A Review of the Diverse Genes and Molecules Involved in Sucrose Metabolism and Innovative Approaches to Improve Sucrose Content in Sugarcane

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Abstract: Sugarcane (Saccharum spp. hybrid) is the chief source of sugar and biofuel globally and is prominent among cash crops. Sucrose is the main required product in sugarcane, and many studies have been performed to understand the phenomena of sucrose synthesis, metabolism, and accumulation in sugarcane. However, none of the studies concluded that a single gene is responsible for the sucrose content. Instead, a complex mechanism consisting of several genes, such as sucrose phosphate synthase genes (SPS1, SPS2, SPS4, SPS5), sucrose synthase genes (SuSy1, SuSy2, SuSy4), invertase genes (INV, CWIN, NIN1, CINV2), and phytohormone, trehalose, transcription factor (TF), protein kinase, and sugar transporter genes are working spatiotemporally in sugarcane. Currently, omics approaches like transcriptomics, proteomics, and metabolomics are also being used to explore the sugar metabolism in sugarcane, but integrated transcriptomic, proteomic, and metabolomic studies have been less reported. The results obtained from the integrated analysis of transcriptomics, proteomics, and metabolomics are more reliable because the strong gene expression, received in the form of abundant mRNA, does not guarantee the plentiful existence of associated proteins or their particular activity in the target cells or tissues, which discloses the restraint of single interpretation and stresses the significance of the integrated analysis of transcriptomics, proteomics, and metabolomics. This review highlights different genes and molecules contributing to sugar metabolism at different stages and the significance of omics approaches in explaining sucrose metabolism, especially sucrose accumulation in sugarcane. It is also a vital source of knowledge for sugarcane breeders, particularly associated with sucrose content improvement and bioethanol energy production.

Keywords: sugarcane; sucrose synthase; sucrose phosphate synthase; phytohormone; invertase; omics approach

1. Introduction

Sugarcane (Saccharum spp. hybrid) is an important member of the grass family Poaceae (Gramineae), subfamily Panicoideae, super tribe Andropogoneae, sub-tribe Saccharinae, and genus Saccharum [1]. Sugarcane is a C₄ perennial plant and is well-cultivated commercially in at least 106 countries of tropical and subtropical areas, which are recognized by their hot and humid atmospheres and extremely productive lands suitable for sugarcane growth and development. Sugarcane is vital among crops because of its high sucrose content in cane [2,3]. Sugarcane has a significant capability for sucrose accumulation in stalks, chiefly in ripened internodes where its quantity drives aloft to 0.7 M [4]. The main objective of sugarcane production is to yield sugar, which can be consumed in various categories of products. The sucrose is synthesized by photosynthesis in the green leaves.
of sugarcane plants and then transfers to sink organs, including consuming and storage sinks. In consuming sinks, sucrose is hydrolyzed to produce energy for growing roots, stems, and flowers while translocated to accumulate in the sink through phloem for storage purposes [5–7]. Sucrose accretion in the parenchyma cells of sugarcane stalk is achieved via incessant cleavage and resynthesis [8], whereas its metabolism is catalyzed by several key enzymes, such as sucrose phosphate synthase (SPS, EC:2.4.1.14), sucrose synthase (SuSy, EC 2.4.1.13), and invertase (INV, EC 3.2.1.26), including neutral invertase (NI), soluble acid invertase (SAI), and cell wall invertase (CWIN) [9].

2. Sugar and Other By-Products

Sugarcane is a vital industrial crop with worldwide importance and a primary source of sugar [10]. Commercial sugarcane varieties have the competence to store up to 18% sucrose in fresh cane [11]. As a whole, about 70% of the world's sugar is produced by sugarcane, making it the most significant crop [12,13]. Sugarcane provides more than 90% of the entire sugar production in China, and the main cane sugar-producing provinces in China are Guangxi, Yunnan, Guangdong, and Hainan [14,15]. Sugarcane and its by-products are used as raw materials in over 25 industries [16]. Being a C₄ plant, sugarcane contributes to reducing carbon footprints and alleviating global warming to some level [17].

Sugarcane production and sugar mills produce various by-products such as falemum, bagasse, cachaça, molasses, rum spent wash, ethanol, press mud, trash, yeast, and subsequent derivatives [18,19]. Sugarcane residues like bagasse have enough lignocellulosic biomass, mainly cellulose, hemicellulose, and lignin. Bagasse is a highly rich raw material used in glucose, xylose, ethanol, and methane production [20,21]. Sugarcane by-products, like press mud and filter cake, are produced in sugar mills during sugar purification by carbonation or sulphitation, described as soft, spongy, amorphous, and dark brown to brownish material [22]. The carbohydrates in sugarcane and their conversion into fuel have attracted worldwide attention. Rising data show that sugarcane could be the top crop for creating renewable energy, which could replace fossil fuels to some extent and will assist in lessening global warming [23]. Molasses is a viscous liquid produced during sugar production from cane juice, and it possesses many microbial activities used to synthesize alcohol or fuel [24]. Sugarcane is used to produce bioethanol which is environmentally friendly and will replace fossil fuels. Sugarcane by-products are an emerging alternative energy source [25]. The use of sugarcane trash as feasible feedstocks for the production of second-generation fuel is abundantly common, as reported by American Energy Department in 2016 [26]. Trashes are an important source of lignocellulose for conversion to biofuel and biochemicals like ethanol, lactic acid, furfural, butanol, and methanol, with the successive creation of electricity [27].

3. Tissue Culture and Mutation

Presently, the progress of somatic embryogenesis through tissue culture has an excessive capacity for propagation at a fast frequency [28]. It has been stated that all the regenerated plants from tissue culture are the same as their parents. However, the phenotypic discrepancy is generally detected between regenerated plants which are related to genetic variations in plants. These deviations have resulted from mutations, epigenetic changes, or a combination of binary processes. Soma clonal disparity is due to genetic inconsistency through tissue culture [29]. The incidence of soma clonal dissimilarity occurring through cryptic gene blemishes can limit micropropagation for clonal multiplication [30]. These differences in the genomic DNA of regenerants limit the usefulness of plant micropropagation practices for extensive multiplication. The inability to rapidly recognize these polymorphisms at cytological, biochemical, phenotypic, and molecular levels in micro-propagated sugarcane poses a challenge. The quick discovery is useful for checking the similarity between mother and in vitro-grown plantlets [31]. The PCR allied DNA molecular markers-based study arrangement, such as random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), simple sequence repeat
(SSR), inter-sequence simple repeats (ISSR), and microsatellite DNA/SSRs hold numerous advantages over the old methods that have been exercised for uncovering of polymorphism and genotyping in the plant [32,33]. The RAPD and ISSR examination have been broadly operated to reveal polymorphism in the genomic DNA of sugarcane and various other plant systems because of numerous advantages such as being a comparative, rapid, simple, cost-effective technique that needs a slight amount of DNA from sugarcane with no initial sequence data for primer design [34–36].

4. Sucrose Content Improvement

Sugarcane is a C$_4$ plant capable of using resources and efficiently producing photosynthetic products, particularly sucrose [37–39]. Improving sucrose production in sugarcane has been an eventual target of breeders [3]. Recently, progressive genomic approaches have been used to insert the diversity of alleles into plants in breeding programs through gene extraction from wild relatives. Next-generation sequencing (NGS) technology, like high throughput sequencing, has importantly increased the volume of information easily available for phylogenetic inference [40,41]. Such advancements are important for challenging groups resulting from fast evolutionary radiation, such as the grass tribe Andropogoneae [42–44].

Mother nature of genotypes, environmental circumstances, and maturity stage are crucial to sucrose storage in sugarcane internodes [45]. During the growing time, all the internodes work like an independent unit, and the bottom internodes get to mature earlier while the top internodes of the stem continue growth. The sugarcane plant continues ripening as time passes, and more internodes store higher sucrose. In the perception of diverse maturity and reaping time, different sugarcane varieties are classed based on the sucrose content in cane and are divided into early, mid-late, or late maturing types. Based on a worldwide economic perspective, sucrose content in cane is a significant trait of commercial sugarcane varieties and is a central focus of crop scientists [46].

5. Sugarcane Breeding

Sugarcane breeding programs develop new varieties with high yield, high sugar, and resistance to abiotic and biotic stresses. Sugarcane breeders frequently pursue improved high-yielding germplasm and use them as parents in breeding [47]. Biotechnological strategies could expand traditional breeding programs to understand genetic structures, genomic locations, and plant transformation. The uncommon complexity in the genome of sugarcane has made its genomic and genetic manipulation a provoking task [48]. Modern sugarcane varieties have been obtained through interspecific hybridization between Saccharum spontaneum and Saccharum officinarum species. The current commercial sugarcane varieties are typically created through crosses between other commercial or pre-commercial hybrids. The chromosome numbers of commercial sugarcane cultivars range from 100 to 130, with 70–80% of the chromosomes resulting from the S. officinarum species, 10–20% from S. spontaneum, and 5–17% derived from recombination of these two species [49].

Sugarcane breeding programs have faced several challenges due to narrow genetic backgrounds, and fewer ancestral clones have been used in the early hybridization schemes. Additionally, this problem has been intensified as only a few well-liked sugarcane hybrids have been broadly utilized as parental lines [50,51]. For instance, over 90% of sugarcane cultivars in America can be found back to 10 hereditary clones [47,52]. The cultivar ROC22 covered 50–60% of China’s cultivation areas in the past 15 years and has been the most regularly adopted parental genetic source for breeding programs [53,54]. Hence, the expanded genetic base for sugarcane cultivars would advance cane yield and decrease seriously upsetting disease eruptions because of planting varieties with similar backgrounds in big areas. Introducing and using exclusive sugarcane clones from other countries or areas can meaningfully accelerate the attainment of sugarcane breeding for two important reasons, one is the top sugarcane clones resulting from diverse breeding programs expectedly have unlike genetic backgrounds, while the other is one of the top sugarcane clones that have
high yield, high sugar and improved vital agronomic characters [55]. Sugarcane breeding is a powerful approach to accumulating desired traits in target varieties according to the circumstances (Figure 1).

### Figure 1. Some major goals of sugarcane breeding.

#### 6. Genetic Engineering

Transgenic technology is merely the option for foreign genes to be incorporated across the species. Sugarcane has been investigated to engineer valuable agronomic traits. Most alteration events in sugarcane are biolistic; *Agrobacterium* and electroporation have also been utilized. The engineered lines' achievement depends on integration and the regular appearance of inserted genes. Recalcitrancy, small transformation proficiency, transgene nonactivation, and tough backcrossing are the main blockages in sugarcane transformation. However, some reports have been found for the field plantation of transgenic sugarcane, and many research groups are working on sugarcane genome engineering [56].

Fresh omics technologies are momentous in comprehensive understandings of sugarcane genome and raising commercial varieties with essential qualities. These technologies have a wide range of applications in genomics, transcriptomics, metabolomics, and proteomics. The result interpretations are built on logical approaches, bioinformatics, computational scrutiny, and numerous successive interdisciplinary biological perceptions [57]. Reliability and predictability of transgenic technologies have a central role in producing crops with excellent yield and quality traits in a short time and durable resistance to biological and non-biological challenges like insects, drought, fungal pathogens, herbicides, salinity, and cold stresses [58,59].

#### 7. Application of Transcriptomic Tools

Transcriptomic investigation of sugarcane delivers the mandatory data about genes of concern through several in silico techniques comprising probe hybridization array, expressed sequenced tag (EST), and recognized genes of other associated crop varieties. EST database of sugarcane in Brazil is considered one of the major databases because it holds about 238,000 ESTs, congregated from 26 diverse cDNA libraries that were built by utilizing, unlike tissues from a big set of Brazilian sugarcane varieties [60,61]. These ESTs have 43,141 putative exclusive transcripts containing 26,803 contigs and 16,338 singletons, and they are jointly itemized as sugarcane assembled sequences (SAS) [62]. The sugarcane gene index database (version 3.0) contains 282,683 ESTs, 499 cDNA sequences and 121,342 unigenes, though there are about 10,000 unknown sugarcane coding genes [63]. Freshly, the sequencing outcomes of transcriptome from 59 F1 individuals (*S. officinarum* LA Purple and *S. robustum*) resulted in 11,157 and 8998 single nucleotide polymorphisms (SNPs), and 83 and 105 linkage groups, respectively [64]. However, the absence of a fundamental and
precise reference genome in sugarcane opposes gene function prediction and application of
the transcriptome dataset [63]. Therefore, *Sorghum bicolor* genome is normally used as a
reference in sugarcane transcriptome exercises due to the significant homology (95%) in
the genic regions between sugarcane and sorghum [65]. Amongst the BLASTx top hits,
around 47% of sugarcane unigenes in transcriptome data were harmonized to *Sorghum
bicolor* proteins, but only 2% of unigenes presented significant homology with sugarcane
hybrid cultivar R570, proposing the high genetic difference between different sugarcane
cultivars [63,66]. Next-generation sequencing technologies (NGS) like high-throughput
RNA-Seq are extensively applied in eukaryotic transcriptome investigations [67]. However,
short reads coming from second-generation sequencing technologies need great computa-
tional assemblies and cannot span full-length transcripts, causing a drop in gene model
forecast [68]. So, single-molecule long-read sequencing technology such as Pacific Bio-
sciences long-read isoform sequencing (Iso-Seq) has been established and broadly used in
transcriptome sequencing because this technique bids a better substitute for sequencing of
complete transcriptomes, effectively foreseeing and confirming gene models. The Iso-Seq
strategy also has been used in the long-read transcriptome of sugarcane [69,70].

8. Application of Proteomic Approaches

Besides transcriptomics, proteomics approaches expose novel understandings of
complex life phenomena [17,71]. The methodology for quantifying proteins and their
post-translational by-products is essential for learning biological schemes. Unlike a stag-
nant genome, the proteome of an organism is dynamically reactive to environmental
provocations and intracellular metabolite degrees by vacillating expression levels and
post-translational alterations, namely glycosylation, phosphorylation, methylation, and
acetylation; moreover, enhancing the inherent complication of the proteome. To investigate
the variance and relative expression concentration of protein, varied protein isolation and
quantitation tools like two-dimensional electrophoresis (2-D), mass spectrometry (MS), and
matrix-assisted laser desorption/ionization-time of flight mass spectrometry (MALDI-TOF-
MS) are applied in sugarcane to explore the effects of various environmental stresses [17].
Moreover, isobaric tags for relative and absolute quantification (iTRAQ) and tandem mass
tag (TMT) quantitative proteomics are the major protein quantification tools applied in
sugarcane and other plants for differential proteomic exploration [72,73]. Several proteomic
studies have been performed in sugarcane to understand the functions of various proteins
like SPS, SuSy, and cellulase [74–77]. Proteomic approaches have characterized proteome
regulation by examining sugarcane developmental processes in various organs. For com-
prehensive knowledge of the modeled developmental processes in sugarcane, gaining
whole proteome features such as high proteome coverage is most important. Several de-
scriptive reports have defined characteristics of sugarcane proteomes, including somatic
embryogenesis in embryogenic and non-embryogenic callus induced by putrescine [78], as
well as under different red and blue lights [79]. Proteomes of the cell wall of different organs
at two developmental stages of sugarcane have been explored [80]. Proteomic research
has also been conducted in sugarcane to understand the stem and cell wall remodeling in
suspension cells [75]. Proteomics-based investigation of sugarcane lignin composition in
stem development has been carried out too [81].

Sucrose content enhancement through the introgression of novel genes is the main
target of sugarcane breeding plans [82]. In recent decades, considerable advancements
have been made in crop plant genome decoding, comprehension of gene expression and
their functional interpretation during various developmental stages, and responses to
numerous environmental inducements [83]. However, sugarcane genome sequencing is
behind because of its large size, polyploidy, and complexity of chromosomes when equated
to other members of the same family, such as sorghum, maize, and rice [84].

Proteins have an imperative protagonist in metabolic activities [85]. The word pro-
teome characterizes the whole protein pool of an organism encoded by the genome. The
term proteomics was first devised in 1995 and was demarcated as the large-scale description
of the total protein complements of a cell, tissue or organism [86,87]. It is the extensive study of various proteins, mainly their compositions, structures, functions, and interpretation of the protein leading to cell characteristics [88]. A proteome is dynamic, unlike a genome, in response to circumstantial impetuses and intracellular metabolite modification by regulating their expressions [89]. Strong gene expression, which results in the form of plenteous mRNA, does not ensure the abundant presence of linked protein or its certain activity in the target cell or tissue; hence, it reveals the limitation of genomics and emphasizes the significance of proteomics.

Proteomic tool application in agriculture is increasing with time [90]. The proteomic analysis approach is an authoritative instrument for documenting the functions of proteins articulated during plant growth and metabolic modifications [91]. Examining variations in the plant proteome, in divergence from the transcriptome, permits recognition of direct effectors of the plant stress response [92]. Throughout the last decades, the most regularly used proteomic method was the two-dimensional gel (2-DE) technique, in which spots with differential expression were cut and investigated by varied mass spectrometry (MS) methods [17]. Now novel protein quantification procedures have been matured utilizing tandem mass tags (TMT) which provide more accurate, precise, and reproducible quantities [93]. The amine specificity of TMT reagents creates maximum peptides in a sample docile to this cataloging approach with no loss of information from samples connected to post-translational alterations, consequently producing further statistical authentication in any certain experiment [94]. Newly, TMT-based quantitative proteomics has been used for proteome investigation, calculation in sugarcane developmental processes, and response to abiotic and biotic stresses [74]. A quantitative proteomics research strategy was also used to know the interaction mechanism between the pathogen and sugarcane [72,95]. Recently, the TMT approach was applied to analyze the protein associated with sucrose metabolism in a high sucrose sugarcane clone GX9 compared with a low sucrose clone B9 in China [96].

9. Sucrose Synthesis

Green plants, by the process of photosynthesis, fix carbon dioxide in chloroplasts through the Calvin cycle and produce triose phosphates, which are moved to the cytosol by translocator, where two triose phosphate molecules are converted into fructose 1,6-bisphosphate (F1,6BP) in a reaction catalyzed by aldolase. Then the F1,6BP is broken down into hexose phosphates like fructose 6-phosphate (F6P) and glucose 6-phosphate (G6P) molecules. The G6P molecule is used to form uridine diphosphate glucose (UDPG), which is combined with F6P to form sucrose 6-phosphate in a reaction catalyzed by sucrose phosphate synthase (SPS). Sucrose phosphate phosphatase (SPP) catalyzes the dephosphorylation of sucrose 6P to yield sucrose. Sucrose is the key product of photosynthetic tissues in sugarcane and the chief sugar transported from the source to consuming and storage sinks. A network of enzymes like SPS, SuSy, and invertases works in sucrose metabolism. Other factors like cellulose, sugar transporter, transcription factors, protein kinases, hormone signaling, miR172-y, miR164-x, miR396, and miR169, which in one way or another control the genes involved in translating cell wall invertase, glucosidase, and hexose shipper protein, sucrose transporter invertase, UDP-sugar pyrophosphorylase, UDP-glucuronate 4-epimerase and trehalose-phosphate synthase and transcription factors, including TFs AP2/ERF, N-acetyl-L-cysteine (NAC), growth-regulating factor (GRF), and bZIP also play roles in sucrose synthesis, transportation, metabolism and accumulation in sugarcane [97–99]. All the genes and molecules, including chlorophyll A-B binding protein (CAB), cytochrome C, UDP-glucose 6-dehydrogenase (UGDH), cytochrome C (CYC), light-harvesting complexes (LHC), chitinase (Chn), ATP synthase subunit (ASYS), sucrose synthase (SUS), alpha-1,4 glucan phosphorylase genes (α-1,4-GPG), sucrose phosphate synthase (SPS), glucose-1-phosphate adenylyltransferase (GPA), invertases (IV), malate dehydrogenase isoform 1 (MDH), fructose-bisphosphate aldolase (FBA), phosphoenolpyruvate carboxylase (PEPC), sucrose transporters (SUT), UTP-glucose-1-phosphate uridylyl-
transferase (UGPU), fructokinase (FRK), starch branching enzyme (SBE) and β-Glucosidase (Bgl) (Figure 2) take part in sucrose accumulation in a very coordinated mechanism.

Figure 2. A systematic co-coordinated role of mRNA and miRNA in sugarcane sucrose accumulation regulation.

10. Relationship between Source and Sink

The basic purpose of sugarcane cultivation is sugar production; after synthesis in the source (green leaves), sucrose is transported to the sink (stalks). In this perspective, sugarcane has a special source-sink relationship. The sucrose stored in the stalk of sugarcane is a soluble disaccharide, which is in divergence from other plant stems where it is stored in the form of insoluble polysaccharides like starch or cellulose. During sugarcane maturation, the assimilated C moves from insoluble and respiratory components toward sucrose, an osmotically functional storage solute [100]. A distinguishing alternative aspect of sugarcane is that sucrose accumulates in parenchyma cells of internodes [101,102], lacking grains and tubers, and fruits as storing sinks.

In contrast to other plants, sugarcane stores sucrose simplistically and apoplectically in cells [103]. Phloem tissues mediate the translocation of sucrose from leaves to immature stalks for growth goals and mature stalks for accumulation [104,105] (Figure 3). Several plants have a mechanism that meristematic tissue sinks are source-limited, and accumulating sinks are sink-limited [106]. In sugarcane, the immature internodes are constrained by the degree of existing photosynthate (sugar), whereas the mature internodes are limited by their capability to import sucrose from the source (leaves). Sink size, and functional activity decide sucrose accretion in internodes, which in response increase photosynthate manufacture by releasing feedback repression at the metabolic and transcriptional levels [107]. Photosynthesis activity in leaves is reduced, and sucrose quantity is significantly increased with the maturity of sugarcane internodes [108], which may indicate sink reg-
ulation through source accumulation capacity [109]. However, further research should be conducted to explore the source-sink relationship, and maybe other factors are also involved in increasing or decreasing sucrose synthesis and accumulation phenomena.

Figure 3. Schematic mechanisms of source-sink relationship in sugarcane.

11. Sucrose Phosphate Synthase (SPS)

Sucrose phosphate synthase (SPS) is an important enzyme in the pathway of sucrose synthesis [110] and is associated with numerous significant agronomic traits like plant height, stalk diameter and millable stalks [111,112]. The SPS activity has also been reported to be correlated with higher final sucrose content in high sucrose sugarcane genotypes [113]. The functional activities of the SPS gene were initially established in wheat crop germplasm [114]. There is a diversity of SPS genes in different plants, showing differential expression of their copies during various tissue developmental stages [115,116]. It indicates that SPS genes play divergent roles under diverse situations. Recent studies have disclosed that most SPS genes have been clustered into three discrete families A, B and C. The different SPS genes seem to have unalike evolutionary chronicle in dicots as family A and in monocots family B [117]. The SPS-related experiments have shown that they are majorly involved in partitioning fixed carbon during photosynthesis in source leaves and storage in plant-storing tissues [118,119]. Studies have exhibited that SPS plays a significant role in sucrose accumulation in plants, particularly in sugarcane [120]. Therefore, it would be important to explore the relative expression of every SPS gene family as a basis for continuing biochemical and genetic research in sugarcane.
12. Sucrose Synthase (SuSy)

Sucrose synthase (SuSy) is a crucial enzyme in the synthesis and breakdown process of sucrose in sugarcane [121]. SuSy gene is supposed to be involved in synthesizing UDPG from the sucrose in sugarcane to generate cell wall substance and starch. It has been linked with internode extension [122,123] and working in sucrose amalgamation in younger culms. SuSy gene expression is controlled through growth, environmental factors, and the sugar status of plants [124]. In crops like maize and sugarcane, multiple SuSy forms are present, which show spatially and temporally distinct expression patterns [125–127]. Sucrose is a compound of interest in nearly all plants and the core storage carbohydrate in plants, like the taproot of sugar beet and the mature sugarcane internodes. In divergence from the mature fruit of tomato, where SuSy activity is extremely reduced, mature sugarcane internodes hold considerable amounts of its activity [128]. In literature, it has been mentioned that SuSy is allied with vascular bundles in sugarcane and other plants [129,130]. Overexpression of SuSy genes in plants is thought to be associated with improved growth, enhanced xylem area, xylem cell-wall width, and increased cellulose and starch contents, which makes the SuSy gene highly powerful contender for the enhancement of agricultural qualities in crop plants, particularly sugarcane [98]. The investigation of SuSy genes localization in tissues would be an effective tool for studying sucrose metabolism especially sucrose accumulation in sugarcane and application in breeding.

13. Invertase

Sucrose synthesis is an irreversible mechanism completed by mediating two enzymes, SPS and sucrose phosphate phosphatase [131]. Because sucrose production is an irreversible pathway, only the sucrose-cleaving enzyme can be used as an energy source. The crucial degrading enzyme is termed invertase (INV) [132], which is present in plants, bacteria, fungi, and some animals [133]. The insoluble acid invertase (INAC-INV) is a cell wall-bound protein, while vacuolar invertase found in the vacuole has a flexible molecular weight, which plays a significant role in plant development [131,134,135]. Sucrose discharged from the phloem in the sugarcane stem is sent to three diverse cellular sections: apoplastic space, cytoplasm, and vacuole [136]. Every compartment has a definite INV isoform, for example, apoplastic space has cell wall invertase (CWIN), the vacuole contains soluble acid invertase (SAI), whereas the cytoplasm holds neutral invertase (NI) [137]. The action of invertase produces a mixture called inverted sugar, which consists of D-glucose and D-fructose equally [138]. The resulting monosaccharides from sucrose and signaling activity during various stress conditions also provide basic substrates for the production of starch and cellulose [139]. Sugarcane invertases play an important role in sucrose metabolism including accumulation, however, they are also involved in unproductive reactions where sucrose is incessantly split throughout the pre and post-harvest passé, thus dropping sugar harvest and retrieval [140].

14. Cellulose Synthase (CeS)

Plant cell walls are compound structures of high molecular mass polysaccharides, proteins, and lignin. Cell wall cellulose is a hydrogen-bonded beta-1,4-linked glucan microfibril component, the main strength-providing part. The cells of plants are enclosed by cell walls, which provide firmness, hardness, and protection during severe environmental pressures on the plant body [141]. Growing cells continually develop cell wall material which may be contrasting in composition and structure because of reliance on the nature of different tissues and their cells according to developmental requirements and spatial arrangement. Various studies have found the existence of two main types of cell walls in plants, the primary and the secondary cell walls, visibly eminent via structure, configuration, and function [142,143]. Sugarcane accumulates high concentrations of carbohydrates in mature stalks in the form of sucrose; however, it also supplies a certain percentage of metabolites to cell wall synthesis and fiber manufacture. Cellulose biopolymer is made by cell membrane-localized cellulose synthase (CeS, EC: 2.4.1.12), which is also called
cellulose synthase complex (CSC) [144]. In a study, two categories of CeS genes were found expressed in the cell wall of sugarcane; one group of CeS genes was associated with primary cell wall syntheses like CesA1, CesA7, CesA9, and bk2l3, while the other group was connected with secondary cell walls synthesis such as CesA10, CesA11, CesA12, and bk-2 [57]. In sugarcane, cleaved sucrose is used for many purposes, including cellulose synthesis [100,145]. Generally, immature sugarcane tissues partition a considerable amount of C into protein and fiber because of rapid growth, whereas mature culms partition C mainly to sucrose accumulation [146].

15. Sucrose Transporter (SUT) and SWEET

Sugar is an important substance in plants produced by photosynthesis which is not only the source of energy in plants and animals but also works as a signaling molecule [147]. Sugar transporters are vital proteins transporting sugar from prototrophic green tissues to heterotrophic tissues like sink tissue. Sugar transporters can be grouped into various types, which play a significant role in the intercellular transport of sugars. Monosaccharide transporter (MST), sucrose transporter (SUT), and SWEET are very important in this perspective [148–151]. The sugar transporter families MST and SUT have been widely understood in higher plants in the last couple of decades [152,153], while the SWEET transporter family has newly recognized as sugar effluxes [154] due to the role of its members in transporting of hexose or sucrose across plasma membranes. Different members of the SWEET family have different functions in sugarcane, for example, SWEET1b is a sucrose starvation-induced sugar transporter in high photosynthetic zones, SWEET13c functions as an important factor in the efflux of sugar transportation in mature photosynthetic tissues, SWEET4a/4b primarily transport sugar in stalk while SWEET1a/2a/4a/4b/13a/16b are supposed to be contributing to the variance in sugar content between S. spontaneum and S. officinarum [155] (Figure 4). SUT1 and SUT4 have been isolated from mature leaves and bundle sheath of maturing internodes in sugarcane [156,157]. SUT2 was expressed in leaves and stems, while SUT5 and SUT6 were highly expressed in sugarcane leaves [158]. Analysis of the storage parenchyma tissues, rind, and vascular bundles discovered that the sugar transporter genes like ShPST2a, ShPST2b, and ShSUT4 were expressed in parenchyma cells and ShSUT1 in vascular bundles of sugarcane [57]. The AtTMT1 and AtTMT2 tonoplast H+/sugar antiporters of Arabidopsis transfer glucose and sucrose into vacuoles and are highly homologous to sugarcane ShPST2a, and ShPST2b linked to sucrose import into parenchyma cell [155,159,160].

Though there are large numbers of SWEET and sugar transporter genes, the phenomenon of how SWEETs and sugar transporters are synchronized with other sugar metabolism genes and how they aid the sucrose accretion in Saccharum continues to be unidentified. So, based on previous findings, future research must be targeted to know the physiological and molecular mechanisms of SWEETs and sugar transporter genes in sucrose metabolism especially sucrose accumulation in sugarcane. Advanced technological approaches, including yeast-one-hybrid screens, spatiotemporal expression analysis, immune chromosome precipitation (ChIP) assays, yeast complementation and uptake evaluations, and CRISPR-Cas9 system, would be assisting in achieving the goals. So, the molecular study of sugar transporters in sugarcane would assist in knowing the mechanisms of sucrose metabolism including sucrose accumulation in sugarcane.
Figure 4. Systematic presentation of SWEET genes activities in sugarcane phloem loading and unloading.

16. Trehalose

Plant growth and development are strongly regulated in response to environmental circumstances that affect the presence of photosynthetic carbon in the shape of sucrose. Trehalose 6-phosphate (T6P) is the predecessor in the biosynthetic pathway of trehalose, an important signaling molecule that mediates plant growth and development. Trehalose is the product of a reaction between UDPG and G6P [161] in the presence of the enzyme trehalose-6-phosphate synthase (TPS). Trehalose-6-phosphate phosphatase (TPP) further metabolizes T6P to trehalose. Trehalase finally resolves trehalase into two glucose molecules [162]. The interaction between T6P and SnRK1 (SNF1-related/AMPK protein kinases) influences the control of plant carbon provision and consumption [163]. The approaches such as genetic alteration, gene discovery through quantitative trait locus (QTL) mapping, and chemical intervention have been used for changing the T6P pathway to advance crop performance under unfavorable circumstances like drought and flooding in three main food crops wheat, maize, and rice. Prokaryotes have five mechanisms of trehalose production, and one of them, a two-step synthesis procedure, is found in eukaryotes [164]. The T6P signaling scheme has appeared as an instrument of resource distribution and has been involved in numerous crop metabolisms like assimilate partitioning and enhancement of production in different environments [165]. The investigation of sweet and grain sorghum showed
Figure 5. Trehalose synthesis and role in the metabolism of carbohydrates. (TPP denoted with an asterisk is assumed to localise to plastids; however, experimental confirmation is still required).
17. Transcription Factor (TF)

The major mechanism for regulating gene expression in eukaryotes looks to be controlled at the transcriptional stages. Transcriptional regulation of gene expression is facilitated by TFs, which initiate or inhibit transcription. These activators and repressors perform via numerous mechanisms like DNA-protein interactions, protein–protein interactions, and amendment of the chromatin structure [177]. In multicellular plants, the expression of thousands of proteins encoding genes is a topic complicated by spatial and temporal regulation patterns. The primary pace in the transcriptional regulation of every gene incorporates several signals to alter the degree of transcription of their required genes [178,179]. The specificity of gene expression is at least governed by transcriptional activators and repressors, many of which bind DNA in a sequence-specific manner [180]. Different TF databases exist, particularly for several crops, such as the plant TF and grass TF databases. Chief TF families like WRKY, MYB, NAC, and AP2/ERF are critical regulators of diverse genes connected to unique stresses, which donate to the perfect choice for genetic engineering to improve the struggle of plants against unlike stress provocations. According to the plant TF database, plentiful TFs have been described in *Oryza sativa* (2389), *Hordeum vulgare* (2620), *Triticum aestivum* (3437), and sugarcane (*Saccharum* spp.) (672). Notably, 39 WRKY, 44 NAC, 38 MYB, and 73 AP2/ERF gene families of TFs in sugarcane have been discovered. In sugarcane, basic helix-loop-helix (bHLH) transcription factors, homologs of Arabidopsis FBH (Flowering-bHLH) that bind to the promoter of *ScACS2*, a sugarcane type 3 ACS isozyme gene. Gene expression examination found that *ScFBHs* and *ScACS2* transcripts are more plentiful in maturing internodes during afternoon and night. These *ScFBHs* transcriptionally regulate ethylene biosynthesis in maturing internodes of sugarcane [181]. A sugarcane MYB in the culm persuades suberin biosynthesis and is involved in the digestion of fatty acids and phenolics [182]. *WRKY* transcription class III, *ScWRKY* gene factors have shown important roles in plant stress responses in sugarcane clone ROC22 [183]. Sugarcane *WRKY3*, *WRKY4*, and *WRKY6* genes were increased under ABA, SA, MeJA, NaCl, and PEG stresses [184,185]. This research indicates that sugarcane WRKY family members of different types may have various functions due to their expression characteristics. The transcription factors potentially relative to regulating sucrose accumulation in sugarcane have been discovered by cDNA microarrays [186]. The signaling hormones and stress response genes, such as *dehydration responsive element binding protein* (DREB), *ethylene response factor* (ERF), *NAC*, *MYB*, auxin response factor *ARF*, ethylene regulator *EIL*, and sugar signaling *TF*, usually interact with other signaling pathways for proper functions in sugarcane [187]. An Arabidopsis homolog TF bZIP11 has sucrose regulated peptide, and its transformation can be suppressed by sucrose to control amino acid metabolism [188]. It reveals that sucrose accumulation may interact with drought and hormone signal pathways in sugarcane.

18. Protein Kinase (PTK)

Protein kinase (PTK, EC: 2.7.11.1) is a group of important enzymes that catalyze the allocation of γ-phosphate of ATP to the protein substrates, which change their functions. These signaling substances have a crucial and complex role in controlling cellular signaling transduction [189]. Several signaling genes encoding PTKs need dynamic regulation, which must be traced incessantly in different living cell compartments and signaling microdomains. Sucrose non-fermenting 1-related protein kinase 2 (SnRK2) plays a central role in plant stress signal transduction. Mitogen-activated PTK (MAPK) has an important role in signal transduction in response to various environmental and developmental situations through the phosphorylation of downstream signaling domains with other kinases, cytoskeletal proteins or transcription factors in all eukaryotic cells. A general MAPK cascade contains at least three successively acting serine/threonine kinases such as MAP kinase kinase-kine (MAPKKK), MAP kinase-kine (MAPKK), and MAP kinase (MAPK) [190]. Several signaling pathways are active in sucrose synthesis, transportation, and accumulation to keep optimal sucrose levels at diverse developmental stages under different growth
conditions. Protein phosphorylation adjusts sucrose accretion and low inorganic phosphate levels to mediate sucrose accumulation [4]. PTKs catalyzing protein phosphorylation are important signal molecules in plants. A category of Ser/Thr PTKs and SNFI connects PTKs (SnRK1), sensing the sugar and energy grade to control source-sink equilibrium in plants [191]. SnRK1 phosphorylates SPS to constrain its activity [192]. Diverse gene expression of PTKs in high and low sucrose content varieties and culms were investigated by cDNA microarrays [186]. Sugarcane ScSnRK1-2 is less expressed in mature internodes and might be induced by sucrose treatment. SnRK1 can be an important signaling molecule to control sucrose accumulation in sugarcane. A receptor protein kinase, ScBAK1, was highly expressed in sugarcane vascular bundle sheath cells of leaves in sugarcane, and individuals with higher sucrose content might control sucrose manufacture in source leaves [193]. Molecular-level research is necessary to clarify PTK genes' role further and define their usefulness in sugarcane sucrose metabolism and accumulation.

19. Phytohormones

Plant hormones are the main regulatory tools involved in growth and development, which play a dominant role in integrating interior and exterior signals that temper development [194]. So, it is assumed that internodal development, source-sink relationship and subsequently, cane yield and quality improvement in sugarcane are regulated by hormones. In this regard, five main plant growth hormones, auxin (IAA), gibberellin (GA), cytokinin (CTK), abscisic acid (ABA), and ethylene (ETH), are important, along with some recently identified growth regulators such as brassinosteroid (BR), jasmonates, salicylic acid, a peptide hormone, and strigolactone [195–197].

19.1. IAA

Previous decades have witnessed several breakthroughs in recognizing a deceivingly simple transcriptional response pathway and cellular and molecular mechanisms of steering auxin transport [198], synthesis and deactivation. At the same time, auxin function has been described in most growth and developmental progressions, interactions with other hormonal signaling pathways [199], which is even valuable in pathogenic microorganisms and viruses [200]. Abundant auxin-associated research has emphasized the activity of the leading naturally occurring auxin, indole-3-acetic acid (IAA). Numerous synthetic analogues, including 2,4-dichloro phenoxy acetic acid (2,4-D) and 1-naphthaleneacetic acid (NAA) have also been extensively utilized. Other naturally originating molecules also have auxin activity, for example, indole-3-butyric acid (IBA) has been the subject of vigorous examination for many years. IBA is closely alike to IAA with the exclusion of a supplementary CH2 group, yet the function of IBA is somewhat more diverse than IAA. It is considered that IBA strongly controls auxin storage form, which permits spatiotemporal control of auxin levels through plant development, mainly in the elaboration of the root system [201]. Auxin regulates various plant growth and development responses containing cellular elongation, expansion, and division in sugarcane. The basic auxin-response gene families comprise auxin/indole-3-acetic acid, auxin-response factor (ARF) [184], Gretchen Hagen3 (GH3), small auxin-up RNAs (SAUR) [202], and lateral organ boundaries (LBD). AUX/IAA, SAUR, and GH3 genes can be stimulated instantly with auxin, leading to diverse cell and growth responses. AUX/IAA is a vital gene family for plant growth regulation, and the process of auxin regulation is via the degradation of repressor genes AUX/IAA and the modulation of gene expressions involved in multiple physiological processes. ARF family contains important genes regulating the auxin-modulated gene expression [203]. The SAUR gene family contains early auxin-responsive genes that are significant for tissue elongation and can donate to biomass variances. LBD is usually regulated by exogenous IAA and are involved in lateral organ development. The GH3 gene family works in regulating and preserving endogenous auxin homeostasis [204]. Much is known about the complex sucrose and auxin nexus that controls plant cell division and growth. Additional research into the complex network of sugar and auxin signaling pathways within plant tissues during...
specific growth stages or environmental conditions will improve our understanding of the regulatory systems underlying developmental processes and help develop new strategies to optimize sugarcane crop yield and stress tolerance.

19.2. ETH

ETH is a multifunctional hormone that controls plants’ growth and senescence [205,206]. Monitoring the ETH responses is a key commercial enterprise due to the widespread effects of ETH on plants of agronomic and horticultural value [50]. ETH signaling can induce the biosynthesis of other hormones, for instance, rice ETH signaling encourages GA in deep water, which signals internode elongation, letting rice plants escape from whole submergence [207]. ETH influences both growth and development of plants; in terms of growth, it is mostly allied with the regulation of cell size and generally limits cell elongation. However, it may also control cell division, while in the case of development, ethylene is normally associated with aging, sometimes required for processes like ripening, senescence, and abscission [208]. These pathways depend deeply on negative regulation and post-translational control [209]. ETH is also an important signaling hormone in various biological mechanisms of sugarcane [202]. ETH not only increases sucrose accumulation but also increases biomass manufacturing and stress tolerance in sugarcane. Sugarcane ripening and sucrose accumulation have also been reported to be influenced by ETH [210,211]. The gene families of reversion to ETH sensitivity (RTE), ETH receptor (ETR), ETH response sensor (ERS), ETH insensitive (EIN) ETP, EIN2, targeting protein genes EIL, EIN3-like, and EBF (EIN3-F) are significantly mediating ETH signaling [212–214]. ETH is a ripening hormone in plants that contributes to increasing sucrose storage in sugarcane [211].

In sugarcane, ETH has been reported to play an important role in sugar synthesis (leaves), transportation, and storage in sink tissues. In a study [210] (Figure 6), sugarcane leaves were treated with ETH, which increased the activity of Rubisco, and genes associated with sucrose synthase, sucrose phosphate synthase and invertases, up-regulated by the action of ERFs which are known as sucrose synthesis stimulators. Sucrose and glucose seem to work as regulatory signals to regulate the photosynthesis process. Once sucrose is prepared in the leaves, it is transported to the phloem via plasmodesmata (symplastic-sugar transporters) and cell wall (apoplastic-wall invertase). Sugar movements from the leaves to the phloem generate gradient potential, which assists the biochemical equilibrium of sugar between the source and sinks in sugarcane. However, it needs further investigation to understand the exact molecular role of ETH in sugar production and storage.

19.3. GA

GA is jointly referred to as a group of diterpenoid acids, and some act as plant hormones and are crucial for normal plant growth and development [215]. GA exploitation in agriculture is a usual practice, and the best-known involvement of GA manipulations is the insertion of dwarfing alleles into vital crops [216]. This alteration resulted in one of the foundation stones of the so-called green revolution and directed a massive increase in global wheat and rice harvests. Documentation of the genes accountable for these traits presented that the encoded proteins are involved in the action or production of GA [217]. More than 130 gibberellic acids (GAs) have been recognized in plants, fungi, and bacteria, and only a subclass of them, GA$_3$, GA$_4$, GA$_5$, and GA$_7$ are believed to function as bioactive hormones [218]. Other forms of Gas that occur in plants are predecessors of the bioactive systems or deactivated metabolites [219]. GA is the most studied signaling hormone in sugarcane [220]. Family A of GA$_3$ is a commercially and scientifically well-known hormone [221,222]. Different isoforms of Gas play significant roles in the growth and development of plants, particularly leaf morphogenesis, floral development and fruit maturation [223]. Alteration of interior Gas surges plant vegetative biomass, alters shoot structure, and regulates fruit and seed development [185,223,224]. Variation in endogenous Gas in sugarcane via altering regulatory genes of its metabolism [225], changing GA action modulator DELLA protein [226], or exterior use of Gas meaningfully improves the stem
growth and biomass [227,228]. GA$_1$, GA$_3$, GA$_{19}$, GA$_{20}$, and GA$_{29}$ were recognized in mature leaf and shoot apical meristem of flowering and nonflowering sugarcane in a study [229]. The maximum rise in length and fresh weight of seven Hawaiian commercial sugarcane cultivars were observed when treated with a proper amount of GA$_3$ [227]. Due to increased sink demand, the immature internodes exhibit a decrease in sucrose and an increase in hexose sugar levels over the shading period. GAs can thus be predicted to increase sucrose accumulation in sugarcane internodes by heightening sink demand, subsequently increasing cane yield [230]. Further investigation is needed to find the role of GA associated with sucrose in sugarcane.

![Diagram](Figure 6. Demonstration of ethylene contribution to sugar synthesis and transportation regulation in sugarcane.)

### 19.4. ABA

ABA is a chief phytohormone that regulates plant growth, development, and stress responses. It plays an important role in various physiological processes of plants, such as stomatal closure, cuticular wax accumulation, leaf senescence, bud dormancy, seed germination, and osmotic regulation. During the last four decades, molecular genetics and biochemical methodologies have recognized the central components of ABA biogenesis and their signaling pathways. The genetic investigation of viviparous mutants in Arabidopsis and maize for fast screening of mutants insensitive to sugar, salt, and ABA during germination brought to the documentation of many components responsible for the biosynthesis of ABA and signaling. The initial isolates were found in the clade A PP2Cs like ABA insensitive ABI$_1$, ABI$_2$, ABI$_3$, ABI$_4$, and ABI$_5$ [231,232]. Biochemical exploration of the ABA stimulation of PTKs caused the recognition of AAPK, a homolog of the Arabidopsis soul PTKs, SnRK2s, in *Vicia faba* [233]. Because of strong functional severance, the ABA receptor pyrabactin resistance 1 (PYR1) and PYR1-like (PYL) proteins were not discovered before 2009 via chemical genetic isolation for mutants that are insensitive to the ABA homologous pyrabactin [234]. At the same time, regulatory types of machinery of the ABA receptors were screened through the yeast two-hybrid screen method [235]. The characteristics of the PYL/RCAR protein family were also established via in vitro reconstruction of the main ABA signaling pathway [236] and later verified by extensive genetic and structural data [231,237]. ABA has dynamic regulatory and signaling regulation in plant physiological processes. During the past few years, ABA biosynthesis and signaling
pathways were well-characterized in abiotic stress tolerance in several crops [238,239]. ABA concentration increases in response to drought, extreme temperature and high salinity to enhance tolerance [240]. Foliar application of ABA in sugarcane enhanced the tolerance against water stress [241]. In relation to stomatal physiology, ABA is one of the most important regulatory signaling molecules [187,226]. Besides its functions in the physiology of abscission, ABA acts in several stress-correlated responses, particularly root and stomatal responses to drought. ABA treatment increased the growth of leaf spindle, stalk, root, and Brix value in internodes of sugarcane reported in a study [242]. ABA response to pathogens in sugarcane has also been reported [158]. As it is evident from the literature that ABA is an important multifunction phytochrome, it should be further studied on the molecular level, particularly in sugarcane, to find its association with the synthesis, transportation, accumulation, and decomposition of sucrose. There are several important phytohormones, other genes and molecules, which have significant role in sugarcane sucrose metabolism, however their pinpoint function still need further investigation (Table 1).

### Table 1. List of major genes and molecules associated with sucrose metabolism in sugarcane.

<table>
<thead>
<tr>
<th>Gene/Molecule</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sucrose phosphate synthase (SPS); SPS1, SPS2, SPS4, SPS5</td>
</tr>
<tr>
<td>Sucrose synthase (SuSy); SuSy1, SuSy2, SuSy4</td>
</tr>
<tr>
<td>Soluble acid invertase (SAI)</td>
</tr>
<tr>
<td>Cell wall invertase (CWI)</td>
</tr>
<tr>
<td>Neutral invertase (NI)</td>
</tr>
<tr>
<td>Sucrose transporter; SWEET1b, SWEET13c, SWEET4a/4b, SUT1, SUT4, SUT5, SUT6, ShPST2a, ShPST2b, ShSUT4.</td>
</tr>
<tr>
<td>SNF1-like kinases</td>
</tr>
<tr>
<td>Trehalose-phosphate synthase</td>
</tr>
<tr>
<td>Cellulose synthase (Ces)</td>
</tr>
<tr>
<td>CesA1, CesA7, CesA9, bk2l3,CesA10, CesA11, CesA12</td>
</tr>
<tr>
<td>Trehalose 6-phosphate (T6P)</td>
</tr>
<tr>
<td>Trehalose-6-phosphate phosphatase (TPP)</td>
</tr>
<tr>
<td>Transcription factors (TF); WRKY, MYB, NAC, AP2/ERF</td>
</tr>
<tr>
<td>Basic helix-loop-helix (bHLH)</td>
</tr>
<tr>
<td>ScFBHs and ScACS2</td>
</tr>
<tr>
<td>Mitogen-activated PTK (MAPK)</td>
</tr>
<tr>
<td>Sucrose-nonfermentation1-related protein kinase1-2 (ScSnRK1-2)</td>
</tr>
<tr>
<td>BCL2 antagonist/killer 1 (ScBAK1)</td>
</tr>
<tr>
<td>Phytohormones; Auxin (IAA), AUX/IAA, Gibberellin (GA), Cytokin (CTK), Abscisic acid (ABA), Ethylene (ETH).</td>
</tr>
<tr>
<td>Brassinosteroid (BR), jasmonates, salicylic acid, a peptide hormone, and strigolactone</td>
</tr>
<tr>
<td>Gretchen Hagen3 (GH3), small auxin-up RNAs (SAUR)</td>
</tr>
<tr>
<td>Ethylene receptor (ETR), Ethylene response sensor (ERS), Ethylene insensitive (EIN) ETP, EIN2, Targeting protein genes EIL, EIN3 like, EBF (EIN3-F)</td>
</tr>
<tr>
<td>GA1, GA3, GA4 and GA7 A19, GA20 and GA29</td>
</tr>
<tr>
<td>ABA receptor pyrabactin resistance 1 (PYR1), PYR1-like (PYL)</td>
</tr>
</tbody>
</table>

### 20. Conclusions and Future Perspective

Sucrose content is a highly desirable trait in sugarcane worldwide by farmers and the sugar industry. It is necessary to investigate diverse genes associated with sucrose and their spatiotemporal analysis and manipulation to meet the sugar demand. High enrichment of genes linked with phytohormones, metabolism, and signaling intensely regulates sugarcane’s source-sink activity, growth, and sucrose accretion. The current review describes the association between sugar, post-transcriptional regulation factors, and sugar-related genes. Since sucrose phosphate synthase (SPS) is crucial for sucrose accumulation, especially in sugarcane, it is vital to investigate each SPS gene family’s relative expression as a foundation for further biochemical and genetic studies in sugarcane. The spatiotemporal research of sucrose synthase (SuSy) gene localization in diverse tissues will be a useful tool for studying sucrose metabolism and accumulation in sugarcane and for breeding purposes. The investigation of sugar transporter molecules holds potential for enhancing our understanding of sucrose metabolism and accumulation in sugarcane.
Protein kinase (SnRK1, 2) has significant functions in sucrose homeostasis regulation; however, how signals are conveyed through SnRK1 about the sucrose status is imprecise. As it is clear that invertases are important for sugarcane metabolism, more studies are required to pinpoint the population and allele specific markers for invertases in order to increase the use of marker-assisted selection in sugarcane breeding. To increase sucrose content, it is crucial to conduct a thorough investigation of the relationship between sucrose accumulation in sugarcane and the primary plant growth hormones, auxin (IAA), gibberellin (GA), cytokinin (CTK), abscisic acid (ABA), and ethylene (ETH), as well as some newly discovered growth regulators, including brassino-steroid (BR), jasmonates, salicylic acid, a peptide hormone, and strigolactone.

The data analysis showed that sucrose content is a significantly required agronomic trait in commercial sugarcane varieties as sugar demand enhances with the increasing global population. Sugarcane researchers ought to focus on improving the sucrose content of sugarcane varieties. It would be better to explore the network of genes associated with sucrose synthesis, transportation, decomposition, and accumulation spatially and temporally on individual bases to obtain comprehensive elucidation in the broader sense of their functions. The focus should be on identifying genes associated with sucrose synthesis, metabolism and their insertion into low-sugar-content varieties using advanced breeding and genome editing technologies. The current paper provides enough knowledge about sucrose-associated genes, involved methodologies and available advanced technologies such as RFLP, DNA-RAPD, AFLP, SSR, SNP, and CRISPR-Cas9. The obtained knowledge and discovered genes will be vital for genetically transforming and engineering sugarcane plants with desired traits. Research through omics approaches is a better choice as it reduces the complexity of data, and only active genes in the target cells or tissues are considered at the time and position of sampling. However, the transcriptomics and proteomics integrated analysis would better elucidate the gene’s spatiotemporal functionality.

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