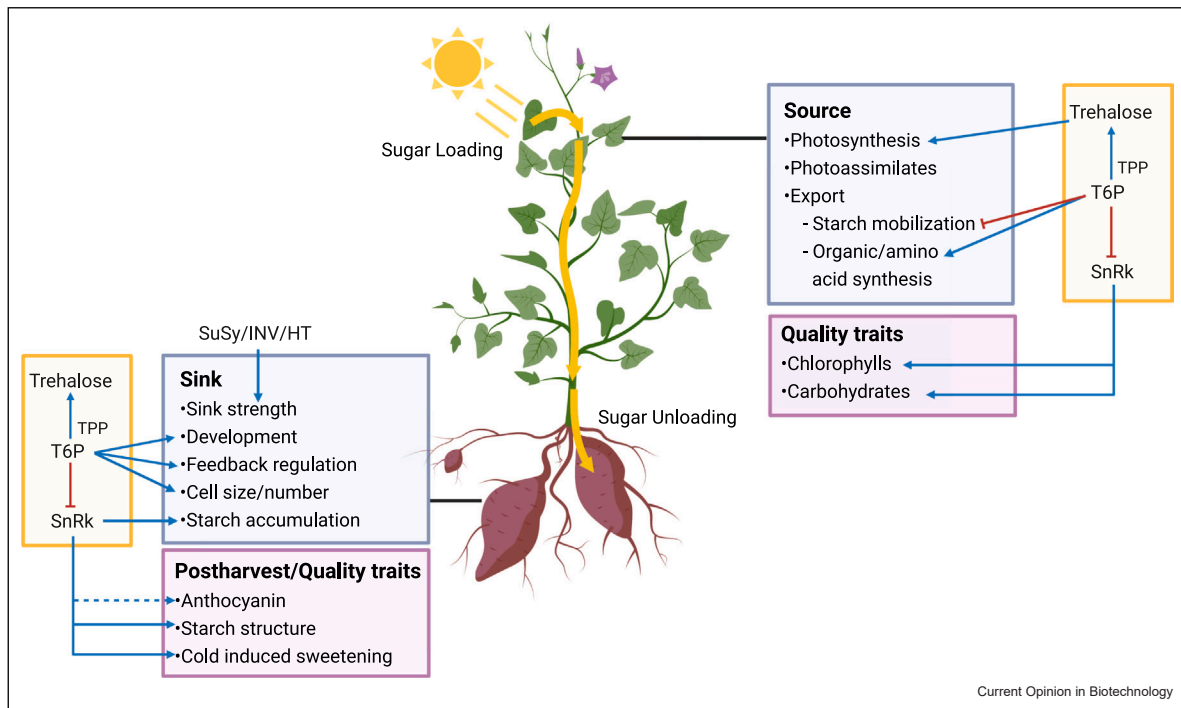
This describes the loss of quality and accelerated spoilage when tropical commodities are stored below 13°C [49]. Postharvest chilling injury (PCI) affects a wide range of species and results in extensive PLW [49]. There is growing evidence for the pivotal role of sugars in mitigating this PCI [49]. Chilling may also trigger higher starch content [50–52], which is degraded to replenish sugars for continued osmoprotection to abate PCI.

An interesting observation is that starch degradation may slow down or even halt as cold storage progresses in tomato, banana, and apple fruit [9,53,54], and even if fruits are rewarmed, starch degradation does not resume. In bananas, TFs that regulate this mechanism have been identified [26,55]. The biological rationale for this mechanism is unclear and should be investigated in more diverse species.

Postharvest physiological deterioration

Cassava root deteriorates 72 h after harvesting due to postharvest physiological deterioration (PPD), a disorder that leads to losses of 20–30% [56]. Silencing AGPase in cassava causes sugars to accumulate in the root. A positive correlation between low PPD and high sugar content was found in the transgenic cassava that extended

Figure 3



Factors affecting crop source and sink relationships. The flux of carbohydrates to the sink (orange arrows), is determined by source and sink capacity, which in turn, are modulated by genetic and preharvest environmental factors (de Ávila Silva et al., 2019). Mobile assimilates, such as sucrose and sugar alcohols, are loaded at the source and are transported to the sinks by mass flow. Sink strength is determined by the factors shown (Alikhani-Koupaei et al., 2022) and also by transporter activity, for example, HT (Aslani et al., 2020), which are developmentally regulated. Starch biosynthesis may play an important role in transitory-storing organs' sink strength by 'pulling' carbon into the sink tissue (Braun, 2022). The model above, represents processes that occur in some, but not all species. Species using sugar alcohols for transportation may have a different mode of regulation. The SnRK/T6P pathway is a central energy signaling hub that regulates carbon allocation and the feedback inhibition of photosynthesis due to stress and development. T6P concentration correlates to the internal sucrose content and inhibits (red arrow) SnRK1. T6P is metabolized to trehalose by the TPP (blue arrow), which also regulates the SnRK/T6P pathway. Depending on sucrose levels, the SnRK/T6P hub activates or represses genes involved in carbohydrate use which may influence PLW. Diverse physiological and metabolic factors promote (red arrows) or inhibit (blue arrows) these processes. Dashed lines indicate that the effect may be species-dependent. SuSy: sucrose synthase; INV: invertase; T6P: trehalose-6-phosphate; SnRK: sucrose nonfermenting-1-related kinase 1; TPP: trehalose-6-phosphate phosphatase.

root longevity, and was likely due to sugars serving as ROS scavengers [56].

Salinity stress

Saline soils trigger sugar accumulation in the leaves, which initially serve as osmoprotectants, but over time, inhibit leaf photosynthesis. The rapid conversion of sugars to starch in tomatofruit promotes sugar export from the leaf to the fruit by mass flow, thus relieving photosynthesis (Figure 3) [57]. The 'extra' starch stored in 'salt-stressed' green fruit is hydrolyzed during ripening, boosting sugar content and intensifying fruit sweetness post harvest [58,59].

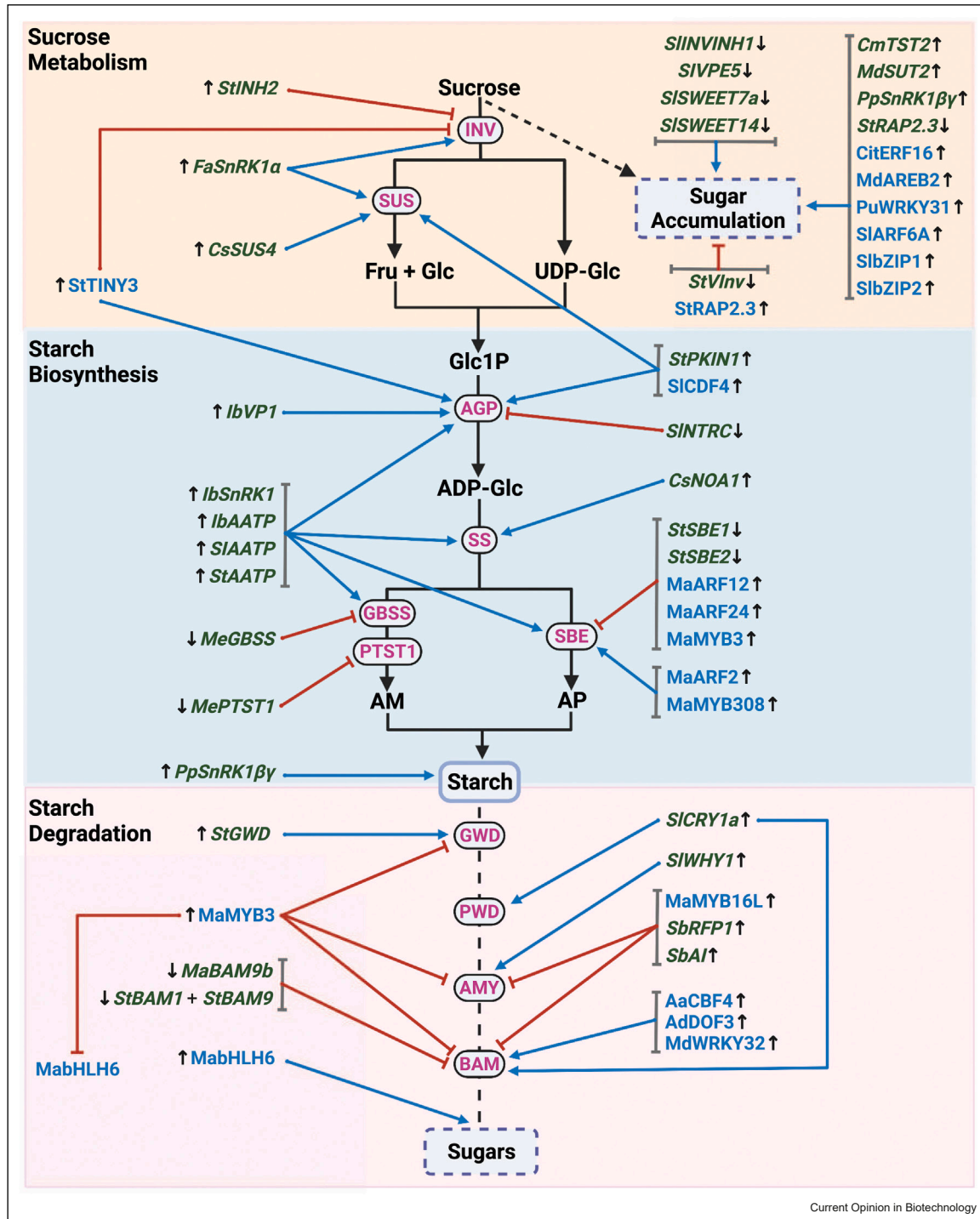
Starch acts as a protectant against biotic stresses

Pathogen infestation decreases postharvest quality, but recent findings showing that pathogen colonization is associated with changes in host carbohydrate levels,

offer new avenues for disease mitigation. Starch may accumulate in the host as an early response after perceiving bacterial effectors or volatile organic compounds in some species. Such accumulation could physically contain the microbes in situ, thus reducing systemic spread [60–63]. If the infestation becomes advanced, accelerated breakdown of the accumulated starch to sugars may provide the host with energy and carbon for the biosynthesis of protective antimicrobial compounds [64,65].

Starch accumulation may also be induced by the pathogen after infection [66–69], and may involve reprogramming carbon allocation between source and sink [50]. This is seen with black Sigatoka disease (BSD) in bananas [50,68], and in citrus greening [67] and grapevine red blotch [66] where phloem starch accumulation is part of the disease response. BSD in bananas not only alters starch metabolism in vegetative tissues, but also

Figure 4



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Enzymes and regulatory factors influencing carbohydrate metabolism. Metabolites (black); Enzymes (pink); Manipulated genes (green); Manipulated TFs (blue); Arrows – blue (activation/ increase) or red (repression/decrease); ↑ – overexpression; ↓ = repression. Abbreviations (metabolites): Glc – glucose; Fru – fructose; UDP-Glc – UDP glucose; Glc1P – glucose-1P; ADP-Glc – ADP-glucose. Enzyme/Gene Abbreviations (enzymes): SUS – sucrose synthase; INV – invertase; AGP/AGPase – ADP-glucose pyrophosphorylase; SS – starch synthase; GBSS – granule-bound starch synthase; PTST1 – protein targeting to starch 1; SBE – starch-branching enzyme; AMY – α -amylase; BAM – β -amylase; GWD – alpha-glucan water dikinase; PWD – phosphoglucan water dikinase; AATP – ATP/ADP transporter; Al – amylase inhibitor; CRY1a – cryptochrome 1a; INH – vacuolar invertase inhibitor; INVINH – invertase inhibitor; NOA1 – nitric oxide-associated 1; NTRC – NADPH-thioredoxin; VP1 – H⁺-pyrophosphatase (H⁺-PPase) gene; PKIN1 – a potato sucrose nonfermenting-1 (SNF1)-related protein kinase gene; SnRK – sucrose nonfermenting-1-related kinase gene; RFP1 – a RING

(really interesting new gene) finger protein; SUT2 — a sucrose-uptake transporter; SWEET — sugars will eventually be exported transporter; TST — Tonoplast sugar transporters; Vlnv — vacuolar invertase; VPE — vacuolar processing enzyme; WHY1 — ssDNA-binding protein 1. Gene nomenclature: The following nomenclature is used to indicate species: Aa- kiwi; Ad-kiwi; At — Arabidopsis thaliana; Cit — citrus; Cs — cucumber; Fa — strawberry; Ib — sweet potato; Ma — banana; Md — apple; Me — cassava; Pp — peach; Sb — potato; Sl — tomato; St — potato. TF Abbreviations: AaCBF4 — a C-repeat-binding factor TF; AdDOF3 — a DNA binding with one-finger TF; CitERF16 — an ethylene-responsive factor family TF; SlbZIP1/SlbZIP2 — basic leucine zipper motif TFs; MaARF2/MaAFR12/MaAFR24/SIARF6A — auxin response factor family TFs; MaMYB3/MaMYB308/MaMYB16L — MYB domain TFs; MabHLH6 — a basic helix-loop-helix TF; MdAREB2 (Ma et al., 2017) — an ABA-responsive element-binding protein TF; MdWRKY32/ PuWRKY31 — WRKY domain TFs; SICDF4 — a cycling DOF-type TF; STRAP2.3 — an ERF-VII transcription factor; StTINY3 — a CBF/DREB TF.

changes the physical and chemical characteristics of starch in the harvested fruit [68]. These examples across host species and pathogen types illustrate that spatial-temporal changes in starch metabolism may be important to host disease response. The *RF1* banana mutant with BSD resistance, was associated with high levels of sugars and starch accumulation [50]. Thus, starch accumulation could be a critical factor that could be modulated pre- and post infection to reduce the damage caused by pathogens.

Preharvest source-sink dynamics determine carbohydrate allocation to harvested organs

The postharvest quality of sink tissues, for example, fruits, roots, and tubers, depends on carbon allocation from the source [37] (Figure 3), and agronomic practices, environmental factors [14,50,52,57], and disease pressure [67,68] can all influence this process. Reconfiguration of carbon allocation in response to development or stress (Figure 3), is mediated in part by the trehalose-6-

phosphate-sucrose nonfermenting-1-related kinase 1 (T6P-SnRK) signaling pathway, a central energy hub that senses sugar status [70]. The T6P-SnRK1 pathway regulates carbohydrate content in potato tuber [71,72], sweet potato [74], and various fruits [73–75]. T6P-SnRK also regulates starch physicochemical properties [74], anthocyanin accumulation [73,76], and CIS [71] in various species, which all have an impact on PLW.

Biotechnological manipulation of carbohydrate genes for improving produce quality

As shown in multiple examples, manipulating the carbohydrate profile of horticultural crops by biotechnology should impact postharvest quality and directly reduce PLW. Increasing starch accumulation, modulating starch degradation, altering starch composition, or changing sugar content are key targets. The composite Figure 4 and accompanying Table 1 illustrate many genes and regulatory factors that influence these processes.

Table 1

Gene targets for improving the postharvest carbohydrate profile of horticultural crops.

Targeted traits	Example gene targets	Reference
Increasing tuber starch and yield	Metabolic enzymes	Plastidial adenylate kinase <i>IbVP1</i> <i>AGPase</i>
	Transporters	<i>IbAATP</i> , <i>SIAATP</i> , <i>StAATP</i>
Modulating the amylose and amylopectin ratio	Metabolic enzymes	<i>GBSS1</i> , <i>SBE</i> ,
	Regulatory proteins	<i>MePTST1</i>
Reducing the flux of sugars from starch in cold-storage potato	Metabolic enzymes	<i>StBAM</i> , <i>StGWD</i> , <i>StVlnv</i>
	TFs	<i>StTINY</i>
		<i>SbRFP1</i>
Manipulating starch degradation during ripening to fruit sugar	Metabolic enzymes	<i>MaBAM9b</i>
	TFs	<i>MaMYB3</i> , <i>MabHLH6</i>
		<i>MaMYB16L</i>
		<i>SIARF10</i>
		<i>MdWRKY32</i>
Altering sugar profiles for better quality	Transporters	<i>MdSUT2.2</i>
	TFs	<i>MdAREB2</i>
		<i>MdbHLH3</i>
		<i>SIRIN</i>
		<i>SlbZIP1/SlbZIP2</i>

Future directions

Throughout this entry, we have pointed to many unanswered questions related to carbohydrate metabolism in horticultural crops and experimental approaches to address them. Here, we highlight additional steps that could yield new knowledge to improve produce for reduced PLW.

- 1) **Determine the extent to which starch metabolism influences fruit quality.** An unresolved question is if the amount, and the rate of sugars released from starch, influence the substrate pool, and the synthesis of downstream flavor compounds (Figure 2a/b).
- 2) **Bioengineer genes encoding carbohydrate enzymes and regulatory proteins for improved postharvest sensory and nutritional quality.** Many of these enzymes are regulated at the post-transcriptional level. A deeper understanding of these regulatory mechanisms could be leveraged to introduce subtle adjustments to the carbohydrate composition of tissues. Fine-tuning the amount and spectrum of carbohydrates produced could be used to optimize shelf life or the flux toward specialized metabolic pathways.
- 3) **Establish the spatial-temporal profile of starch in fruit tissues.** A starch-to-sugar atlas in fruit, through development and in response to pre- and postharvest stress, would provide fundamental and high-resolution data on core energy and carbon metabolic processes. Such an atlas would serve as a baseline to identify targets for gene editing.
- 4) **Determine the role of fruit photosynthesis, in determining fruit quality.** Fruit chloroplasts have photosynthetic and CO₂ fixation capacity, an internal source of CO₂ [20], and fruit chlorophyll correlates with fruit quality [77]. Fruit photosynthesis was activated when source photosynthesis was impaired under drought stress, and was accompanied by starch accumulation [19]. Yet, the role of fruit photosynthesis in fruit growth, carbohydrate production, and stress response is unclear [20]. Data that clarify these potential relationships are needed as the first step to exploiting these processes for enhanced fruit quality.
- 5) **Leverage data from Arabidopsis to study starch metabolism in leafy greens.** There is a growing mechanistic understanding of starch metabolism in *A. thaliana*. These data could be applied to starch-rich leafy greens such as spinach, or those of the related Brassicaceae, that is, cabbage, kale, collards, and so on. This would largely fill the knowledge gap between the current models of starch metabolism and their real-world application toward crop improvement.
- 6) **Identify factors controlling carbon allocation from source to sink for postharvest quality and shelf life.** Although it is tempting to focus on the harvested

product, source-sink relationships help determine produce size, abiotic and biotic stress responses, and quality attributes (see Figure 3). Varying the expression of key genes, for example, T6P-SnRKs, SWEETs, INVs, and so on, combined with precision agronomical practices, could improve many of these critically important attributes that influence marketability (Figure 3).

Conclusions

Carbohydrate biosynthesis and degradation denote changes in energy conversion and storage, with consequences for postharvest quality. Despite the multifaceted role of starch and sugars in plant tissues, rarely are these compounds seen beyond serving as bulk reserves for direct consumption. Here, we argue that their metabolic dynamism is pivotal to the physiology and quality of the harvested organ, which, through their effect on organ size, aroma, taste, flavor, texture, and visual appearance, will reduce postharvest waste at the consumer end. Further, because carbohydrates are vital substrates for respiration, and act as ‘stress-protectants,’ they influence storage and shelf life, and as a result, postharvest loss. We also show that carbohydrate movement from source tissues to the harvested organ should not be ignored when investigating produce quality. Finally, the identified genes, enzymes, and regulators involved in carbohydrate metabolism we present, offer opportunities for precision modification of postharvest attributes to reduce waste and loss.

CRedit authorship contribution statement

Jingwei Yu: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Dave Tseng:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Kien Pham:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Margaret Liu:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Diane M. Beckles:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision.

Conflict of interest statement

The authors declare that they have no conflict of interest.

Data availability

No data were used for the research described in the article.

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Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.copbio.2022.102844](https://doi.org/10.1016/j.copbio.2022.102844).

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

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