

Review Article

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Biosynthesis and Metabolism of Plant Sugars: From Molecular Mechanisms to Agricultural Applications

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Abstract This study reviews how plant sugar metabolism works and why it is important for plant growth, stress response, and agriculture. Sugars like glucose, fructose, sucrose, and starch are not only energy sources but also act as signals that control how plants grow and react to the environment. The paper explains how sugars are made, moved, and used in plants through enzymes and transporters. It also discusses how sugar metabolism connects with nutrient use, hormone signals, and stress resistance. Research has shown that changing sugar-related genes can improve yield, quality, and stress tolerance in crops. New tools such as CRISPR/Cas, systems biology, and metabolic modeling help scientists study sugar pathways more deeply and use this knowledge in real farming. Understanding sugar metabolism can support better crop breeding, stronger stress resistance, and sustainable agriculture in the future.

Keywords Plant sugars; Sugar metabolism; Sucrose transport; Stress tolerance; Crop improvement; CRISPR/Cas; Sustainable agriculture

1 Introduction

Carbohydrates play a fundamental role in plant development and survival, serving as the primary outputs of photosynthesis. They supply energy and carbon skeletons for biosynthetic processes while modulating numerous physiological functions. Over evolutionary time, plants have developed sophisticated mechanisms for sugar production, distribution, and utilization, allowing them to thrive under diverse environmental conditions and optimize resource allocation. Advances in molecular biology and genetics have significantly enhanced our comprehension of these complex regulatory networks.

Sucrose acts as the principal soluble sugar transported within plants. It is produced in photosynthetically active tissues and then distributed to non-photosynthetic organs (Li et al., 2017; Ciereszko, 2018; Stein and Granot, 2019; Gautam et al., 2022). The spatial and temporal regulation of sugar partitioning influences key developmental processes such as cell proliferation, seed dormancy release, flowering initiation, and aging (Eveland and Jackson, 2012). Additionally, sugar metabolism interacts with nutrient uptake systems, particularly for nitrogen and potassium—elements critical for photosynthetic efficiency and carbohydrate translocation (Shah et al., 2024). Under abiotic stresses like drought, high salinity, or heat, plants accumulate monosaccharides (e.g., glucose, fructose) and disaccharides (e.g., sucrose) to stabilize cellular structures, maintain osmotic balance, and scavenge reactive oxygen species (Afzal et al., 2021; Nägele et al., 2022).

Cells can detect specific sugars, including glucose, sucrose, and trehalose-6-phosphate (Tre6P), which function as signaling molecules that influence gene transcription and metabolic flux (Rolland et al., 2006; Choudhary et al., 2022). Key regulators in sugar sensing include hexokinase (HXK), the target of rapamycin (TOR) kinase, and SNF1-related protein kinase 1 (SnRK1), all of which integrate metabolic status with hormonal pathways (Sakr et al., 2018; Li et al., 2021). Cross-talk between sugar signals and phytohormones, such as auxin, shapes organogenesis in roots, shoots, and reproductive structures (Eveland and Jackson, 2012; Mishra et al., 2021). Furthermore, carbohydrates contribute to cell wall biosynthesis and serve as precursors for various secondary metabolites (Figueroa et al., 2021; Tang et al., 2023). Glycosyltransferases facilitate the assembly of intricate polysaccharides, reinforcing cellular integrity and improving resistance to biotic and abiotic challenges.

Manipulating sugar metabolism offers promising strategies to boost agricultural productivity, enhance crop quality, and increase stress tolerance (Patrick et al., 2013; Julius et al., 2017; Ji et al., 2022; Nägele et al., 2022). Emerging gene-editing tools enable precise modulation of sugar transporters such as SWEET and SUT family proteins, thereby optimizing carbohydrate allocation and storage (Breia et al., 2021; Gautam et al., 2022). Moreover, efficient conversion and utilization of sugars position plants as vital feedstocks for bioenergy and biobased materials (Tang et al., 2023).

This study reviews recent research on sugar metabolism in plants. It focuses on: (1) sugar production and breakdown; (2) the role of sugars in energy and structure; (3) sugar metabolism under environmental and nutrient conditions; and (4) applications of sugar metabolism engineering in crop improvement and the bioeconomy. Finally, it points out research gaps and looks ahead to future directions.

2 Types and Functions of Plant Sugar

2.1 Classification: monosaccharides, disaccharides and polysaccharides

Monosaccharides are the simplest sugars, such as glucose, fructose and galactose. They are soluble in water and can provide energy directly or participate in the synthesis of other substances (Qi and Tester, 2019; Niyigaba et al., 2021; Zhu et al., 2024).

Disaccharides such as sucrose, maltose and lactose are composed of two monosaccharides. Sucrose is the most common. After synthesis in leaves, it is transported to roots and fruits and then decomposed into glucose and fructose for energy supply (Koch, 2004; Liu et al., 2025b).

Polysaccharides are composed of many monosaccharides. Starch and cellulose are homopolysaccharides, while pectin and hemicellulose are heteropolysaccharides. They are respectively responsible for energy storage and structural support (Mohammed et al., 2021).

2.2 Main sugars: glucose, sucrose, fructose and starch

Glucose is produced during photosynthesis, providing energy for cells and also serving as a carbon source for the synthesis of molecules such as amino acids (Couee et al., 2006; Qi and Tester, 2019). Fructose often coexists with glucose and is also a component of sucrose.

Sucrose is synthesized in leaves and transported through the phloem to roots, fruits and seeds, where it is decomposed for energy supply or storage (Koch, 2004; Gautam et al., 2022; Liu et al., 2025b).

Starch is composed of amylose and amylopectin and is the main energy storage substance. Synthesis during the day and decomposition for energy supply at night to maintain energy balance (Dong and Beckles, 2019; Cho and Kang, 2020).

2.3 Functions and roles: energy supply, osmotic regulation and stress response

Glucose and sucrose produce ATP during respiration to provide energy for growth (Couee et al., 2006; Qi and Tester, 2019). The transport of sugar is accomplished by proteins such as SWEET, SUT and MST, ensuring normal nutrient distribution (Koch, 2004; Saddhe et al., 2020; Gautam et al., 2022).

Under drought, high temperature or salt stress, plants accumulate soluble sugars, such as sucrose and trehalose, to retain moisture, stabilize membrane structure and reduce oxidative damage (Couee et al., 2006; Afzal et al., 2021; Nägele et al., 2022).

In addition, sugar regulates gene expression and hormone balance, and participates in growth and stress response together with hormones such as abscisic acid (Liu et al., 2025b).

3 The molecular mechanism of carbohydrate biosynthesis

3.1 Photosynthesis and carbohydrate production

In chloroplasts, light energy is used to produce ATP and NADPH. These two molecules enter the Calvin cycle, converting carbon dioxide (CO₂) into a small sugar molecule called 3-phosphoglyceraldehyde (GAP). After GAP,

larger sugars can be synthesized, such as glucose. Some of the glucose remains in the chloroplast to form starch, while the other part is transported to the cytoplasm to synthesize sucrose (Johnson, 2016).

The thioredoxin system in chloroplasts helps plants maintain a balance among light energy utilization, energy generation and sugar synthesis, enabling plants to remain stable under different light and stress conditions (Nikkanen and Rintamaki, 2019; Chauhan et al., 2023). Photosynthesis and the utilization of sugar are related to the growth, environmental adaptation and yield of plants.

3.2 Synthetic pathways of sucrose and starch

The carbon produced by photosynthesis is used to synthesize sucrose and starch. Sucrose is synthesized in the cytoplasm. The three-carbon phosphate generated by chloroplasts is acted by various enzymes, such as aldolase, fructose-1, 6-diphosphatase and sucrose phosphatase synthase (SPS), and eventually sucrose is produced and transported to other tissues through the phloem (Stein and Granot, 2019; Wang et al., 2022b).

Starch synthesis occurs in plastids. The enzyme ADP-glucose pyrophosphorylase (AGPase) catalyzes the formation of ADP-glucose from glucose-1-phosphate and ATP. Then, starch synthase extends the sugar chain, and branched enzymes generate amylose and amylopectin. Studies have shown that sucrose synthase (SuSy) can also generate ADP-glucose in different tissues, indicating that there are multiple pathways for starch synthesis (Baroja-Fernandez et al., 2003; Munoz et al., 2005; Li et al., 2013; Qu et al., 2018) (Figure 1). The ratio of sucrose to starch varies with the growth stage of the plant, the environment and energy requirements.

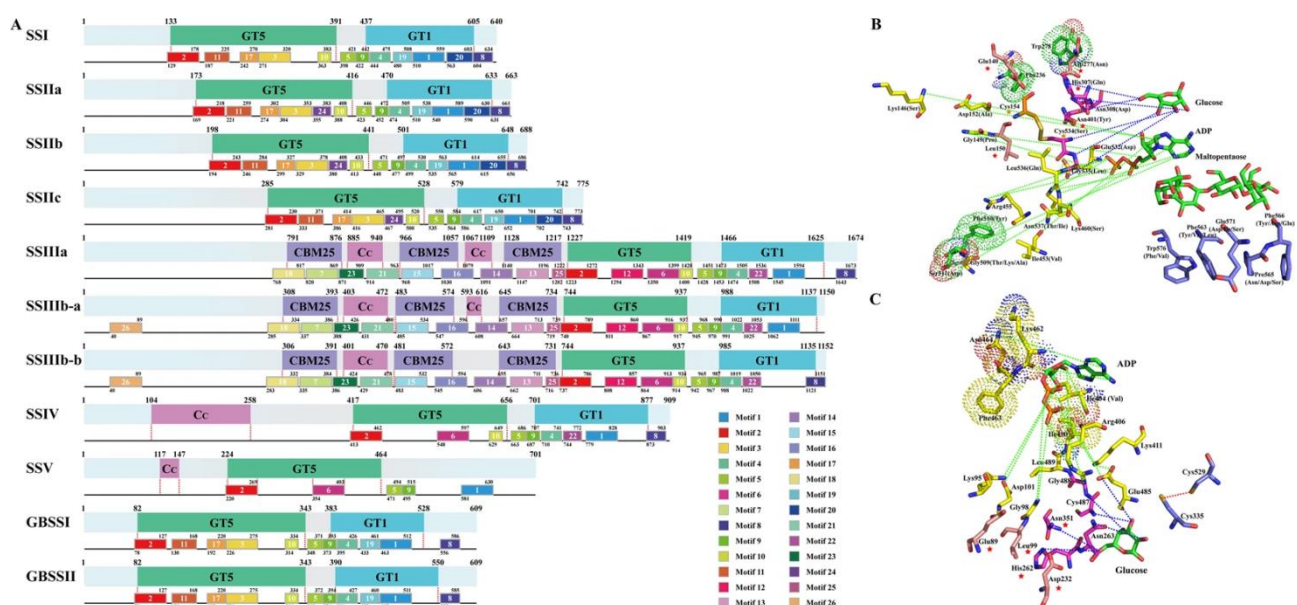


Figure 1 Structural features and active site analysis of SS isoforms. Maize is shown as an example. (A) Compositions and distributions of domain structures and conserved motifs of SS proteins are marked and annotated in different colours. (B) Stereo view of the active sites of SS isoforms based on the sequence of SSI and (C) GBSSI isoforms based on the sequence of GBSSI. The same site with different amino acids is marked with dots in SS isoforms. Interaction sites between SSs and ADP are shown as linked broken green lines. Interaction sites between SSSs and glucose are marked in pink. Red stars and lines shown in light pink represent catalytic sites. Amino acid sites that interact with maltopentaose are marked in blue, and these active sites are not conserved in SSIII, SSIV and SSV. Additionally, disulfide bonds were found only in SSI and GBSSI and are marked with orange stars in SSSs and as blue amino acids in GBSSI (Adopted from Qu et al., 2018)

3.3 The role of key enzymes

Sucrose phosphosynthase (SPS) is responsible for transferring glucose from UDP-glucose to fructose-6-phosphate to form sucralose-6-phosphate, which subsequently forms sucrose. Its activity is regulated by signaling and phosphorylation (Rocher et al., 1989; Wang et al., 2022b).

Adp-glucose pyrophosphorylase (AGPase) is a key enzyme in starch synthesis, activated by 3-phosphoglyceric acid, inhibited by inorganic phosphoric acid, and regulated by REDOX (Qu et al., 2018). Sucrose synthase (SuSy) can break down sucrose into UDP- or ADP- glucose and fructose. Different types of SuSy are involved in cellulose synthesis, stress resistance and growth in different parts of plants (Stein and Granot, 2019; Li et al., 2024).

3.4 Genetic regulation of carbohydrate biosynthesis

The expression of enzymes such as SPS, AGPase and SuSy is controlled by multiple transcription factors, such as bZIP, MYB, AP2/ERF, which respond to changes in glucose concentration, hormones and environment (Ma et al., 2017; Yoon et al., 2021; Finegan et al., 2022; Li et al., 2024a). In cassava, MebHLH68 links ABA signaling to glucose metabolism genes and regulates sucrose and starch pathways (Li et al., 2024c), while AREB2 activates glucose storage-related genes under stress (Ma et al., 2017).

Sugars can also act as signal molecules. Sucrose and trehalose 6-phosphate affect gene expression by regulating SnRK1 kinase (Baena-Gonzalez and Lunn, 2020; Wang et al., 2020; Gobel and Fichtner, 2023). The perception of glucose depends on hexokinase, which regulates metabolism according to energy levels (Stein and Granot, 2019; Finegan et al., 2022). Studies have shown that when the corn starch synthesis gene changes, the sugar transport gene also responds rapidly (Finegan et al., 2022).

4 Sugar Metabolism and decomposition pathways in Plants: Integration of energy, Transport and Regulation

4.1 Glycolysis and respiratory metabolism

Glycolysis breaks down glucose and other sugars into pyruvate and generates ATP and NADH, which is completed in the cytoplasm. This provides rapid energy for plants and also offers raw materials for the synthesis of amino acids and fats. Subsequently, pyruvate enters the mitochondria to undergo the TCA cycle and continues to generate ATP. Glycolysis, in conjunction with respiration, converts stored sugar into energy, which is particularly important when plants have high energy demands or are under stress (Rolland et al., 2006; Smeekens and Hellmann, 2014).

Sugar concentration, light, temperature and other factors can all affect enzyme activity. Sugar is not only an energy source, but also can act as a signaling molecule to regulate gene expression and help plants maintain balance during growth and stress (Koch, 2004; Rolland et al., 2006; Smeekens and Hellmann, 2014).

4.2 Glucose Transporters and cellular compartmentalization

Plants transport sugar from leaves to roots, seeds and other parts through sugar transporters. The main types include sucrose transporter (SUT), SWEET protein and monosaccharide transporter (MST). SUT is responsible for long-distance transportation, SWEET regulates the inflow and outflow of sugar, and MST transport glucose and fructose (Selvam et al., 2019; Saddhe et al., 2020; Xue et al., 2021; Garg and Kuhn, 2022).

These proteins are distributed in the cell membrane, vacuole membrane and endoplasmic reticulum, and can regulate the flow of sugar inside and outside the cell. They are influenced by protein interactions, signal molecules and the environment, thereby flexibly controlling sugar transport under different conditions (Saddhe et al., 2020; Xue et al., 2021; Garg and Kuhn, 2022).

4.3 Sugar metabolism and amino acid and lipid synthesis

The intermediate products of glycolysis can be used for amino acid synthesis, and acetyl-coenzyme A participates in the synthesis of fatty acids and lipids. When sugar is insufficient, gluconeogenesis converts amino acids or lipid metabolites back into sugar for energy supply, especially during seed germination or when energy is insufficient (Walker, Chen and Famiani, 2021).

Glucose signals such as T6P can regulate enzymes and transcription factors of lipid metabolism and also affect the activity of amino acid synthesis genes (Zhai et al., 2021).

4.4 Feedback regulation and sugar perception

Hexokinase (HXK) is a major glucose receptor that regulates metabolism and growth. Systems such as SnRK1, TOR and T6P are jointly involved in glucose signaling and interact with hormone and environmental responses (Rolland et al., 2006; Sheen, 2016; Li et al., 2021; Stephen et al., 2021; Li and Zhao, 2024).

When sugar levels are high, plants reduce their photosynthetic rate. When sugar is insufficient, the energy-saving mechanism is activated (Rolland et al., 2006; Smeekens and Hellmann, 2014; Stephen et al., 2021). Sugar signaling also interacts with nutritional and hormonal signaling to help plants adapt to the environment, but the overall mechanism remains to be further studied (Sakr et al., 2018).

5 Sugar Signaling and Plant Development: Pathways, Hormone Interactions and Developmental Outcomes

5.1 Glucose sensing pathways (dependent on hexokinase pathways and trehalose 6-phosphate signaling pathways)

Plants can "sense" sugar in various ways and thereby regulate their growth. The most common one is the sensing pathway dependent on hexokinase (HXK). HXK can recognize glucose and convert it into glucose-6-phosphate. At the same time, it can also act as a signaling molecule and play a regulatory role in cells. When there is a relatively high amount of glucose in plants, HXK can inhibit the expression of genes related to photosynthesis and also affect the activity of some transcription factors, thereby altering cell division and organ formation. The HXK pathway also affects plant hormones, such as regulating the transport and response processes of auxin (Avonce et al., 2005; Rolland et al., 2006; Ciereszko, 2018; Vanderwall and Gendron, 2023).

Another important pathway is related to trehalose 6-phosphate (T6P). T6P is closely related to sucrose metabolism. It is synthesized by trehalose 6-phosphate synthase and reflects the level of sucrose in cells. When T6P is abundant, the plants grow well. When T6P is low, the growth of plants will slow down. T6P functions by inhibiting SnRK1, a protein kinase. SnRK1 will limit its growth when there is insufficient energy. It can be said that the T6P-SNRK1 system acts like a "switch", linking sugar levels with processes such as plant flowering, embryonic development, and branch formation. If plants cannot synthesize T6P, such as *tps1* mutants, growth disorders will occur (Avonce et al., 2005; Xing et al., 2015; Fichtner and Lunn, 2021; Wang et al., 2021b; Gobel and Fichtner, 2023).

5.2 Interaction between glucose signaling and plant hormones (ABA, auxin, cytokinin)

The relationship between sugar signals and plant hormones is very close. They will affect each other's content, transportation and function. Glucose can regulate the ability of plants to synthesize and distribute auxin. Through the action of HXK, sugar can promote the synthesis of auxin and activate related genes. In turn, auxin can regulate the utilization and transportation of sugar, thus forming a feedback loop. This interaction is particularly important for the formation of roots and stems because they both control cell division and organ growth (Ciereszko, 2018; Robert, 2019; Kotov, Kotova and Romanov, 2021; Mishra et al., 2021; Rashid et al., 2022).

Sugar and cytokinin also interact to jointly regulate the development of stems, roots, seeds and flowers. They can all control the activity of meristem and the growth of organs. At different growth stages, they may promote each other or inhibit each other. Absciscic acid (ABA) is often associated with stress responses and dormancy, but it is also influenced by sugar signaling. When sugar is low, SnRK1 is activated, which initiates the expression of ABA-related genes, thereby linking the state of carbon hunger with the stress response and slow growth of plants (Liu, Offler and Ruan, 2013; Xing et al., 2015; Ciereszko, 2018; Wang et al., 2021b).

5.3 Effects on flowering, seed development and fruit ripening

When plants shift from vegetative growth to reproductive growth, sucrose and T6P are key signals. Before many plants are about to flower, the level of sucrose in the apical meristem will increase, thereby promoting the formation of flowers. External supplementation of sucrose can also make plants flower earlier. T6P is downstream of the sucrose signaling pathway and can activate genes such as FLOWERING LOCUS T (FT) to help plants

flower at the right time. In *Arabidopsis thaliana*, plants lacking the ability to synthesize T6P do not flower, which indicates that T6P is very important in flowering regulation (Xing et al., 2015; Cho et al., 2018; Fichtner and Lunn, 2021; Wang et al., 2021b; Wingler and Henriques, 2022; Gobel and Fichtner, 2023).

During the seed development stage, sugar signals help seeds accumulate nutrients. As the seeds mature, the contents of sucrose and T6P increase, promoting the utilization of carbon and the development of endosperm. T6P can also inhibit the activity of SnRK1, regulate ABA signals, and ensure normal seed development (Wang et al., 2021b). In fruits, sugar not only determines the sweetness but also affects genes related to ripening, pigment formation and hormone activity. Sugar interacts with ABA, auxin and ethylene to jointly control the time and process of fruit ripening (Robert, 2019; Duran-Soria et al., 2020; Rashid et al., 2022; Rossouw et al., 2024).

6 Environmental Regulation of Sugar Biosynthesis and Metabolism

6.1 Effects of light, temperature, and water supply

Light gives energy for photosynthesis and also controls sugar-related genes. These genes regulate enzymes that make sucrose and starch. Changes in light strength, time, or color affect enzymes like UDP-glucose pyrophosphorylase and glucan synthase, which then change sugar types and amounts.

Light signals through photoreceptors and redox factors help plants adjust sugar production and storage under different light conditions (Borbély et al., 2022; Wu et al., 2025).

Temperature affects enzyme activity and respiration. Heat speeds up sugar breakdown, while cold slows it, causing sugar buildup that protects cells from freezing.

When water is low, plants collect sugars like sucrose, trehalose, and raffinose to keep water and protect cells. Sugar transporters and starch-degrading enzymes become more active to help plants survive drought (Dong and Beckles, 2019; Gurrieri et al., 2020; Saddhe et al., 2020; Nägele et al., 2022).

6.2 Responses under abiotic stress (drought, salt stress, low and high temperature stress)

Drought, salinity, low temperatures and high temperatures can all slow down plant growth and reduce yields. Under these pressures, plants usually change the way they use sugar. For instance, under drought or salt stress, plants accumulate soluble sugars such as glucose, fructose, sucrose, trehalose and raffinose. These sugars can help cells retain water, protect proteins and membrane structures, and eliminate reactive oxygen species (ROS) (Kosar et al., 2018; Nagele et al., 2022).

To ensure the supply of sugar, plants make the enzymes and transport proteins involved in sugar synthesis more active, while releasing sugar by breaking down starch. For instance, in arid environments, plants enhance the activities of sucrose synthase and glucan hydrolase to convert stored carbohydrates into energy and maintain cellular water balance (Dong and Beckles, 2019; Gurrieri et al., 2020).

At low temperatures, plants convert starch into soluble sugar, which can lower the freezing point of the cell fluid and prevent it from being damaged by freezing (Thalmann and Santelia, 2017; Dong and Beckles, 2019). When under salt stress, plants tend to accumulate more starch to support growth and enhance salt tolerance. High-temperature stress, especially when drought coexists, can disrupt the sugar balance and eventually lead to a reduction in biomass and yield (Das, Rushton and Rohila, 2017; Wang and Wang, 2023).

6.3 Role of sugars in biotic stress resistance

Sugars act as both energy and defense signals. Pathogens take sugars through transporters like SWEETs, but plants reduce sugar loss by changing transporter and enzyme activity (Tauzin and Giardina, 2014; Bezruczyk et al., 2018; Breia et al., 2021).

During infection, invertase increases glucose, which moves to the infected area to support defense compounds (Wingler and Roitsch, 2008).

Sugar signals also work with hormones such as ethylene and jasmonic acid to turn on defense genes and boost ROS response (Morkunas and Ratajczak, 2014). High sugar levels give energy and strengthen cell walls, though some pathogens can still use sugar signals to weaken defenses.

7 Agricultural Applications of Plant Sugar Research

7.1 Improving crop yield by enhancing photosynthesis and sugar flow

Gene engineering helps plants use light more efficiently. Scientists improve enzymes like Rubisco and the cytochrome b6f complex to increase CO₂ uptake and sugar production. Adding genes from C4 plants such as phosphoenolpyruvate carboxylase or NADP-malic enzyme to C3 crops raises CO₂ near Rubisco, reduces photorespiration, and boosts photosynthesis.

Sucrose transporters (SUTs) move sugar from leaves to roots or fruits. When SUT genes are active, plants grow faster and yield more (Li et al., 2020; Croce et al., 2024; Nazari et al., 2024). Improving photosynthesis in the whole canopy also helps crops like rice and wheat produce more biomass, though results depend on species and environment (Wu et al., 2019; Araus, Sanchez-Bragado and Vicente, 2021).

7.2 Genetic engineering to increase starch and sugar storage

Key enzymes like starch synthase and branching enzyme control starch buildup. Using CRISPR/Cas9, scientists can edit these genes to make more amylose or resistant starch in rice and maize (Bahaji et al., 2014; Baysal et al., 2020; Zhong et al., 2022). In sugarcane and beets, adjusting enzyme and transporter activity increases sugar storage, but balance with water and nutrients is needed. Modern tools like CRISPR help create crops with higher starch and sugar for food and industry (Patrick et al., 2013; Ahmad and Ming, 2024).

7.3 Sugar metabolism and its effects on fruit and grain quality

Sugar metabolism affects sweetness and texture. Levels of sucrose, glucose, and fructose depend on genes and environment. Editing transcription factors like S1-bZIP through CRISPR can make fruits such as strawberries sweeter (Wang et al., 2022a; Du et al., 2024a; 2024b). Conditions like light and temperature also change sugar content. For example, controlling the S6PDH gene in plums raises sugar levels and improves flavor (Chen et al., 2021).

7.4 Applications in bioenergy, biofuels, and industry

Sugarcane's high sugar and biomass make it ideal for bioethanol. CRISPR/Cas9 creates varieties with higher yield and cleaner fuel (Patrick et al., 2013; De Carvalho Silvello et al., 2021; Shi et al., 2023; Ahmad and Ming, 2024). Other crops and microalgae are modified to produce biofuels like ethanol and hydrogen. Turning plant cell walls into sugars for fermentation also supports making bioplastics and other green products.

8 Case Studies on Plant Sugar Metabolism: From Sweeter Taste to Better Stress Resistance

8.1 Case 1: sugar metabolism and sweetness in tomato

People like sweeter tomatoes, so increasing sugar content has been a big goal. But when sugar goes up, the fruits often get smaller or yield less. Studies found that two calcium-dependent protein kinases, SICDPK27 and SICDPK26, act like “brakes” on sugar levels. They add phosphate groups to sucrose synthase, making it break down faster and slow sugar build-up.

When scientists knocked out SICDPK27 and SICDPK26, glucose and fructose levels rose by about 30%. The fruits became sweeter, but their size and yield stayed the same. The seeds were smaller and lighter, but germination was normal. This means changing sugar metabolism directly can make fruits sweeter without reducing yield (Wang et al., 2021a; Zhang et al., 2024; Fernie and Martinez-Rivas, 2025).

Other teams also improved sugar levels by changing genes for invertase and sugar transporters. Deleting SIINVINH1 and SIVPE5 raised glucose, fructose, and total soluble solids. They also found key QTLs such as Lin5 that affect sugar accumulation. These studies show that plants can use different ways to control sugar metabolism, giving new ideas for improving fruit taste and processing quality (Wang et al., 2021a). Similar work in sugarcane also increased sugar yield, but storage remains a big problem (Patrick et al., 2013).

8.2 Case 2: improving starch synthesis in rice and maize

Scientists have built a complex network that controls starch synthesis in rice endosperm. It includes many transcription factors and enzyme genes. Each enzyme gene can be controlled by several transcription factors. By adjusting these regulators, they can change the ratio of amylose to amylopectin.

When OsSPL7 and OsB3 were knocked out, rice tasted better and cooked better, without changing grain shape (Huang et al., 2025). Editing starch synthesis genes can also increase resistant starch (RS). When SSIIa and SSIIb lost their function, RS went up by about 10%. More mutations made it even higher. But too much RS may affect yield or texture, so a balance is needed between health and productivity (Figure 2). In maize, overexpressing ZmCBM48-1 raised starch content and changed the structure of the endosperm (Peng et al., 2022; Dong et al., 2024; Wang et al., 2024).

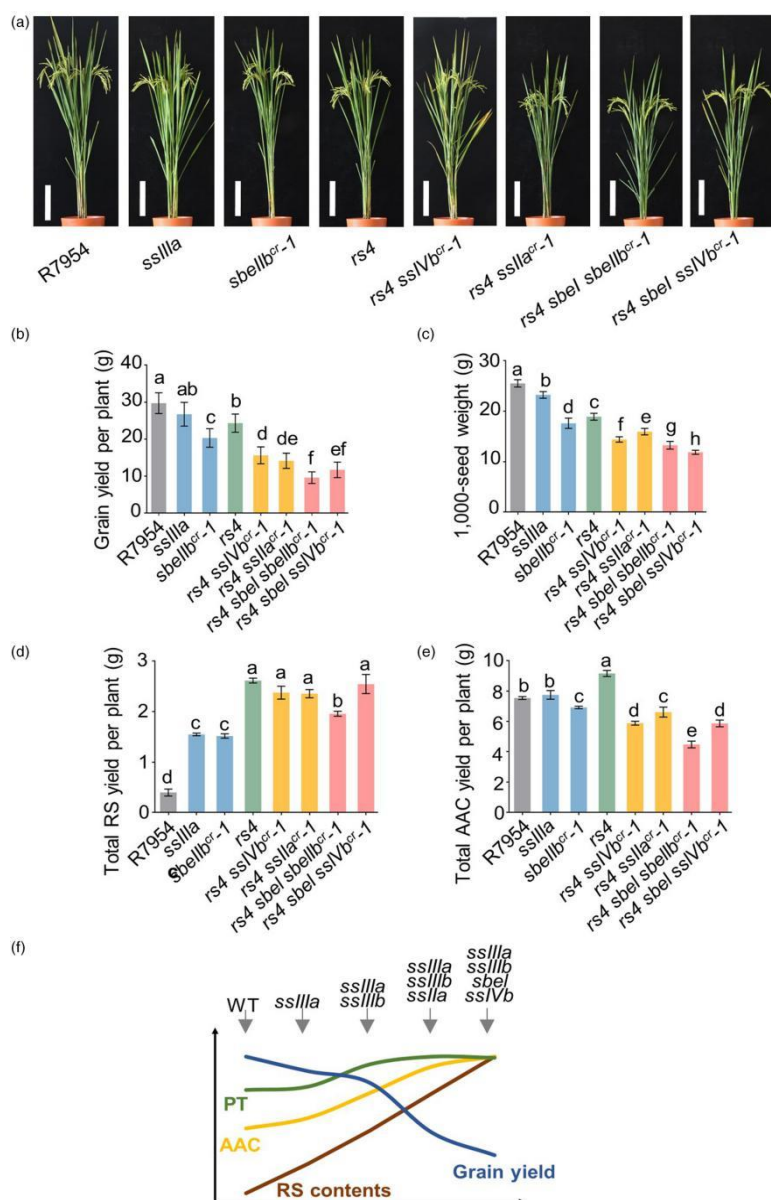


Figure 2 Yield-related traits were significantly affected in eight selected RS lines. (a) Plant morphologies of eight selected RS lines, bars = 20 cm. (b-c) Grain yield per plant (b) and 1000-seed weight (c) of eight selected RS lines in Beijing. (d-e) Total RS (d) and AAC yield (e) per plant of eight selected RS lines. (f) Model of relative RS contents, AAC, PT, and grain yield in the wild type (WT), ssIIa, ssIIa ssIIb (rs4), rs4 ssIIa, and rs4 sbelI ssIVb mutants. In (b-c) values are means $\pm$ s.d. (n = 10 plants), in (d - e) values are means $\pm$ s.d. (n = 3 biological replicates) and different letters at the top of each column indicate a significant difference at $P < 0.05$ determined by Tukey's HSD test (Adopted from Wang et al., 2024)

8.3 Case 3: sucrose transport and drought resistance in wheat

Sucrose transport is very important in plants, especially under stress. It moves sugar from leaves to other parts. In wheat, drought slows sugar movement and reduces yield. Research shows that drought-tolerant wheat keeps higher invertase activity and increases the expression of sugar transport proteins like STP, SWEET, and SUT. These proteins help move sucrose to grains, so the plant can still produce more fertile flowers and grains under drought (Li et al., 2024b).

Also, spraying spermidine after drought can help move sugar in the spikes and stems, increasing fertile flower numbers. Adding zinc can raise SUT1B expression, improve sucrose transport and starch accumulation, and help maintain yield under drought (Zarea and Karimi, 2023).

9 Challenges and Future Prospects in Plant Sugar Research

9.1 Knowledge gaps in sugar signaling and metabolic integration

Hexokinase (HXK), SnRK1, and TOR are main factors that control sugar and energy signals. But we still don't know well how these signals work in different plants, where they overlap, or how they changed during evolution. Sugar signals also connect with nitrogen and hormones, but this system is very complex (Sakr et al., 2018). We also know little about how sugar-related proteins are changed after they are made and what genes they control. This makes it hard to use sugar signals to improve crops (Eom et al., 2024). The link between sugar and microbes is also not clear. Sugar may help or harm microbes, but we don't understand how. We still don't know how sugar moves in infected plants, how it spreads between cells, or what role transport proteins play in disease resistance (Bezruczyk et al., 2018).

9.2 Balancing sugar accumulation, growth, and stress resistance

High sugar levels are good for crops like sugarcane and fruits, but too much sugar can slow growth and make plants weaker under stress. Sugar can also act as a signal or a protector to help plants fight stress by turning on certain genes and processes (Saddhe et al., 2020; Eom et al., 2024). To solve this, we need to understand how sugar and nitrogen metabolism work together and how they affect other processes (Sakr et al., 2018; Liu et al., 2025a). Future studies should combine photosynthesis, sugar storage, and stress response, especially as climate change becomes more serious.

9.3 Emerging Tools: CRISPR, Systems Biology, and Metabolic Modeling

CRISPR/Cas tools make it easier to change genes related to sugar production, transport, and signaling. Scientists have used CRISPR in many crops to improve yield, quality, and stress tolerance, even in plants with big genomes like sugarcane. But editing large genomes is still hard (Ricroch et al., 2017; Zhu et al., 2020; Hussin et al., 2022; Devi et al., 2023). Synthetic biology and systems modeling also help us understand sugar metabolism. Machine learning and omics methods are now used to study sugar pathways and to design better ways to improve crops. But there are still limits, like poor control of gene networks and weak tools for gene delivery (Lü et al., 2022; Cardiff et al., 2024).

9.4 Future Opportunities for Breeding and Sustainable Agriculture

Knowing more about sugar signals and metabolism can help us grow crops that yield more, have better nutrition, and resist stress. CRISPR can quickly find and change key genes, helping crops deal with climate change (Ricroch et al., 2017; Zhu et al., 2020; Hussin et al., 2022; Devi et al., 2023). Improving how plants use sugar and nitrogen can also make farming more sustainable and reduce pollution (Liu et al., 2025a). Sugar studies can support other fields too, like bioenergy, biomaterials, and green industries. For example, sugar-based seed treatments (biopriming) can help seeds sprout and grow better under stress (Bozdar et al., 2025). In the future, combining molecular biology, systems research, and smart breeding will help create crops that meet food and environmental needs.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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