

Trait Basis and Breeding Strategies for the Coordinated Improvement of Yield and Sugar Content in Sugarcane

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Abstract This study explores the trait basis, genetic mechanisms, and breeding strategies for the coordinated improvement of yield and sugar content in sugarcane. Yield and sugar content are the two key traits determining sugar yield per unit area and industrial value, and their formation is jointly influenced by agronomic traits, physiological processes, and molecular regulatory networks. Cane yield is mainly determined by millable cane number, single stalk weight, plant height, and stalk diameter, while sugar content is characterized by quality traits such as Brix, Pol, CCS, juice purity, and fiber content. Photosynthetic efficiency, dry matter accumulation, source-sink relationships, and assimilate partitioning constitute the fundamental physiological basis linking biomass formation and sucrose accumulation. Genetically, the complex polyploid genome of sugarcane makes both traits typical quantitative traits controlled by multiple genes, allele dosage effects, and strong environmental interactions. This study further summarizes breeding strategies, including conventional hybrid breeding, marker-assisted selection, genomic selection, and gene editing, as well as the roles of agronomic management such as water and fertilizer regulation, population structure optimization, and proper harvesting time. Overall, achieving high yield and high sugar content relies on integrating yield- and quality-related traits and their underlying mechanisms within a genotype-environment-management framework to promote multi-trait coordinated improvement.

Keywords Sugarcane; Yield; Sugar content; Source-sink relationship; Coordinated improvement

1 Introduction

Sugarcane (*Saccharum* spp.) is one of the most important sugar crops globally, contributing approximately 80% of the world's sugar supply, and also serves as a major source of biomass energy and bio-based materials (Wu et al., 2024). In tropical and subtropical countries such as Brazil, India, and China, the sugarcane industry not only supports the sugar production system but is also closely linked to rural economic development, employment, and regional agricultural stability. With the advancement of biorefinery systems, sugarcane is no longer merely a traditional sugar crop, but has evolved into an integrated industrial feedstock capable of producing sugar, fuel ethanol, electricity, and various bio-based products. Its strategic importance in the circular economy and low-carbon bioeconomy continues to increase (Wang et al., 2025). Under the pressures of global population growth, limited arable land, and climate change, improving the efficiency with which sugarcane converts solar energy into fermentable sugars and structural biomass has become a key scientific challenge for sustainable agricultural and energy systems (Lu et al., 2024; Mehdi et al., 2024).

In sugarcane production systems, sugar yield per unit area is determined by both cane yield and sucrose content, making it a core indicator of cultivar value and cultivation efficiency. Theoretically, maximizing industrial benefits requires simultaneous improvement in biomass accumulation and sugar concentration. However, in practical breeding, increases in sugar yield have relied more on improvements in cane yield, while gains in sugar content have progressed more slowly. This is closely associated with the physiological and genetic trade-offs between the two traits: high-biomass genotypes tend to allocate more assimilates to structural carbon pools, whereas high-sugar genotypes may divert carbon toward storage tissues at the expense of sustained vegetative growth. Thus, although yield and sugar content jointly determine final sugar yield, their formation processes are not fully synchronized and often exhibit complex coordination and trade-offs. This carbon assimilation, transport,

and allocation-driven mechanism constitutes a major bottleneck in achieving coordinated improvement of high yield and high sugar content in sugarcane breeding (Lu et al., 2024; Wu et al., 2024).

From a breeding perspective, modern sugarcane cultivars are mainly derived from interspecific hybridization between *Saccharum officinarum* and *S. spontaneum*, followed by repeated backcrossing. This system has significantly improved yield, adaptability, and stress resistance, leading to the development of many widely adopted and representative cultivars (Li et al., 2024; Wu et al., 2024). However, in recent years, genetic gains for complex traits in sugarcane breeding programs have shown signs of plateauing. This is largely due to the highly polyploid and heterozygous genome of sugarcane, long breeding cycles, complex genotype \times environment \times management interactions, and limitations in high-throughput and precise phenotyping (Lu et al., 2024). These factors constrain the effective utilization of genetic variation and have led traditional breeding to remain biased toward yield improvement rather than coordinated trait optimization. With the development of whole-genome sequencing, genome-wide association studies (GWAS), multi-population QTL mapping, and multi-omics approaches, researchers have gradually elucidated the genetic architecture of key traits such as cane yield, plant height, stalk diameter, tiller number, and sucrose content. In addition, key enzymes and regulatory networks involved in sucrose metabolism have been identified as critical factors in sugar accumulation (Li et al., 2024; Mehdi et al., 2024). Meanwhile, emerging technologies such as genomic selection, RNA interference, and gene editing provide new molecular tools to improve selection efficiency and precisely regulate carbon allocation (Brant et al., 2025; Wang et al., 2025).

This study aims to explore the theoretical basis and technical pathways for the coordinated improvement of sugarcane yield and sucrose accumulation. Although previous studies have reviewed sugarcane improvement from perspectives such as breeding history, genomics, or biorefinery applications, there is still a lack of an integrated framework that systematically links the multi-trait basis of yield and sugar accumulation, their genetic and physiological interactions, and coordinated improvement strategies under different environmental conditions. Therefore, developing a coordinated optimization framework centered on multi-trait (N-Trait) integration has become a key direction for advancing efficient sugarcane breeding. This study analyzes the genetic associations and regulatory networks between yield- and sugar-related traits, summarizes advances in QTL mapping, association analysis, marker-assisted selection, and genomic selection, and further discusses multi-trait-driven breeding strategies and ideotype design. The objective is to provide a clearer theoretical foundation and methodological framework for the coordinated improvement of high yield and high sugar content, and to support the efficient utilization of sugarcane in sugar production and bioenergy systems.

2 Trait Basis of Sugarcane Yield and Sugar Content Formation

2.1 Key agronomic traits related to sugarcane yield formation

Sugarcane yield is a typical complex quantitative trait, commonly expressed as tons of cane per hectare (TCH), and primarily determined by millable cane number and single stalk weight. Traits such as plant height, stalk diameter, and internode characteristics further influence yield by affecting single stalk biomass (Tolera et al., 2024). Multi-environment trials and path analysis consistently indicate that millable cane number and single stalk weight exert the strongest direct effects on yield, making them key selection targets in breeding. Thus, yield improvement depends on the coordinated optimization of multiple component traits rather than reliance on any single trait.

At the population level, millable cane number represents the fundamental determinant of yield, integrating germination rate, emergence uniformity, tillering ability, and stalk formation efficiency. Strong early germination and tillering promote rapid canopy establishment, while a high stalk formation rate ensures effective conversion of tillers into harvestable canes, thereby stabilizing yield per unit area (Tolera et al., 2024; Vennela et al., 2024). Accordingly, genotypes combining high tillering potential with stable stalk formation capacity are more likely to achieve consistently high yields.

Single stalk traits and resource-use efficiency largely determine the upper limit of biomass accumulation. Longer and thicker stalks with well-developed internodes generally exhibit greater fresh weight and dry matter

accumulation, contributing substantially to cane yield (Navya et al., 2025). In addition, physiological traits such as leaf area index, canopy structure, stay-green ability, root distribution, and nutrient balance support yield formation by enhancing photosynthetic efficiency and resource acquisition (Lu et al., 2025). Genetic studies further indicate that key yield-related traits-including stalk number, plant height, stalk diameter, and single stalk weight-are polygenically controlled and have been consistently targeted during sugarcane improvement (Li et al., 2024).

2.2 Major quality traits related to sugar content accumulation

Sugar content is a key indicator of cane quality, processing efficiency, and sugar yield, and is typically evaluated using traits such as Brix, Pol, juice purity, commercial cane sugar (CCS), and fiber content. Among these, Brix reflects total soluble solids, Pol represents sucrose concentration, purity indicates the proportion of sucrose within soluble solids, and CCS more directly reflects industrial value. These traits are generally positively correlated with each other and with sugar yield, suggesting a shared genetic and metabolic basis (Eltaher et al., 2025).

Physiologically, sucrose accumulation mainly occurs in stem internodes during the maturation stage and depends on continuous assimilate supply, phloem transport, and sink storage capacity. Leaves function as the primary carbon source, while assimilates are transported in the form of sucrose to stem sink tissues, where they accumulate in parenchyma cells. Therefore, sugar accumulation depends not only on assimilate production but also on transport efficiency, internode maturation, and sink strength. Genotypic differences in maturity timing and sugar accumulation patterns underpin the classification of early-, mid-, and late-maturing varieties.

At the biochemical and genetic levels, key enzymes such as sucrose phosphate synthase (SPS), sucrose synthase (SuSy), and invertases (INV) regulate sucrose synthesis, degradation, and storage, while cell wall-related processes influence carbon partitioning between structural and storage carbohydrates. High-sugar genotypes typically exhibit enzyme activity and expression patterns favorable for sucrose accumulation, along with structural features such as higher stem maturity, greater parenchyma proportion, and appropriate fiber content (Lu et al., 2025). Genome-wide and candidate gene studies have identified numerous loci associated with Brix, Pol, CCS, and fiber content, providing a molecular basis for improving sugar-related traits (Li et al., 2024; Eltaher et al., 2025).

2.3 Common trait basis for coordinated improvement of yield and sugar content

Although sugarcane yield and sugar content may exhibit negative correlations under certain genotypes and environments, they are not independent breeding targets. Instead, they share a common trait basis involving plant structure, source-sink relationships, carbon allocation patterns, and genetic networks. Sugar yield is the combined outcome of cane yield and sugar content; therefore, traits that enhance biomass production while maintaining or increasing sugar concentration are key targets for coordinated improvement.

Photosynthetic efficiency and assimilate production serve as the common source for both yield formation and sugar accumulation. Traits such as higher leaf area index, optimized canopy structure, prolonged functional leaf duration, and enhanced photosynthetic efficiency increase total carbon assimilation, providing substrates for both stem growth and sucrose accumulation (Lu et al., 2025). In addition, assimilate transport and partitioning efficiency represent the key physiological link between these traits. Efficient transport to stem tissues, coupled with progressive allocation toward sucrose storage, enables the simultaneous improvement of stalk weight and sugar concentration (Singh et al., 2024).

Furthermore, maturation dynamics and shared genetic bases play critical roles in coordinated improvement. An optimal maturation pattern allows extended biomass accumulation followed by efficient sucrose deposition, reducing the risk of either insufficient biomass or delayed sugar accumulation (Singh et al., 2024). Multivariate and genome-wide analyses have identified SNPs and haplotypes associated with both yield-related traits (e.g., stalk number, plant height, and diameter) and sugar-related traits, indicating a shared genetic basis (Li et al., 2024).

3 Physiological Basis of Sugarcane Yield and Sugar Content Formation

3.1 Effects of photosynthesis and dry matter accumulation on yield and sugar formation

Photosynthesis is the fundamental physiological basis for sugarcane yield and sugar accumulation. As a typical C₄ crop, sugarcane possesses high photosynthetic efficiency and carbon assimilation capacity, enabling it to maintain high net photosynthetic rates under conditions of high temperature and strong light. It efficiently converts solar radiation into dry matter, providing the primary carbon source for cane yield and sucrose accumulation. Assimilates fixed by leaves are converted into sucrose through primary metabolism and transported via the phloem to the stem, supporting stalk elongation, tissue development, and subsequent sugar deposition. Therefore, parameters such as net photosynthetic rate, stomatal conductance, chlorophyll content, leaf area index, and radiation use efficiency are closely associated with biomass production and final yield (Figure 1).

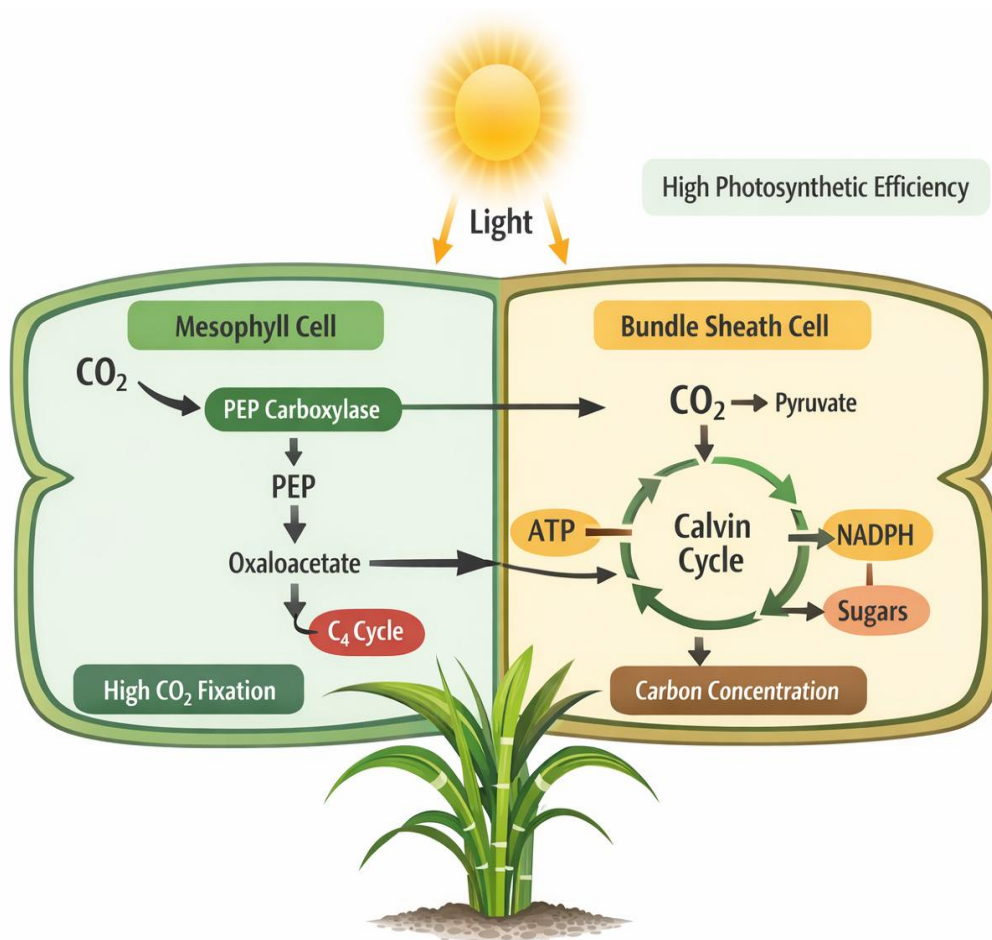


Figure 1 Schematic representation of the C₄ photosynthetic pathway in sugarcane

Image caption: CO₂ fixation in mesophyll cells and carbon concentration in bundle sheath cells to enhance photosynthetic efficiency

Dry matter accumulation serves as the key link between photosynthesis and both yield and sugar formation, reflecting the dynamic balance among carbon assimilation, respiratory consumption, and structural construction costs. During the early growth stage, sugarcane is dominated by vegetative growth, and photosynthates are mainly used for the development of leaves, stems, and roots. In the mid- to late-growth stages, as internodes mature, assimilates shift from structural carbon synthesis to soluble sugar accumulation, leading to gradual sucrose enrichment in parenchyma tissues (Martins et al., 2024; Mehdi et al., 2024). Thus, higher dry matter production efficiency, longer functional leaf duration, and sustained photosynthetic capacity are generally favorable for maintaining both high biomass and high sucrose accumulation. In essence, dry matter accumulation determines not only how many stalks are produced but also how much sugar can be stored within them.

In addition, canopy structure and ecological regulation further influence photosynthetic efficiency and dry matter production. Populations with more erect leaves, uniform canopy distribution, and good ventilation and light penetration typically exhibit higher canopy photosynthetic efficiency and biomass production (Mehdi et al., 2024). Water and nitrogen are key environmental factors affecting this process: adequate supply supports leaf area development and photosynthetic activity, whereas severe drought or nitrogen deficiency significantly suppresses photosynthetic efficiency, stalk formation, and yield (Mehdi et al., 2024). Under certain maturation stages, moderate stress may promote carbon allocation toward stem sugar storage, but excessive stress can simultaneously reduce biomass and sugar accumulation. Therefore, sustained high photosynthetic capacity, stable dry matter accumulation, and proper ecological regulation are essential prerequisites for achieving high yield and high sugar content in sugarcane.

3.2 Role of source-sink relationships and assimilate partitioning in sugar accumulation

Sugar accumulation in sugarcane is regulated by a typical source-sink relationship. Leaves act as the primary source, fixing CO₂ and synthesizing carbohydrates, while the stem serves as the main sink, particularly mature internodes that accumulate high concentrations of sucrose (Önder et al., 2025). Therefore, the capacity of source assimilation, phloem transport efficiency, unloading mechanisms, and sink storage capacity collectively determine sugar accumulation. High sugar accumulation in sugarcane is not merely the result of increased sugar production in leaves, but rather the coordinated balance between source supply and sink demand.

This source-sink relationship varies significantly across developmental stages. During early growth, leaves and young stems function mainly as growth sinks, and assimilates are primarily used for cell division, organ formation, and structural dry matter production. As internodes elongate and mature, stem sink strength increases, and mature internodes become the main carbon sinks where sucrose is extensively accumulated. Strong sink capacity allows continuous uptake and storage of sucrose from leaves, enhancing sugar content. Conversely, if transport or unloading is limited, sugars may accumulate in leaves and feedback-inhibit photosynthesis, reducing overall productivity. Thus, high photosynthetic capacity does not automatically translate into high sugar yield; the key lies in whether the sink has sufficient pull strength.

At the molecular level, source-sink coordination is finely regulated by sucrose transport, unloading, and metabolic pathways. Key enzymes such as SPS, SuSy, and various invertases determine whether sucrose entering the stem is directly stored, degraded for respiration and growth, or converted into structural carbohydrates. High-sugar genotypes typically exhibit higher SPS activity and lower acid invertase activity during maturation, favoring sucrose storage. In contrast, high-biomass genotypes often show higher SuSy and invertase activities, supporting rapid growth and cell wall synthesis but potentially reducing sugar concentration per unit fresh weight (Martins et al., 2024). Therefore, assimilate partitioning efficiency is the key link between biomass formation and sugar accumulation. If early growth prioritizes population establishment and stem elongation, followed by a gradual shift toward sugar storage in later stages, it is possible to enhance sugar accumulation without significantly compromising biomass, thereby achieving coordinated high yield and high sugar content.

3.3 Effects of hormonal regulation and stress responses on high yield and high sugar formation

Plant hormones are key integrators regulating sugarcane growth, maturation, stress adaptation, and carbon allocation. Hormones such as indole-3-acetic acid (IAA), gibberellins (GA), and cytokinins (CK) are primarily involved in stem elongation, cell division, tillering, and maintenance of leaf function, thereby influencing population structure, biomass accumulation, and sustained photosynthetic capacity (Ain et al., 2024; Lu et al., 2025). Appropriate levels of GA promote internode elongation, while IAA and CK support organ development and functional leaf maintenance, collectively forming the physiological basis for high yield. However, optimal performance depends not on the increase of a single hormone, but on the balance among different hormones and their coordination with metabolic networks (Lu et al., 2025).

Hormones closely related to maturation and carbon metabolism, such as abscisic acid (ABA), ethylene, and jasmonic acid (JA), play critical roles in sugar accumulation and stress responses. ABA is involved in maturation induction, sugar metabolism regulation, and stress signaling integration, and can promote assimilate transport to

the stem and enhance sucrose accumulation at specific stages. Ethylene is often associated with maturation promotion and increased sink strength, improving sugar storage capacity in some low-sugar genotypes (Lu et al., 2025). In contrast, sustained high levels of defense-related hormones such as JA and salicylic acid may redirect resources toward defense metabolism, inhibiting growth and sugar accumulation (Lu et al., 2025). Therefore, from the perspective of coordinated improvement, the key lies in balancing growth promotion, maturation initiation, and defense responses, rather than enhancing a single hormonal pathway.

Environmental stresses further influence yield and sugar formation through hormonal signaling and redox regulation. Drought, high temperature, nutrient deficiency, and biotic stresses can reduce photosynthesis, disrupt reactive oxygen species (ROS) balance, and alter carbon metabolism and sugar partitioning via ABA, ethylene, JA, and calcium signaling pathways (Mehdi et al., 2024). Moderate water deficit during certain maturation stages may promote sucrose accumulation, but excessive or premature stress can lead to stomatal closure, impaired electron transport, and reduced net photosynthesis, thereby decreasing both biomass and sugar accumulation (Mehdi et al., 2024). Additionally, exogenous regulators such as ethylene, seaweed extracts, and indole-3-butyric acid can improve high-yield and high-sugar performance by enhancing sink strength, promoting root development, and improving photosynthesis and antioxidant capacity (Zhang et al., 2025). Overall, the formation of high yield and high sugar content in sugarcane results from the coordinated interaction of hormonal balance, stress adaptation, and carbon allocation, and can only be fully realized under suitable environmental conditions and proper management.

4 Genetic Basis of Sugarcane Yield and Sugar Content

4.1 Characteristics of the complex sugarcane genome and its impact on trait studies

Sugarcane is a typical complex polyploid crop. Modern cultivars are mainly derived from hybridization and backcrossing between the high-sugar species *Saccharum officinarum* and the wild species *S. spontaneum*, resulting in a genome that combines high sugar content with strong adaptability but is also highly complex and mosaic in nature (Healey et al., 2024; Brant et al., 2025). Compared with most diploid crops, sugarcane exhibits higher ploidy levels, strong heterozygosity, and pronounced aneuploidy. Each chromosome often has multiple homologous copies and is accompanied by extensive structural variations, copy number variations, and large-scale rearrangements (Healey et al., 2024). This makes sugarcane one of the most genetically complex cultivated crops.

In terms of genome size, elite sugarcane hybrids typically possess genomes of approximately 8-10 Gb, rich in repetitive sequences and structurally complex regions. Although sugarcane shares partial micro-collinearity with sorghum, the relationship is not strictly one-to-one, making it difficult to directly use the sorghum genome to precisely dissect complex sugarcane traits (Healey et al., 2024). The combination of high ploidy, high repetition, and high heterozygosity has long posed major challenges for genetic map construction, allele dosage estimation, variant detection, and reference genome assembly, leading to slower progress in sugarcane genetic research compared with crops such as rice, maize, and sorghum.

This complex genomic background directly affects the study of quantitative traits such as yield and sugar content. These traits are typically controlled by numerous minor-effect loci, allele dosage effects, and non-additive genetic interactions rather than a few major genes. Ignoring ploidy variation and dosage effects in linkage analysis, GWAS, or genomic prediction can reduce the accuracy of effect estimation. In recent years, advances in high-throughput sequencing, whole-genome resequencing, and reference genome assembly—such as the release of R570 and *S. spontaneum* reference genomes—have greatly improved variant detection and candidate gene identification, providing a solid foundation for dissecting complex traits and advancing molecular breeding in sugarcane (Healey et al., 2024; Brant et al., 2025).

4.2 Advances in genes, QTLs, and molecular markers related to yield and sugar content

Sugarcane yield and sugar content are typical polygenic traits, whose genetic basis is determined by multiple QTLs, QTNs, and complex regulatory networks. In recent years, significant progress has been made in QTL mapping, association analysis, and molecular marker development for traits such as plant height, stalk number, single stalk weight, cane yield, Brix, and fiber content. Early linkage maps constructed using TRAP, DArT, SSR,

and GBS-based single-dose markers identified multiple QTLs associated with yield and quality traits, some of which showed stability across environments and crop cycles (Figure 2).

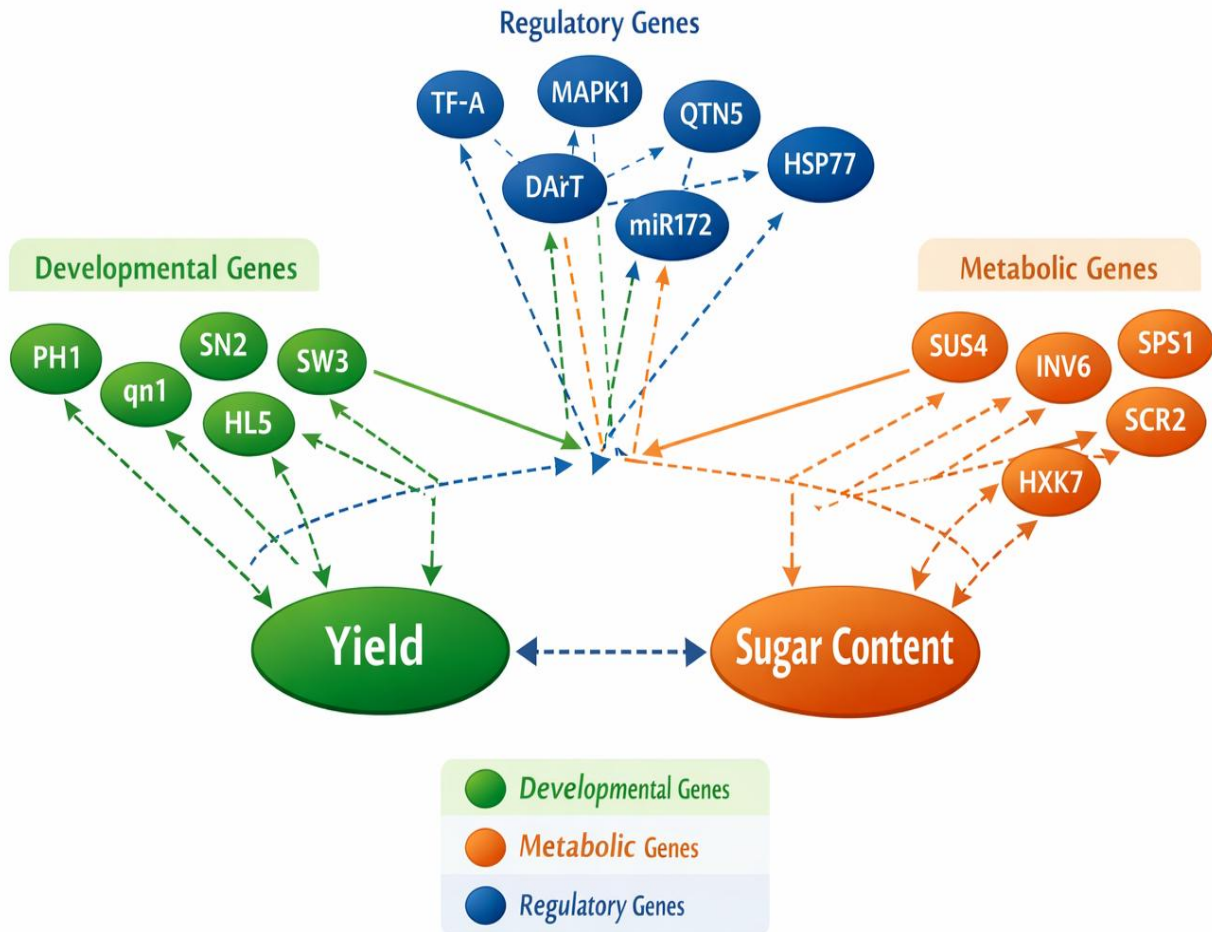


Figure 2 Conceptual model of the polygenic architecture underlying sugarcane yield and sugar content
 Image caption: The interactions among multiple QTLs, QTNs, and regulatory networks

With the application of high-density SNP data, GWAS has greatly improved the resolution of genetic analysis. In Brazilian sugarcane germplasm populations, multiple marker-trait associations related to Brix, plant height, stalk number, stalk weight, and cane yield have been identified, and strong genotypic correlations among these traits suggest shared developmental and metabolic pathways (Barreto et al., 2019). In Zhang's (2023) study, more than 100 QTLs related to Brix and other yield traits were identified across the entire genome., including 35 candidate genes involved in internode development, cell wall formation, signal transduction, and carbon metabolism. These findings indicate that sugarcane yield formation is regulated by multiple developmental and metabolic processes.

For sugar content and quality traits, high-density GWAS and candidate gene analyses have identified numerous SNPs associated with Brix, Pol, CCS, sucrose content, and sugar yield (Li et al., 2024; Eltaher et al., 2025). Notably, a functional SNP in the sucrose synthase gene SoSUS1 (mSoSUS1_SNPCh10.T/C) shows significant associations with Pol, CCS, Brix, fiber content, and sugar yield across multiple environments, demonstrating clear pleiotropy and serving as an important candidate marker for selecting high-sugar genotypes with appropriate fiber content (Li et al., 2024). Meanwhile, studies on fiber-related QTLs further reveal the genetic trade-off between sugar accumulation and biomass formation (Chen et al., 2025b). With the transition to high-density SNP arrays and high-throughput sequencing platforms, QTL mapping, functional marker development, and genomic prediction are jointly driving sugarcane breeding from single-marker selection toward multi-locus integrated prediction.

4.3 Application of transcriptomics, metabolomics, and multi-omics in trait dissection

With the advancement of omics technologies, transcriptomics, metabolomics, and multi-omics integration have become essential tools for dissecting complex quantitative traits in sugarcane. Due to the highly complex genome, traditional forward genetics faces significant limitations in gene identification and functional analysis. Therefore, approaches focusing on gene expression regulation and metabolic networks have become effective strategies for studying yield and sugar formation mechanisms. In particular, RNA-seq enables systematic comparisons of gene expression across tissues, developmental stages, and genotypes, facilitating the identification of key regulatory factors associated with yield and sucrose accumulation.

Transcriptomic studies comparing high- and low-sugar materials, as well as elite and control varieties, have identified numerous differentially expressed genes involved in carbon fixation, starch and sucrose metabolism, plant hormone signaling, secondary metabolism, and cell wall formation. Pan-transcriptome analyses have further distinguished core and variable gene clusters and identified important candidate genes (Li et al., 2024). In the study by Chen et al. (2025a), ScHCT has been proposed as a key regulator of lignin biosynthesis, showing a negative correlation with sugar content and a positive correlation with lignin content, indicating a genetic coupling between secondary cell wall formation and sugar accumulation. This provides molecular insight into the balance between high sugar-low fiber and high biomass-high fiber traits.

Metabolomics reveals the dynamic processes of carbon allocation and sugar formation at the metabolite level. High-sugar varieties are enriched in sugars and sugar-phosphate intermediates related to sucrose accumulation, while secondary metabolites such as phenylpropanoids and flavonoids can indirectly regulate sugar formation by influencing carbon allocation and stress responses. In recent years, multi-omics integration has combined genomic, transcriptomic, metabolomic, and phenotypic data to dissect regulatory networks of yield and sugar content at multiple levels. Such studies have identified over 18 000 differentially expressed genes and 175 differentially accumulated metabolites, and highlighted around 100 key genes that may significantly influence high-yield and high-sugar phenotypes (Li et al., 2024). Additionally, transcription factor families such as MYB, WRKY, bHLH, NAC, TIFY, and C2C2-Dof have been identified as key regulatory nodes coordinating sugar metabolism and secondary metabolism.

5 Key Constraints on the Coordinated Improvement of Sugarcane Yield and Sugar Content

5.1 Negative correlation or trade-off between yield and sugar content

In sugarcane breeding, yield and sugar content often exhibit a certain degree of negative correlation, which is a key constraint on their coordinated improvement. Cane yield is generally positively correlated with traits such as stalk length, stalk diameter, and single stalk weight, but negatively correlated with quality traits such as Brix, sucrose percentage, juice purity, and CCS%. This indicates that although yield and sugar content jointly determine final sugar yield, they do not always increase simultaneously during trait formation, and high yield does not necessarily correspond to high sugar content.

From a physiological perspective, this trade-off reflects competition in carbon allocation between structural growth and sugar storage. Yield mainly depends on biomass accumulation in the stalk, whereas sugar content depends on sucrose concentration and storage within the stem. During vigorous vegetative growth, assimilates are preferentially allocated to cell division, elongation, and cell wall synthesis to support stalk development. In contrast, during the maturation stage, carbon flow gradually shifts toward sucrose accumulation. Under limited carbon resources, biomass increase and sugar storage tend to compete with each other.

However, this negative relationship is not absolute. Long-term breeding results indicate that increases in sugar yield have mainly been driven by biomass improvement, while gains in sugar content have been relatively slower. Nevertheless, this does not imply a permanent antagonism. Mehdi et al. (2024) mentioned in their study that there is no fixed negative trend between biomass and sugar content; instead, their relationship is strongly influenced by environmental conditions. Under favorable environments, sugarcane can simultaneously achieve high biomass and high sugar content (Mehdi et al., 2024). Therefore, this trade-off should be regarded as a conditional constraint influenced by environment, maturity process, and genetic background.

5.2 Effects of environmental factors on the stability of yield and sugar accumulation

Sugarcane yield and sugar content are not only controlled by genetic background but are also strongly influenced by environmental factors. Temperature, light, water availability, soil nutrients, and biotic stresses jointly affect photosynthesis, dry matter accumulation, carbon allocation, and maturation processes, thereby altering the stability of biomass formation and sugar accumulation (Figure 3) (Mehdi et al., 2024). Suitable temperatures and sufficient light generally enhance photosynthetic efficiency and sucrose synthesis, whereas extreme temperatures can inhibit photosynthesis, increase respiratory consumption, and disrupt sugar storage, ultimately reducing both yield and quality.

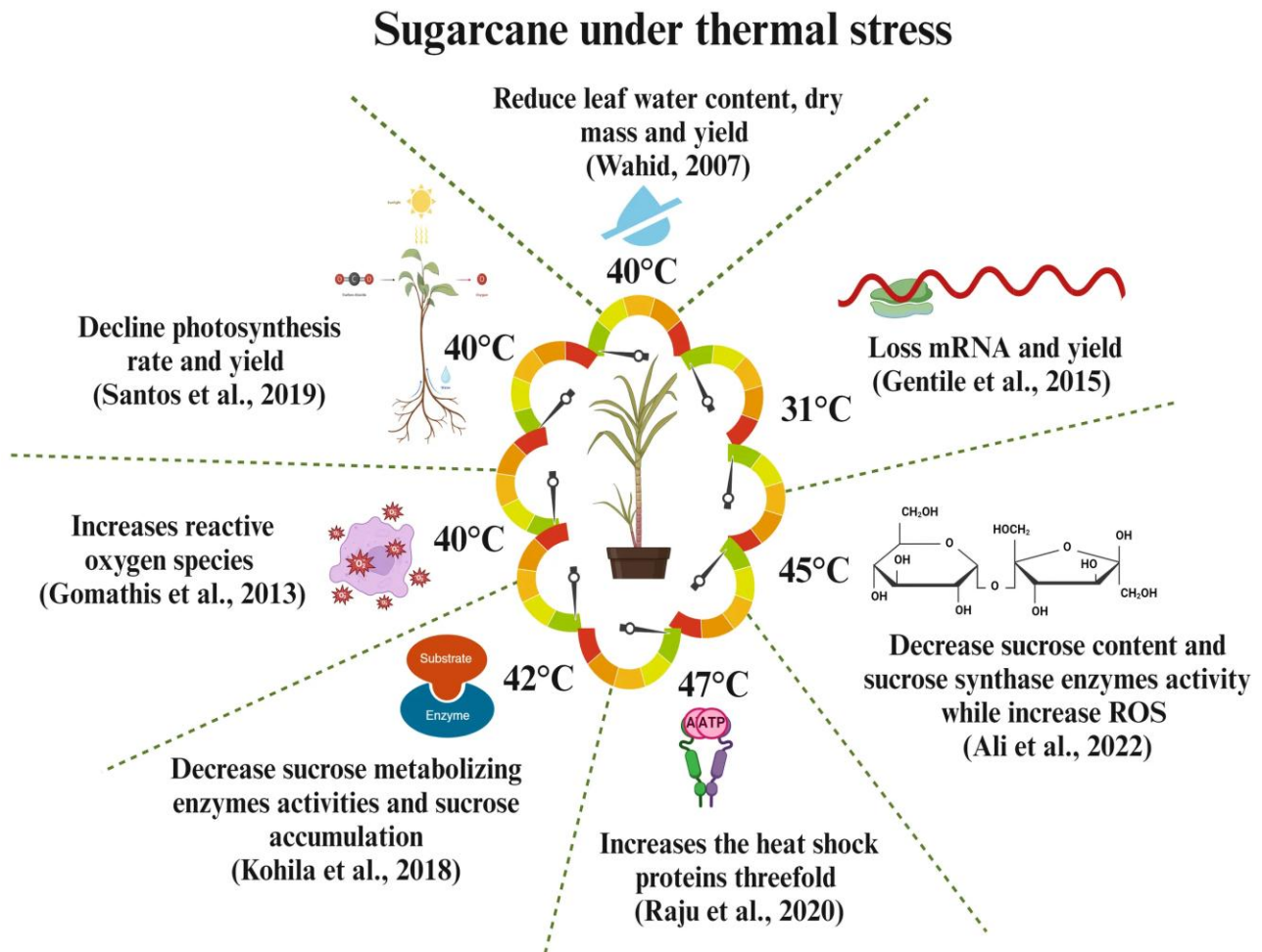


Figure 3 Response of sugarcane crop to different thermal stress conditions (Adopted from Mehdi et al., 2024)

Image caption: High temperatures can affect molecular, physiological, and biochemical processes in sugarcane, leading to reduced yield and sucrose production (Adopted from Mehdi et al., 2024)

Water conditions are particularly critical for the coordinated formation of high yield and high sugar content. Water deficit during the growth stage reduces stomatal conductance and radiation use efficiency, thereby limiting biomass production. Conversely, excessive rainfall or high soil moisture during the maturation stage may increase fresh weight but dilute sucrose concentration in the stalk, leading to the phenomenon of high yield but low sugar. It was mentioned in the article by Saavedra-Diaz et al. (2024), in humid production regions, high rainfall in the late growth stage promotes stalk growth but significantly reduces sucrose accumulation, resulting in lower sugar yield per unit area (Saavedra-Diaz et al., 2024). In addition, nutrient imbalance can disrupt coordination between yield and sugar content, as excessive nitrogen delays maturity and reduces sugar content, while nutrient deficiency suppresses overall growth.

Environmental variation also amplifies genotype×environment (G×E) interactions, leading to unstable performance of high-yield and high-sugar genotypes across regions, years, and ratoon cycles. Improvements in sugar content are generally smaller than those in biomass and are less responsive to environmental improvements, making it more difficult to maintain stable sugar levels across different ecological conditions (Amaresh et al., 2025). With increasing climate variability, factors such as drought, heat waves, extreme rainfall, and pest pressures are expected to further exacerbate instability. Therefore, multi-environment trials, environment-specific ideotype design, and refined environmental characterization are essential for improving the stability of yield and sugar content (Mehdi et al., 2024).

5.3 Breeding challenges arising from complex genetic backgrounds

The highly complex genetic background of cultivated sugarcane is another major constraint on the coordinated improvement of yield and sugar content. Modern sugarcane is a highly polyploid, aneuploid interspecific hybrid with a large genome, high heterozygosity, and complex homologous chromosome composition (Kumar et al., 2024; Wang et al., 2024; Amaresh et al., 2025). Most commercial cultivars derive the majority of their genome from *S. officinarum*, with a relatively smaller contribution from *S. spontaneum*. While this composition helps maintain high sugar traits, it also results in a relatively narrow genetic base, limited available variation, and reduced adaptive potential (Lu et al., 2024).

This complex genetic structure means that most economically important traits in sugarcane are not controlled by single major genes but by numerous small-effect QTLs, accompanied by allele dosage effects and complex interactions (Kumar et al., 2024). For traits such as high biomass and high sucrose accumulation, which may involve inherent trade-offs, combining sufficient favorable alleles within a single genotype is inherently slow and stochastic. In addition, the long breeding cycle of sugarcane, typically 10-15 years and largely reliant on clonal selection, further reduces the efficiency of improving complex traits (Amaresh et al., 2025).

Moreover, reproductive biology and quantitative genetic characteristics further complicate breeding. Asynchronous flowering, partial sterility, and limited effective crosses reduce recombination opportunities and hinder the rapid accumulation of favorable alleles. At the same time, early-stage phenotypic evaluation of yield and sugar content is highly influenced by environmental factors, reducing selection accuracy. These traits often exhibit low narrow-sense heritability and strong non-additive genetic effects, limiting the effectiveness of traditional marker-assisted selection (MAS). Although advances in reference genomes, high-density SNP platforms, and high-throughput sequencing have accelerated molecular breeding, challenges remain in accurate genotyping, allele dosage modeling, and integration of high-quality phenotypic data in polyploid contexts (Amaresh et al., 2025).

6 Breeding Strategies for the Coordinated Improvement of High Yield and High Sugar in Sugarcane

6.1 Conventional hybrid breeding and parental optimization strategies

Conventional hybrid breeding remains the core approach for sugarcane improvement, and most widely cultivated varieties are derived from this system. The basic process includes parental selection, artificial crossing, seedling population establishment, and multi-stage clonal selection and regional trials over 1014 years. In early generations, selection focuses mainly on yield-related traits such as tillering, stalk number, and vigor, while in later stages, greater emphasis is placed on sugar content, maturity, and resistance. Long-term practice shows that although this system can continuously increase yield, the gains mainly come from biomass improvement rather than significant increases in sugar content, reflecting its limitations in achieving coordinated high yield-high sugar improvement (Figure 4).

Under the goal of coordinated improvement, optimizing parental combinations becomes critical. High-biomass genotypes typically exhibit strong stalk growth, whereas high-sugar genotypes excel in sucrose accumulation and quality. Hybridizing these types can expand recombination variation in progeny. However, relying solely on empirical parental selection is inefficient; current approaches increasingly emphasize scientifically guided design based on genetic background, trait complementarity, and combining ability. Studies have shown that specific

combining ability (SCA) may contribute more to yield variation than general combining ability (GCA), indicating that identifying superior hybrid combinations is more important than selecting individual elite parents.

In practice, parental design should focus on N-Trait-based complementarity, such as crossing high-biomass but moderate-sugar genotypes with high-sugar parents to develop ideotypes with strong source-large sink-optimal maturity. Successful cases demonstrate that systematic parental design combined with multi-trait selection can overcome traditional trade-offs and achieve simultaneous improvements in yield and sugar content (Wu et al., 2024; Liu et al., 2025). Additionally, a comprehensive multi-trait evaluation system should be established during progeny selection, integrating early-stage elimination with multi-environment validation in later stages, thereby shifting conventional breeding from experience-driven to target-oriented design.

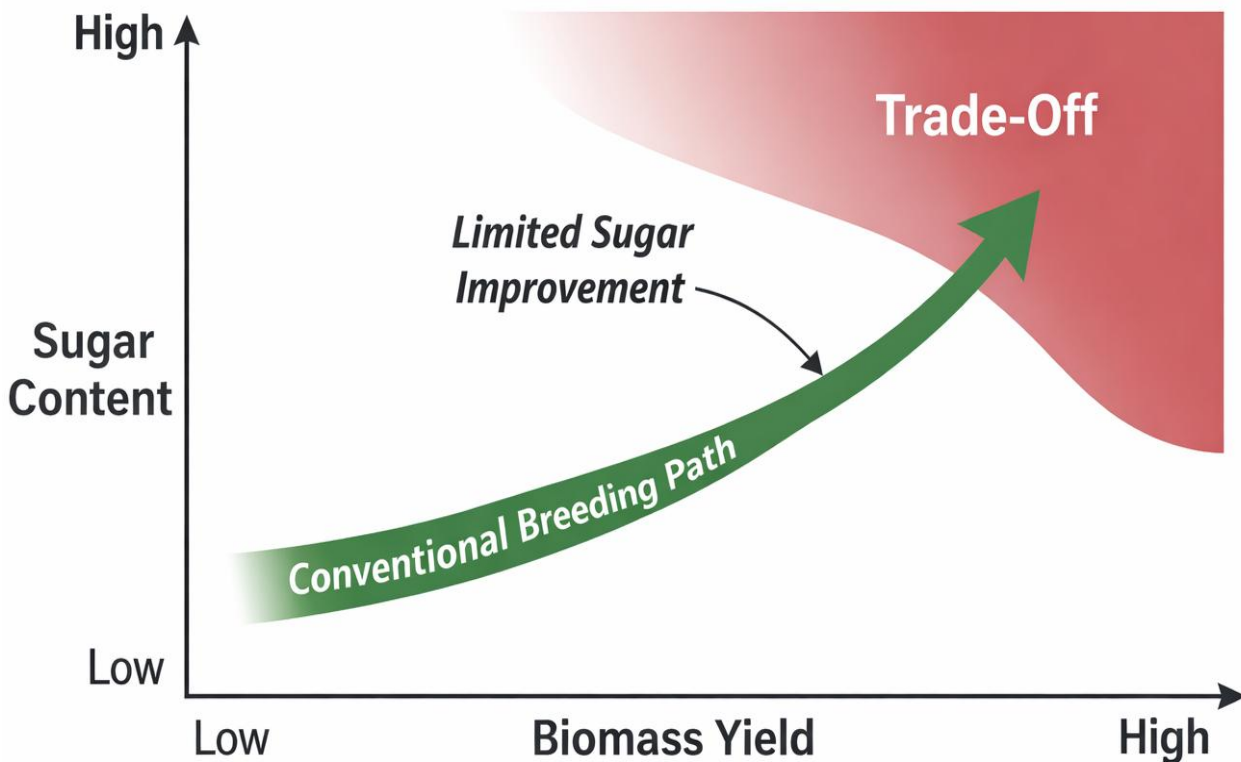


Figure 4 Conceptual relationship between biomass yield and sugar content in conventional breeding
Image caption: Limited improvement in sugar content despite yield gains

6.2 Applications of marker-assisted Selection, genomic selection, and gene editing

Advances in molecular breeding technologies have significantly improved sugarcane breeding efficiency. Marker-assisted selection (MAS) enables early-generation screening based on genotypic information and has been successfully applied to relatively simple traits such as disease resistance—for example, the use of Bru1-associated markers in rust resistance breeding (Lu et al., 2024). However, for complex quantitative traits such as yield and sugar content, which are controlled by multiple genes and environment interactions, the explanatory power of single markers is limited, and MAS is mainly used as a supplementary tool.

With the development of high-density SNP markers and GWAS, an increasing number of loci associated with yield and sugar traits have been identified, providing a foundation for pyramiding favorable alleles (Eltaher et al., 2025). In contrast, genomic selection (GS) is more suitable for complex traits, as it uses genome-wide markers to predict breeding values and capture the combined effects of numerous small-effect loci. Studies have shown that GS can improve selection accuracy, shorten breeding cycles, and provide stable predictions across environments, making it a key tool for future coordinated improvement in sugarcane.

Future trends involve integrating GS with high-throughput phenotyping, environmental data, and machine learning approaches to build a genotype-phenotype-environment predictive framework, thereby improving the understanding of G×E×M interactions and enhancing selection efficiency (Amaresh et al., 2025). Meanwhile, gene editing technologies such as CRISPR/Cas offer new opportunities for precisely regulating genes involved in sucrose metabolism, cell wall synthesis, and stress responses, with the potential to optimize carbon allocation and mitigate the physiological trade-offs between high yield and high sugar (Amaresh et al., 2025; Brant et al., 2025). Although the polyploid genome of sugarcane presents challenges, these technologies are rapidly advancing.

6.3 Integrated breeding approaches for coordinated high yield and high sugar

Because sugarcane yield and sugar content are complex traits, no single technology can achieve major breakthroughs; therefore, future improvement requires an integrated breeding system combining multiple approaches. Within the breeder's equation framework, it is necessary to simultaneously increase genetic variation, selection accuracy, and selection intensity while shortening breeding cycles. This relies on genome-wide data mining, multi-environment phenotyping, and modeling of G×E×M interactions (Amaresh et al., 2025). Thus, coordinated improvement should be conducted under a unified NTrait framework, rather than focusing on single traits independently.

In terms of germplasm resources, expanding the genetic base and strengthening pre-breeding are essential. Introducing wild species and diverse ecotypes can help identify genes associated with high biomass, high sugar content, and stress resistance (Eltaher et al., 2025). A continuous strategy of germplasm expansion-pre-breeding-targeted improvement can provide richer genetic resources for ideotype development. At the same time, breeding objectives should shift from single-trait selection to multi-trait ideotype design, incorporating NTrait components such as tillering, root system architecture, canopy structure, and carbon allocation efficiency to improve indirect selection efficiency.

At the implementation level, a hierarchical breeding pipeline should be established, integrating molecular prediction-phenotypic validation-multi-environment calibration. Early generations can be rapidly screened using molecular markers and GS; intermediate stages can evaluate key traits using high-throughput phenotyping and physiological indicators; and final stages can validate yield, sugar content, and stability through multi-environment trials (Amaresh et al., 2025). In addition, strategies such as recurrent genomic selection (RGS) and reciprocal recurrent genomic selection (RRGS) can be incorporated to accumulate favorable alleles while exploiting heterosis, thereby improving both parental development and hybrid performance and accelerating the coordinated breeding of high-yield and high-sugar sugarcane.

7 Effects of Agronomic Management on the Coordinated Improvement of Sugarcane Yield and Sugar Content

7.1 Regulation of stalk growth and sugar accumulation by water and fertilizer management

Water and nutrient management directly influence the balance between biomass formation and sucrose accumulation in sugarcane by regulating root uptake, canopy structure, and photosynthesis. Adequate water supply during early growth promotes germination, tillering, and rapid stalk elongation, thereby increasing millable cane number and single stalk weight and laying the foundation for high yield. However, excessive water supply in later stages may delay maturation, stimulate vegetative growth, and dilute sucrose concentration, reducing sugar accumulation efficiency. Studies on integrated water-fertilizer management indicate that water and nitrogen jointly promote population establishment and individual growth, but high water and high fertilizer inputs do not necessarily result in high sugar content, reflecting the trade-off between biomass and sugar concentration. Therefore, optimizing the timing and amount of water supply is critical for balancing yield and quality.

In terms of nutrient management, nitrogen, phosphorus, potassium, and micronutrients play distinct roles at different growth stages. Nitrogen promotes leaf area expansion and vegetative growth, but excessive application can delay maturity and reduce sugar content. Phosphorus supports root development and early population establishment, while potassium plays a key role in sucrose transport and synthesis. Recent studies have shown that combined application of potassium with micronutrients such as boron and zinc can improve both yield and sugar

quality (Manzoor et al., 2023). In addition, fertilizer source, placement, and timing are important factors, and synchronizing nutrient supply with crop demand can significantly enhance nutrient use efficiency. Overall, stage-specific and precise water and nutrient management-promoting biomass accumulation in early stages and moderately restricting water and nitrogen in later stages-can redirect carbon flow toward sucrose storage and achieve coordinated improvement of yield and sugar content.

7.2 Effects of planting density and population structure on yield and quality

Planting density and spatial configuration influence sugarcane yield and quality by regulating canopy structure and resource use efficiency. Moderate increases in planting density can enhance millable cane number, leaf area index, and light interception, thereby improving canopy photosynthesis and dry matter accumulation (Joseph et al., 2024). However, excessive density intensifies competition among plants, reduces light penetration and ventilation, inhibits individual stalk development, and lowers sucrose accumulation efficiency. Therefore, optimal density should achieve a dynamic balance between increasing population size and maintaining individual plant quality, rather than simply maximizing or minimizing density.

From a long-term production perspective, moderate density is generally more favorable for maintaining population stability across both plant cane and ratoon crops. Although low density may promote individual plant growth, it is less conducive to sustained high yield. Spatial arrangements, such as row spacing and double-row planting, also affect the coordination between yield and quality, with different configurations favoring either biomass production or sugar accumulation (Joseph et al., 2024). In addition, varietal characteristics and belowground conditions can modify density effects, as plants may compensate through adjustments in stalk number and individual stalk weight. An ideal population should have a moderate leaf area index, good light penetration and ventilation, and uniform stalk distribution to balance photosynthetic efficiency and sugar accumulation, thereby achieving both high yield and high sugar content.

7.3 Importance of growth stage regulation and timely harvest for high yield and high sugar formation

The formation of sugarcane yield and sugar content is highly dependent on developmental stages. The tillering and elongation phases determine population size and biomass foundation, while the maturation phase governs sucrose accumulation and quality improvement. By regulating planting time, water and nutrient supply, and irrigation withdrawal, it is possible to coordinate the timing of peak biomass formation and peak sugar accumulation. Moderate restriction of water and nitrogen during maturation can suppress excessive vegetative growth and promote carbon allocation to sucrose storage. In contrast, continuous high water and nutrient supply may increase biomass but often reduces sugar concentration. Therefore, proper regulation of the maturation process is essential for achieving synchronized improvements in yield and quality.

Planting and harvesting windows are also closely related to varietal maturity types and regional climatic conditions. Appropriate planting time is critical for achieving high yield, whereas delayed planting often results in yield reduction. Different maturity types require different optimal harvest times, and moderately delayed harvesting generally improves quality traits such as Brix, purity, and CCS. Moreover, harvest season and scheduling significantly affect sugar yield, and optimized harvest planning can greatly enhance overall production efficiency and economic returns (Gebrehiwot et al., 2025). Therefore, timely harvesting should be determined based on variety characteristics, environmental conditions, and processing capacity, ensuring coordination between production and processing to maximize the potential for high yield and high sugar content.

8 Future Research Directions and Development Trends

8.1 Multi-omics integration for deciphering mechanisms of high yield and high sugar traits

With advances in genomics, transcriptomics, and metabolomics, the coordinated improvement of yield and sugar content in sugarcane increasingly relies on multi-omics integration to systematically elucidate the continuum from genetic variation-physiological processes-agronomic performance. Since yield and sugar content are complex quantitative traits involving multiple layers such as carbon fixation, sucrose metabolism, source-sink partitioning, and hormonal regulation, single-omics approaches are insufficient to fully explain their formation. Therefore, integrating genomic, transcriptomic, proteomic, metabolomic, and phenomic data has become a key strategy for

uncovering trait mechanisms. Studies have shown that multi-omics analyses can identify differentially expressed genes, metabolites, and key pathways associated with high yield and high sugar, mainly involving carbon metabolism, secondary metabolism, and hormone signaling networks (Li et al., 2024). Further integration with co-expression and metabolic network analyses enables the identification of key modules and hub genes related to sugar content, fiber, and yield, providing targets for NTrait marker development and molecular breeding.

In the regulation of sucrose accumulation, multi-omics approaches have moved beyond transcript-level analysis toward integrated protein-metabolite-phenotype systems. Evidence suggests that enzymes, transporters, and regulatory factors involved in sucrose metabolism act coordinately in time and space, with an expanding number of candidate proteins highlighting the importance of photosynthesis and primary carbon metabolism in high sugar formation (Fan et al., 2025). This indicates that future research should focus more on the integrated regulation of functional proteins and metabolic pathways. In addition, multi-omics studies reveal dynamic changes in carbon allocation during development, shifting from early growth and structural formation to later sugar storage and stabilization, providing insights into the regulation of maturation and source-sink relationships. In the future, integrating pan-omics with machine learning frameworks is expected to enable precise identification of key regulatory modules and trait prediction, advancing sugarcane breeding from association analysis to predictive design.

8.2 Integration of high-throughput phenotyping, smart breeding, and digital agriculture

In sugarcane breeding, low efficiency and limited accuracy of phenotyping have long been major bottlenecks for studying complex traits. Traditional field measurements are labor-intensive and subject to human error, making them unsuitable for large-scale population evaluation. Therefore, high-throughput phenotyping (HTP) technologies have emerged as a key breakthrough for improving breeding efficiency and precision. In recent years, UAV-based systems, multispectral/hyperspectral imaging, LiDAR, and field sensors have enabled rapid acquisition of key traits such as canopy structure, biomass, water status, and photosynthesis-related parameters. These traits are not only closely related to yield but can also serve as intermediate indicators in genomic selection models, transforming phenotypic data from static end-point measurements into dynamic traits across the entire growth cycle.

Future research should expand the scope of HTP to include NTrait indicators such as tillering dynamics, stalk number changes, early growth vigor, canopy temperature, and sugar accumulation processes, and evaluate their genetic relationships with final yield and sugar content (Amaresh et al., 2025). This will improve prediction accuracy for complex traits and enable early selection of superior genotypes. At the same time, integration of phenotypic, genomic, and environmental data is driving the development of smart breeding. Under the “Breeding 4.0” framework, machine learning-assisted genomic selection models can more accurately predict breeding values across environments, optimizing parental selection and breeding strategies. In addition, digital agriculture technologies integrating remote sensing, environmental monitoring, and management data can enable precise regulation of water and fertilizer use, pest control, and harvest timing. More advanced developments include the construction of digital twin breeding systems, which simulate breeding and management strategies in virtual environments and optimize decisions in real time (Wang et al., 2024a). Combined with data sharing and blockchain technologies, such systems will significantly enhance collaborative breeding and supply chain management efficiency.

8.3 Breeding directions for multi-objective coordinated improvement

With the diversification of the sugarcane industry toward sugar production, bioenergy, and biomaterials, future breeding objectives are shifting from single traits to multi-trait optimization. Ideal varieties should simultaneously possess high yield, high sugar content, strong stress resistance, wide adaptability, and suitability for mechanized harvesting (Lu et al., 2024; Wang et al., 2025). Thus, breeding targets are evolving into a comprehensive system encompassing yield, sugar content, stress resistance, mechanization, and industrial adaptability. In ideotype design, a series of NTrait intermediate traits play key roles, including optimal canopy structure, appropriate leaf angle, deep root systems, stay-green ability, and high single stalk weight. These traits contribute to efficient light use,

balanced source-sink relationships, and enhanced stress tolerance, and should be incorporated into multi-trait selection frameworks.

Multi-omics studies further reveal that certain key regulatory factors can simultaneously influence sucrose accumulation, cell wall composition, and stress responses, providing opportunities for coordinated improvement of high sugar-high biomass-high resilience. For mechanization requirements, ideal varieties should also exhibit uniform plant architecture, strong lodging resistance, and synchronous maturity, traits that have begun to be elucidated at molecular and metabolic levels (Li et al., 2024). In terms of stress resistance, greater use of wild germplasm resources is needed to broaden the genetic base, combined with molecular markers, genomic selection, and gene editing technologies to achieve coordinated improvement of stress tolerance, yield, and sugar content (Lu et al., 2024). At the same time, future varieties should also meet the needs of processing and biorefinery applications, with cell wall structures optimized for both sugar extraction and bioenergy conversion (Wang et al., 2025), thereby promoting the transition of sugarcane from a single-purpose crop to a multifunctional industrial resource.

9 Conclusion

Sugarcane yield and sugar content are the two core traits determining the economic value of raw cane and sugar yield per unit area. Their formation is not governed by a single factor but results from the coordinated interaction of agronomic traits, physiological processes, and molecular regulatory networks. At the agronomic level, traits such as tiller number, millable cane number, single stalk weight, plant height, and stalk diameter jointly determine cane yield, while sucrose content, maturity, and juice quality directly influence sugar levels. At the physiological level, photosynthetic efficiency, dry matter accumulation, source-sink relationships, and assimilate transport and partitioning are key processes linking biomass production and sugar accumulation. From a genetic perspective, these traits are typical complex quantitative traits controlled by multiple genes with significant non-additive effects. Their essence lies in the dynamic balance of carbon allocation between biomass and sugar, rather than a fixed antagonistic relationship.

The realization of high yield and high sugar content in sugarcane depends on the synergistic interaction of genotype \times environment \times management (G \times E \times M). Relying solely on genetic improvement or agronomic practices is insufficient to achieve optimal performance. In breeding, it is necessary to optimize parental combinations, broaden the genetic base, and apply multi-trait selection strategies, combined with molecular markers, genomic selection, and gene editing technologies to identify genotypes with both high biomass and strong sugar accumulation potential. In agronomic management, optimizing variety selection, nutrient supply, and input levels-particularly the balance of nitrogen, potassium, magnesium, and calcium-is essential to promote tillering, population structure formation, and sucrose accumulation. Studies indicate that under suitable environmental conditions and appropriate management, high biomass and high sugar content can coexist, highlighting the importance of an integrated genotype-environment-management framework for stabilizing sugar yield.

For the high-quality development of the sugarcane industry, future efforts should focus on advancing coordinated improvement of yield and sugar content at theoretical, resource, and technological levels. Theoretically, an N-Trait-based framework should integrate outcome traits (e.g., tillering, stalk number, single stalk weight, sugar content, and fiber) with mechanistic traits such as carbon allocation, nutrient use efficiency, and maturation regulation to enable precise ideotype design. In terms of resources, pan-genomics, whole-genome resequencing, and GWAS should be used to identify key loci and favorable haplotypes. Technologically, integrating genomic selection, rapid breeding approaches, and CRISPR-based gene editing will improve the efficiency of complex trait improvement. Meanwhile, incorporating high-throughput phenotyping, digital agriculture, and artificial intelligence into breeding and management, along with strengthening germplasm innovation and international collaboration, will facilitate the development of a modern sugarcane breeding system that integrates theoretical models, molecular tools, and region-specific applications, thereby supporting the sustained improvement of high yield and high sugar content and the sustainable development of the sugarcane industry.

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Conflict of Interest Disclosure

The authors affirm 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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