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REVIEW

Molecular basis for optimizing sugar metabolism and transport during fruit development

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Abstract Sugars are fundamental metabolites synthesized in leaves and further delivered to fruit in fruit crops. They not only provide "sweetness" as fruit quality traits, but also function as signaling molecules to modulate the responses of fruit to environmental stimuli. Therefore, the understanding to the molecular basis for sugar metabolism and transport is crucial for improving fruit quality and dissecting responses to abiotic/biotic factors. Here, we provide a review for molecular components involved in sugar metabolism and transport, crosstalk with hormone signaling, and the roles of sugars in responses to abiotic and biotic stresses. Moreover, we also envisage the strategies for optimizing sugar metabolism during fruit quality maintenance.

Keywords Abiotic and biotic stress, Fruit quality maintenance, Postharvest diseases, Sugar metabolism, Transporter

INTRODUCTION

Sugars are primary metabolites providing building blocks and energy for cells (Dai et al. 2013; Ruan 2014). Previous studies have indicated that sugars are not only crucial for maintaining cellular turgor and promoting cell expansion, but also function as signaling molecules to modulate fruit development (Ruan et al. 2014; Chen et al. 2020). In fruit, sugar content is often measured as the total soluble solid content, which determines fruit sweetness and ultimately fruit quality (Ruan et al. 2012; Chen et al. 2021). In fruit crops, sucrose, sorbitol and occasionally trehalose or raffinose are synthesized and delivered from leaves (source organs) to fruit, tuber and seeds (sink organs) (Ruan et al. 2014; Li et al. 2018), thereby involving in metabolic activities of plants. Moreover, sugar transport is synergistically mediated by transporters from different superfamilies, which are elaborately tuned at transcriptional, posttranscriptional and posttranslational levels. A part of the sugars transported to fruit is utilized in physiological processes, whereas the other part is stored in vacuoles. Therefore, a comprehensive understanding of these processes is important for uncovering important players in physiologically relevant processes (Wipf et al. 2021).

Major sugar-related metabolic activities in fruit

Sugar metabolic and transport processes function differentially among fruit species. In apple, sorbitol and sucrose are synthesized in leaves and further delivered and metabolized in fruit (Fig. 1), whereas sucrose is the major translocated sugar in many citrus varieties (Shangguan et al. 2014; Sadka et al. 2019). As compared with leaf photosynthesis, fruit photosynthesis seems not important for primary metabolism in tomato fruit, as suppression of glutamate 1-semialdehyde aminotransferase (GSA), a rate-limiting enzyme involved in chlorophyll biosynthesis, did not obviously affect normal fruit development (Lytovchenko et al. 2011).

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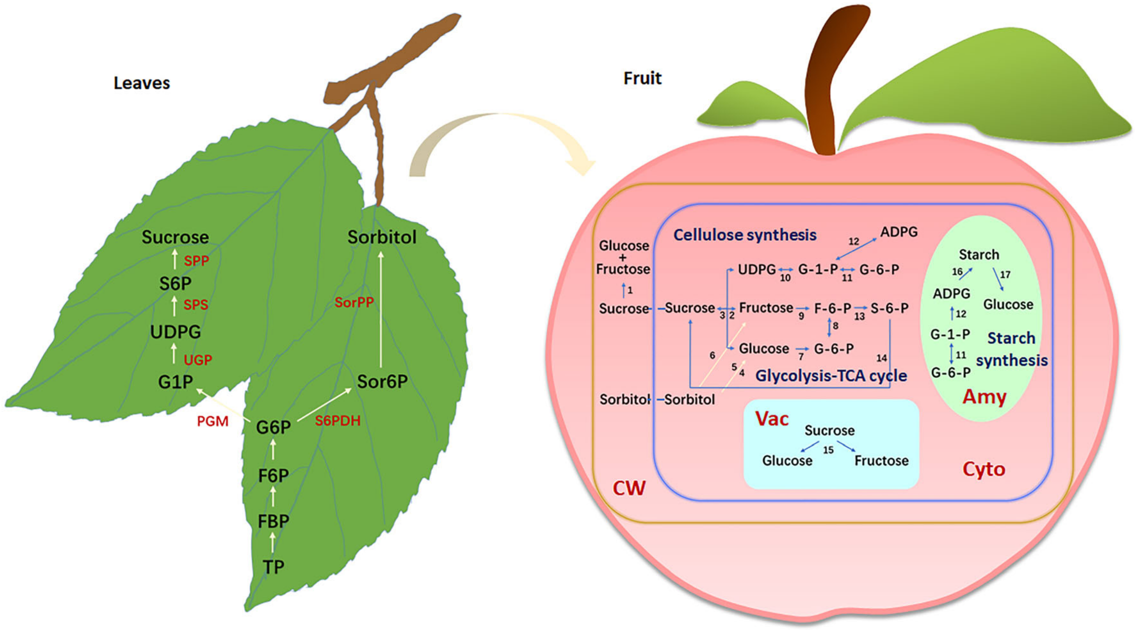

Fig. 1 A simplified model for sugar metabolism in leaves and fruit. Taking apple as an example, sorbitol and sucrose are synthesized in leaves mainly by the enzymes as follows: *F6P* fructose-6-phosphate; *FBP* fructose-1,6-bisphosphate; *G1P* glucose-1-phosphate; *G6P* glucose-6-phosphate; *S6P* sucrose-6-phosphate; *Sor6P* sorbitol-6-phosphate; *TP* triose phosphate; *PGM* phosphoglucomutase; *S6PDH* sorbitol-6-phosphate dehydrogenase; *SorPP* sorbitol-6-phosphate phosphatase. Sorbitol and sucrose are further transported to fruit. Major enzymes involved in sugar metabolism in fruit: 1. apoplastic invertase; 2. cytosolic invertase; 3. sucrose synthase; 4. $NADP^+$-sorbitol dehydrogenase; 5. sorbitol oxidase; 6. NAD^+-sorbitol dehydrogenase; 7. hexokinase; 8. phosphoglucose isomerase; 9. fructokinase; 10. UDP-glucose pyrophosphorylase; 11. phosphoglucomutase; 12. ADP-glucose pyrophosphorylase; 13. sucrose phosphate synthase; 14. sucrose phosphate phosphatase; 15. soluble acidic invertase; 16. granule-bound starch synthases and other enzymes; 17. α-amylase and other enzymes (refer to Li et al. 2012b). Note: *Amy* amyloplasts, *Cyto* cytosol, *CW* cell wall, *Vac* vacuoles

Moreover, there seems no strict relationship between leaf photosynthesis rate and fruit yield, as overexpression of maize sucrose-6-phosphate synthase in tomato showed increased photosynthetic activity and sucrose synthesis in leaves but did not influence the final fruit yield (Micallef et al. 1995). These results implied that sugar-related metabolic activities in fruit are modulated by specific mechanisms.

Sucrose metabolism has pivotal functions in normal development and stress responses of plants. The sucrose cycle plays a central role in sugar metabolism in fruit (Nguyen-quoc and Foyer 2001; Wind et al. 2010), substantially connecting sugar metabolic activities with other primary metabolic processes (including starch synthesis, glycolysis, tricarboxylic acid cycle, and cell wall biosynthesis). This metabolic cycle consists of several steps: sucrose degradation by sucrose synthase and cytosolic invertase in the cytosol or acidic invertase in the vacuole/apoplastic space, subsequent phosphorylation of the resulted hexoses, transformation between UDP-glucose and hexose phosphates, and ultimately sucrose re-generation catalyzed by sucrose-6-phosphate phosphatase and sucrose-6-phosphate synthase (SPS). Upon antisense suppression of aldose-6-phosphate reductase, the transgenic apple fruit showed lower sorbitol level, much higher glucose level but comparable concentrations of fructose, sucrose, and starch to the control, indicating that the sucrose cycle and the sugar translocation system function effectively in maintaining the fructose level in apple fruit (Li et al. 2018).

Sucrose utilization depends on its degradation into glucose and fructose by sucrose synthase and invertases in fruit (Zhang et al. 2004; Ruan et al. 2014). Sucrose synthase is a cytosolic glycosyl transferase converting sucrose into UDP-glucose and fructose, thus is closely related to the growth rate and the quantity of starch in fruit (Yelle et al. 1988). Invertases hydrolyze sucrose into glucose and fructose, which are crucial for normal development and responses to biotic and abiotic stresses in plants (Qin et al. 2016). According to their specific sites of action, invertases are categorized into three groups, i.e., cell wall (apoplastic) invertases (CWIN), vacuolar invertases (VIN), and cytoplasmic invertases

(CIN) (Li et al. 2012b). Invertases have crucial roles in fruit set and ripening (Palmer et al. 2015; Qin et al. 2016). LIN5 is one of the CWIN enzymes responsible for sugar uptake into tomato fruit (Zanor et al. 2009; Vallarino et al. 2017). A study demonstrated that both *CWIN* and *INH* (the gene encoding LIN5 inhibitor) mRNAs displayed a phloem-specific pattern during tomato fruit development. The CWIN LIN5 specifically functions in the walls of sieve elements with increasing activity, thereby facilitating phloem unloading and generating sugar signaling to regulating cell division (Palmer et al. 2015).

Upon phloem unloading into sink cells apoplasmically or symplasmically (Li et al. 2018), sucrose is hydrolyzed by apoplastic invertase into glucose and fructose before being transported into cytosol. It has been reported in model plants that apoplastic glucose may be perceived by Regulator of G protein Signaling 1 (RGS1) coupled with heterotrimer G protein (Liu et al. 2019), whereas extracellular glucose may promote the endocytosis of RGS1 and thus release RGS1 from the coupling machinery with G protein. Further efforts should be made to examine whether the sensing of apoplastic glucose may be involved in the regulations on development and responses to biotic factors in fruit (Urano et al. 2012; Liang et al. 2018). In contrast, the sucrose transported via plasmodesmata or by sucrose transporters is degraded by cytosolic invertase and sucrose synthase. The intracellular hexose is utilized for glycolysis as well as synthesis of starch, cellulose and other carbohydrate polymers (Ruan et al. 2014). Since the vacuole is a storage organelle for sugars, vacuolar invertase is supposed to modulate the sucrose/hexose ratio in fruit. Antisense suppression of *TIV1* in tomato resulted in lower hexose accumulation (Klann et al. 1996). Similar results were also reported in grape berry and muskmelon (Davies and Robinson 1996; Yu et al. 2008). In contrast, vacuolar invertase activity is tightly regulated by various signals, including corresponding invertase inhibitors. Qin et al. (2016) reported that RIPENING-INHIBITOR (RIN) transcriptionally activated the expression of *SlVIF* (a gene encoding a vacuolar invertase inhibitor in tomato), and the color transition of the transgenic *SlVIF*-RNAi fruit was retarded as compared to wild type, further suggesting a role for vacuolar invertase in regulating tomato fruit development (Qin et al. 2016).

Being the major photosynthate in Rosacea species, sorbitol accounts for about 80% of soluble carbohydrates synthesized in leaves, but only 3%–8% of soluble carbohydrates in fruit, suggesting that sorbitol is rapidly metabolized in fruit (Loescher 1987; Cheng et al. 2005). Both sorbitol and sucrose are translocated to and utilized in apple fruit, in which sorbitol accounts for about 60%–70% of the photosynthates synthesized in leaves (Li et al. 2012b). The enzymes related to sorbitol metabolism in apple are mainly sorbitol-6-phosphate dehydrogenase (S6PDH), sorbitol dehydrogenase (SDH) and sorbitol oxidase (SOX). S6PDH mainly catalyzes sorbitol biosynthesis in leaves, whereas SDH and SOX are involved in sorbitol metabolism in apple fruit. Their functions have also been defined. NAD^+-SDH reversibly catalyzes the production of fructose from sorbitol (NAD^+ functions as a co-enzyme) and SOX catalyzes the irreversible conversion from sorbitol to glucose (Li et al. 2012b; Shangguan et al. 2014).

Sugar transport

Sugar transporters are indispensable for sugar export, phloem loading and unloading (Wei et al. 2014; Durán-Soria et al. 2020; Li et al. 2020a). As the main transporter families, sorbitol transporters (SOTs), sucrose transporters (SUTs), monosaccharide transporters (MSTs) [including hexose transporters, tonoplast transporters, vacuolar glucose transporters, ERD six-like transporters, and plastid glucose transporters], and Sugar Will Eventually be Exported Transporters (SWEETs) function coordinately in sugar transport (Jeena et al. 2019) (Fig. 2). Occurring either apoplasmically, symplasmically, or synergistically, SWEETs and SUTs are involved in sucrose export during phloem unloading. SUTs are energy-requiring sucrose/H^+ symporters (Chen et al. 2010) and SWEETs function as facilitated diffusers in four phylogenetic clades for transmembrane delivery of sugars (Chen et al. 2012; Braun et al. 2014; Eom et al. 2015). These transporters are elaborately regulated at transcriptional, translational and epigenetic levels. The overexpression of sucrose transporter gene *MdSUT2.2* promoted sugar accumulation and drought tolerance in apple plants, which depended on the phosphorylation by MdCIPK22 upon drought treatment (Ma et al. 2019). In another Rosacea species *Pyrus ussuriensis*, *PuSWEET15*, a clade III member transporting sucrose, showed a high expression level in the bud sport variety of 'Nanguo' fruit, which was attributed to the activation by PuWRKY31 and the high acetylation level in *PuWRKY31* promoter (Li et al. 2020b).

After cell wall invertases degrade sucrose into hexoses in apoplasmic unloading (Ruan et al. 2014), sugar transporters translocate sucrose, fructose, and glucose in the vacuole (Durán-Soria et al. 2020). In this process, tonoplast sugar transporters (TSTs) play important roles (Liu et al. 2016b; Ren et al. 2018). *ClTSaT2* expression was positively correlated with tonoplast

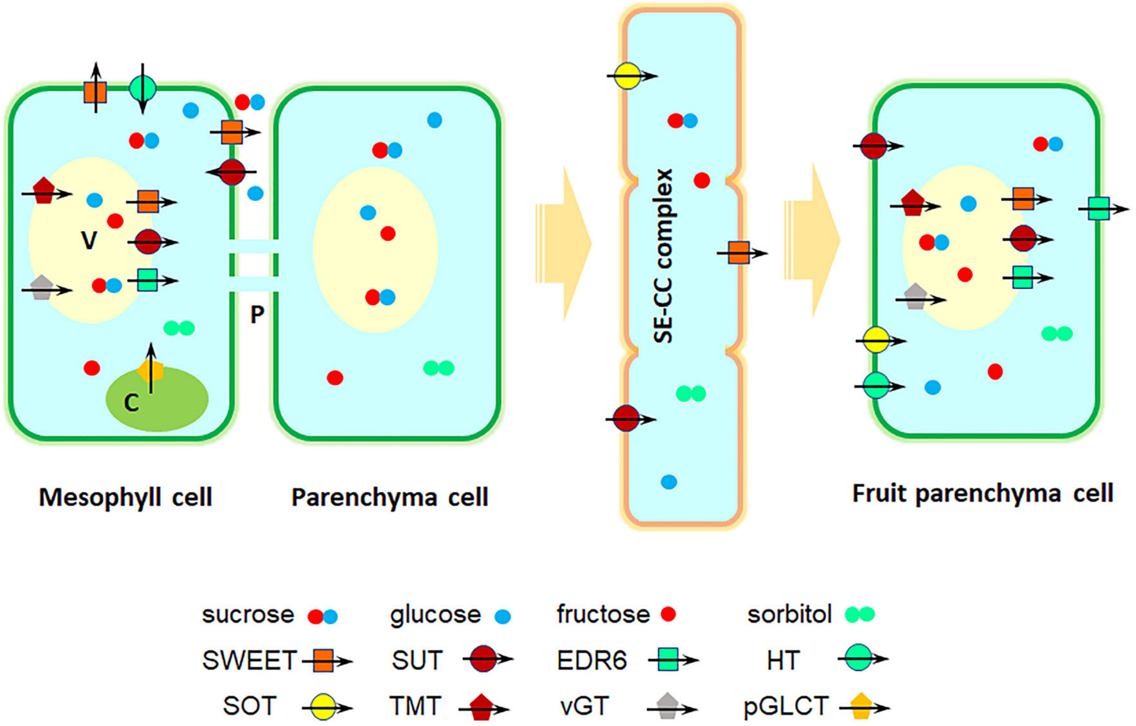

Fig. 2 Sugar transport from leaves to fruit in apple. Sorbitol and sucrose are loaded into phloem and then unloaded into fruit parenchyma cells (Ruan et al. 2014; Wei et al. 2014). In apples, sorbitol transporters (*SOTs*), sucrose transporters (*SUTs*), SWEETs, monosaccharide transporters (*MSTs*) [including hexose transporters (*HTs*), tonoplast membrane transporters (*TMTs*), vacuolar glucose transporters (*vGTs*), ERD six-like transporters (*EDR6*), and plastid glucose transporters (*pGLCT*)] are major enzymes involved in sugar transport. SWEETs are uniporters mainly mediating the export of sugars. SUTs, SOTs, and HTs are H$^+$/sugar importers importing Sor, Suc, and hexose. vGTs and TMTs function as sugar/H$^+$ antiporters mobilizing sugars into vacuoles, while EDR6 and SWEET IV subfamilies are involved in sugar efflux from vacuoles. In addition, pGLCTs modulate sugar efflux from plastids. Note: *C* chloroplasts, *P* plasmodesmata, *SE-CC complex* sieve element/companion cell complex, *V* vacuoles

uptake and sugar accumulation in fruit flesh cells in watermelon, which was regulated by a sugar-induced transcription factor SUSIWM1 (Ren et al. 2018). In addition, raffinose family oligosaccharides are also major sugars translocated in the vascular bundle in cucurbits. ClAGA2, ClSWEET3 (a plasma membrane-localized clade I hexose transporter) and ClTST2 function in raffinose hydrolysis, transmembrane sugar transport and sugar storage in vacuoles, respectively, thereby contributing to the derivation of sweet watermelon from non-sweet ancestors during domestication (Ren et al. 2021). Moreover, it was reported recently that MdERDL6-1, a tonoplast glucose/H$^+$ symporter, exports glucose to cytosol and up-regulates *MdTST1* and *MdTST2* expression, thus facilitating sugar accumulation from cytosol to vacuole in apples (Zhu et al. 2021). In contrast, the glucose, fructose and sucrose contents decreased during apple fruit senescence during storage, which was partly explained by the differential expression of ERD six-like transporter and tonoplast monosaccharide transporter 1, suggesting a efflux of sugars from the vacuole during storage (Zhu et al. 2013).

CROSSTALK BETWEEN SUGAR METABOLISM AND HORMONES DURING FRUIT DEVELOPMENT AND RIPENING

Crosstalk between sucrose and abscisic acid

Sugar signaling is closely related to the function of ABA in climacteric fruit ripening. Prior to the onset of tomato fruit ripening, an ABA content peak appears ahead of the ethylene peak, suggesting that both hormones function in promoting fruit ripening in climacteric fruit (Li et al. 2016; Chen et al. 2020). ABA positively modulates sugar accumulation in apple fruit by integrating multiple pathways. Besides the induction in the transcript levels of the tonoplast monosaccharide transporters MdTMT1 and MdSUT2, ABA also triggered the CIPK22-dependent phosphorylation of an ABA-responsive transcription factor MdAREB2 (Ma et al. 2017a). MdAREB2 directly activates the expression of amylase and sugar transporter genes to promote soluble sugar accumulation in *M. domestica* (Ma et al. 2017b). The crosstalk between sucrose and abscisic acid has also been reported in nonclimacteric fruit. *FaSUT1* overexpression increased endogenous sucrose level, *FaNCED* expression of and ABA level in strawberry fruit, suggesting a synergistic action between ABA and sucrose (Jia et al. 2013). RNAi knockdown of 9-cis-epoxycarotenoid dioxygenase (NCED), a key enzyme regulating ABA biosynthesis, significantly delayed the ripening process of strawberry (Jia et al, 2011). Moreover, simultaneous application with sucrose and ABA exerted a more pronounced effect to accelerate the ripening of strawberry fruit, suggesting coordination between ABA and sucrose signaling in promoting ripening (Jia et al. 2016). However, Siebeneichler et al. reported that ABA and sucrose application on harvested strawberry fruit resulted in altered chemical composition and firmness, implying that postharvest ripening of strawberry fruit induced by ABA and sucrose may differ from that in natural ripening (Siebeneichler et al. 2020). Further investigations are still required to ascertain the underlying mechanisms.

Crosstalk between sugars and other hormones

Sugar metabolism and transport are also intersected with the signaling of other hormones, including auxin, ethylene, jasmonic acid and others. Besides the contribution of ABA and sucrose to strawberry fruit ripening, auxin (indole acetic acid, IAA) showed a negative role in sucrose accumulation as it suppresses the expression of genes related to sugar accumulation during tomato and strawberry fruit ripening (Jia et al. 2016). Moreover, in young pear fruit, auxin functioned in preventing fruit abscission by accumulating in the peduncle and allowing sucrose transport to sink cells in which it is degraded by CWIN (Murayama et al. 2015). Consequently, the produced glucose may inhibit the incidence of programmed cell death (PCD) at the abscission site and further guarantee fruit development (Ruan 2012). As a gas hormone, ethylene has been known for its function in fruit ripening, particularly in climacteric fruit (Chen et al. 2020). Upon the onset of fruit ripening for tomato, apple and grapes, the expression of ethylene receptor genes displayed increasing patterns, which was in accordance with the increase in sugar accumulation (Li et al. 2016). Moreover, ethylene promoted sucrose accumulation in kiwifruit and grapes during fruit ripening (Farcuh et al. 2018), while sucrose can also promote ethylene production and tomato fruit ripening at postharvest stage (Li et al. 2016), suggesting the existence of potential modulators involved in sugar and ethylene signaling. Moreover, evidence has been shown that methyl jasmonate (MeJA) promoted ethylene biosynthesis by regulating *MdERFs* and ethylene biosynthetic genes via MdMYC2 (Li et al. 2017). However, it has also been reported that JA may inhibit ethylene biosynthesis and delay fruit ripening in other fruit species, including sweet cherries and pears (Kondo et al. 2000; Lindo-Garcia et al. 2020). Therefore, it seems that the relationship between sugars and hormones depend on fruit species and environmental conditions, which requires in-depth investigations in specific contexts.

SUGAR METABOLISM INVOLVED IN RESPONSES TO ABIOTIC STRESS

Adverse environmental conditions often result in the accumulation of excess reactive oxygen species (ROS) and ultimately oxidative stress, during which sugar metabolism has its contribution to the responses of fruit crops to abiotic stress (Tian et al. 2013; Wang et al. 2019). RNA sequencing (RNA-seq) profiling for the antisense-*A6PR* apple line showed that sorbitol had important roles in the responses to abiotic and biotic stresses by modulating the genes involved in ABA, salicylic acid and JA signaling as well as nucleotide-binding site leucine-rich repeat (NBS-LRR) resistance (Wu et al. 2015). Moreover, as glucose contributes to the pentose phosphate pathway and the production of non-enzymatic antioxidants (including phenolics and flavonoids), sugar metabolism may function in maintaining fruit quality through modulating intracellular redox homeostasis and preventing oxidative stress under unfavorable conditions (Liu et al. 2013).

It has been documented that fruit development are sensitive to temperature (Zhang et al. 2010; Wang et al. 2019). After measuring CWIN, VIN, and sucrose synthase activities among the tomato cultivars showing differential heat sensitivity at normal and high temperature, Li et al. (2012a) found that that both CWIN and VIN activities were higher in the heat-tolerant cultivar (CLN2413R), suggesting that these two enzymes were involved in the responses of reproductive organs to heat stress. In accordance with the phenotype for *CWIN* overexpression (Liu et al. 2016a), the transcript level of PLDa1, a PCD regulator, was higher in the heat-sensitive cultivar (T9246), which may be related to invertase activities. The authors hypothesized that the suppression on the expression of PLDa1 and other PCD regulators may be attributed to the higher hexose content in the heat-tolerant cultivar (Li et al. 2012a). Taken together, these findings confirm that invertases have crucial roles in correlating sugar signaling and heat tolerance of fruit. Moreover, sucrose metabolism also functions in the responses to low temperature. Exogenous JA alleviated chilling injury in peach fruit by preventing the decrease in soluble sugar content, which was resulted from the scavenging of reactive oxygen species and the stabilization of membranes (Zhao et al. 2021). Similarly, the chilling resistant 'Ninghaibai' loquat fruit showed higher hexokinase and fructokinase activities, higher hexose contents, and higher sucrose degrading activities. These results suggest that the higher hexose contents and hexose sensor activity may also contribute to the chilling tolerance of loquat fruit (Cao et al. 2013). In addition, high salinity also interferes with sugar metabolism in tomato fruit, leading to lower sink activity and yield loss (Albacete et al. 2014). Overexpression of *CIN1*, a CWIN gene, alleviated the impairment of high salinity on fruit yield. Therefore, the authors proposed that globally activated hormonal signaling had positive roles in this process. However, the underlying mechanisms still require further clarifications.

Besides hexose contents and sensor activity, the trehalose pathway also contributes to the responses of fruit to abiotic stress (Durán-Soria et al. 2020). The trehalose precursor trehalose-6-phosphate (T6P) has been proposed to function via the sucrose non-fermenting-related kinase-1 (SnRK1) pathway, in which SnRK1 acts as a key modulator activated by stress conditions, such as hypoxia and submerging. It was reported that heterologous overexpression of *SnRK1* from *Malus hupehensis* and *Prunus persica* in tomato accelerated fruit ripening, which was attributed to the interaction with RIN (Yu et al. 2018; Wang et al. 2012). In the presence of abundant sucrose, T6P inhibited SnRK1 activity but activated the expression of growth-promoting genes, whereas SnRK1 functioned as a growth repressor to regulate normal growth and stress responses (O'Hara et al. 2013). Nevertheless, the exact roles of T6P and SnRK1 in abiotic responses of fruit still require further exploration.

SUGAR METABOLISM INVOLVED IN RESPONSES TO BIOTIC STRESS

Sugar metabolism and transport have important roles in the interaction between fruit and pathogens. Exogenous sucrose increased endogenous sucrose, glucose and fructose levels, further stimulated the phenylpropanoid metabolic activity, resulting in higher levels of isoflavone glycosides and defense responses to *Fusarium oxysporum* in lupine (Morkunas et al. 2005). Interestingly, Sigha et al. reported that mitogen-activated protein kinase (MAPK) activities and *LIN6* expression were substantially induced by non-metabolizable sugars, which were similar to the variations substantially triggered by fungal elicitors from *F. oxysporum* (Sigha et al. 2002). The authors proposed that non-metabolizable sugars may be perceived as stress signals. In addition to trehalose synthesis, pathogens may synthesize trehalose or trehalose-6-phosphate (T6P), thereby triggering metabolic reprogramming of plant cells. An interesting study showed that Snf1-related kinase (SnRK) 2.8, a member in the SnRK-CDPK module, may be hijacked by pathogens to phosphorylate bacterial effectors (Lei et al. 2020). These data identify a strategy co-opted by pathogens to promote disease incidence, which may be utilized for genetic breeding to improve resistance. Sugar transporters also play roles in fruit-pathogen interaction. The transcript level of *VvSWEET4* (a clade II member) was strongly stimulated upon the invasion of the necrotrophic fungus *Botrytis cinerea* (Chong et al. 2014), which may be explained by the manipulation on sugars in hosts by *B. cinerea*. Coincidently, the knock-out mutants for *AtSWEET4* (a gene encoding a clade II SWEET) displayed cell death phenotype and higher resistance to *B. cinerea* (van Kan 2006). Another line of evidence showed that *B. cinerea* infection induced SlSWEET15 (a clade III SWEET) but down-regulated VvSWEET7 (a clade II SWEET), thereby providing sugars to facilitate mycelial growth of *B. cinerea* (Asai et al. 2016; Breia et al. 2020), suggesting that sugar transporters in the same superfamily may respond differentially to pathogen invasion.

Pathogens compete for sugars as nutrient sources to gain access to their hosts, whereas host sugar metabolism may contribute to the variations in host environment, thereby affecting the consequence for interactions between fruit and pathogens (Prusky and Yakoby 2003; Tian et al. 2016; Wang et al. 2019). It was reported that excessive sugar content in fruit contributed to pH modulation in host tissues by oxidation of glucose to gluconic acid by glucose oxidase 2 in acidifying pathogens. In contrast, the deamination reaction catalyzed by glutamate dehydrogenase 2 led to ammonia production, indicating that fungus-induced pH modulation was affected by sugar content in hosts (Bi et al. 2016). Similarly, in the analysis on the interactions of *Colletotrichum gloeosporioides* and *Penicillium expansum* with different tomato cultivars, *P. expansum* showed enhanced colonization in the high sugar content cultivar, whereas *C. gloeosporioides* showed enhanced colonization in the low sugar content cultivar. Moreover, the specific gene responsive profiles for the two host lines differed significantly, which depended on the sugar level. The authors suggested that such differential response patterns may contribute to the differential host ranges for both pathogens (Ziv et al. 2020).

Sugar may also function as a signaling molecule to modulate the resistance of plants to pathogens (Meng et al. 2018). Antisense suppression of *A6PR* led to reduced sorbitol synthesis in *M. domestica* leaves, downregulation of Nucleotide-binding Leucine-rich Repeat (NLR) genes, and ultimately susceptible responses to *Alternaria alternata*. Overexpression of *MdNLR16* in *A6PR* lines improved the resistance, whereas sorbitol promoted the transcriptional activation of *MdNLR16* by MdWRKY79, suggesting sorbitol could modulate the resistance to *A. alternata* through the interaction between MdNLR16 and fungal effector in a classical gene-for-gene manner in apple (Meng et al. 2018). To our knowledge, this is the only report on the signaling roles of sugars in modulating disease resistance to fungal pathogens up to now.

STRATEGIES FOR METABOLIC ENGINEERING ON SUGAR CONTENT

Sweeter fruit with higher sugar content is often favored by consumers. A gene co-expression analysis on citrus fruit transcriptome showed that most the sugar/acid ratio-related genes are involved in transport, signaling, transcription and metabolic enzymes, only few genes are weakly correlated with sugar level and none corresponded to acid-associated genes, suggesting that a fruit-specific dissection for sugar metabolic processes may be necessary for genetic engineering (Qiao et al. 2017). Latest studies on gene regulatory elements have provided new targets for future work. An interesting study generated the transgenic tomato lines harboring the main open reading frames (ORFs) of *SlbZIP1* and *SlbZIP2* (driven by the fruit-specific *E8* promoter), whereas the sucrose-induced repression of translation (SIRT)-responsive uORFs were removed (Sagor et al. 2016). The contents of sugar (sucrose/glucose/fructose) and several amino acids (such as asparagine and glutamine) were significantly higher in the transgenic fruit. This strategy is promising as it substantially increases the sweetness of fruit without substantially affecting normal growth of fruit crops. Similar results have also been reported to modulate the growth/immunity tradeoff of plants in cereal crops (Xu et al. 2017).

In return, the genes involved in sugar metabolism, such as some *SWEET* genes, may be co-opted by fungal pathogens, as revealed in the gray mold caused by *B. cinerea* (Chen et al. 2010). *SWEET* genes play a major role in growth and development of plants, but also act as susceptibility (*S*) genes in response to pathogen invasion. Therefore, these dual-function genes modulating the balance between growth and defense should be further explored, and their functions as *S* genes in regulating pathogen susceptibility might be elucidated. The use of *SWEET* genes may potentially enable the improvements for fruit crops, including tomato and banana, as their substantial functions as *S* genes has already been demonstrated (Gupta et al. 2020). However, the clustering of a SWEET in a specific clade does not guarantee a definite physiological process for the protein, which requires in-depth studies on the exact functions (Eom et al. 2015). In addition, during the production of botrytized wines using some white-skinned grape berries, noble rot reprograms the metabolism of cv. Sémillon berries by inducing stress responses and fruit ripening, resulting in accumulation of sugars, aroma substances, and flavor compounds, as well as enhancement of phenylpropanoid metabolism and anthocyanin biosynthesis (Vannini and Chilosi 2013; Blanco-Ulate et al. 2015). Although the underlying mechanisms have not been elucidated so far, this represents another example for the engineering of primary and secondary metabolism of fruit utilizing "beneficial" fungal pathogens.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

In conclusion, metabolic and transport activities synergistically contribute to composition and concentrations of sugars in various fruit species, ultimately determining fruit quality and commodity. Sugars may function coordinately with ABA and other phytohormones. Moreover, sugars also act as crucial modulators of stress responses and disease resistance to fungal pathogens. Importantly, the development of different fruits is underpinned by different transport and metabolic processes, and transporters or catalytic enzymes also changes substantially during development of different fruit crops. Therefore, an in-depth understanding in the molecular networks involving sugar metabolism and transport in specific biological context may greatly intensify and accelerate future metabolic engineering of fruit crops.

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Author contribution ST conceives, writes the original manuscript, revises and approves the final version; TC, ZZ, BL and GQ discuss on the data and write the original manuscript.

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Declarations

Conflict of interest The authors declare that there is no conflict of interest.

Compliance with ethical standards Not applicable.

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