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Genome-Wide Association Studies in Sugarcane: Unlocking the Genetic Basis of Yield and Agronomic Traits

Wanru Wang [1,2], Xiping Yang [1,2]
1 State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, Guangxi University, Nanning, 530005, Guangxi, China
2 College of Agricultural, Guangxi University, Nanning, 530005, Guangxi, China
Corresponding email: xipingyang@gxu.edu.cn

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Abstract This study provides a comprehensive overview of genome-wide association studies (GWAS) applications in sugarcane, highlighting the key findings related to yield and agronomic traits. Major GWAS studies conducted in sugarcane have identified numerous genetic markers associated with important traits. Significant loci linked to high sucrose content, overall yield, disease resistance, and abiotic stress tolerance have been discovered, offering valuable insights for breeding programs. The integration of these findings into marker-assisted selection (MAS) and genomic selection (GS) has enhanced breeding efficiency, leading to the development of superior sugarcane varieties. A detailed case study on the Brazilian Panel of Sugarcane Genotypes (BPSG) study exemplifies the practical application of GWAS in sugarcane research. The BPSG study identified key genetic regions associated with yield and disease resistance, demonstrating the potential of GWAS to accelerate genetic improvements. In the future, it is expected to improve the resolution and applicability of GWAS, address current challenges in translating findings to field applications, and unleash the full potential of GWAS in improving sugarcane yield and agronomic traits.

Keywords Sugarcane (*Saccharum* spp.); Genome-wide association studies (GWAS); Genetic basis; Yield; Agronomic traits

1 Introduction

Sugarcane (*Saccharum* spp.) is a vital crop globally, contributing significantly to the production of sugar, ethanol, and electricity. It is a C4 plant known for its high biomass production and is cultivated extensively in tropical and subtropical regions (Budeguer et al., 2021; Mahadevaiah et al., 2021). Modern sugarcane varieties are complex hybrids derived from interspecific and intergeneric hybridization between *Saccharum officinarum*, *Saccharum spontaneum*, and other wild relatives. The crop's economic importance is underscored by its role in supplying up to 80% of the world's sugar and approximately 60% of biofuel (Yang et al., 2020; Zan et al., 2020).

The yield and agronomic traits of sugarcane are critical for meeting the growing global demand for sugar and biofuels, especially in the context of climate change. Key agronomic traits include cane yield, sucrose content, disease resistance, and tolerance to abiotic stresses such as drought and salinity (Racedo et al., 2016; Fickett et al., 2019). Improving these traits is essential for enhancing sugarcane productivity and sustainability. However, the genetic complexity of sugarcane, characterized by its polyploidy and high heterozygosity, poses significant challenges to traditional breeding methods (Budeguer et al., 2021; Meena et al., 2022).

Genome-wide association studies (GWAS) have emerged as a powerful tool for dissecting the genetic basis of complex traits in sugarcane. Unlike biparental mapping, GWAS leverages natural genetic variation within a population to identify marker-trait associations (MTAs) (Fickett et al., 2019; Yang et al., 2020). This approach is particularly advantageous in sugarcane due to its large linkage disequilibrium, which allows for the identification of markers associated with important agronomic traits. Recent studies have successfully utilized GWAS to identify markers linked to yield, sucrose traits, and other agronomic characteristics, providing valuable genetic resources for sugarcane improvement (Racedo et al., 2016; Yang et al., 2020).

The objective of this study is to summarize recent advances in sugarcane genomics and the identification of favorable alleles for superior agronomic traits, highlight the challenges and limitations associated with GWAS in sugarcane, and discuss the potential of integrating GWAS findings with other genomic tools, so as to provide insights into future research directions and the potential impact of GWAS on sugarcane improvement. By consolidating findings from multiple studies, this study expects to offer a comprehensive understanding of how GWAS can be harnessed to improve sugarcane yield and agronomic traits, ultimately contributing to the development of more resilient and productive sugarcane varieties.

2 Overview of Sugarcane Genetics

2.1 Genetic complexity of sugarcane

Sugarcane is characterized by an exceptionally complex genome, which includes high levels of polyploidy and frequent aneuploidy. This complexity poses significant challenges in understanding the relationships between genotype and phenotype (Racedo et al., 2016; Barreto et al., 2019). The genome of modern sugarcane hybrids is derived from *Saccharum officinarum*, *Saccharum spontaneum* as well as wild relatives, and includes sub-genomes from those, with some chromosomes resulting from recombination between these sub-genomes (Thirugnanasambandam et al., 2018). The high heterozygosity and autopolyploid nature of sugarcane further complicate the development of a comprehensive genetic map (Meena et al., 2022).

2.2 Key traits of interest

Key traits of interest in sugarcane breeding include yield, disease resistance, and tolerance to abiotic stresses. Yield traits such as cane yield, sugar content, and biomass are critical for both sugar and biofuel production (Racedo et al., 2016; Fickett et al., 2019; Yang et al., 2020). Disease resistance, particularly against major pathogens, is another crucial trait, with significant efforts directed towards identifying and incorporating resistance genes into breeding programs. Additionally, tolerance to abiotic stresses such as drought and salinity is essential for maintaining productivity in varying environmental conditions (Mahadevaiah et al., 2021).

2.3 Historical breeding efforts and challenges

Historically, sugarcane breeding has relied on conventional methods, which are time-consuming and labor-intensive, often requiring 12~14 years to develop new varieties (Mahadevaiah et al., 2021). The high genetic complexity and polyploidy of sugarcane have made it difficult to achieve desired rates of genetic gain through traditional breeding methods. Despite these challenges, significant progress has been made in identifying superior agronomic traits and genes through quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), and transcriptome approaches (Meena et al., 2022). Recent advances in genomic selection and next-generation sequencing technologies have opened new avenues for improving breeding efficiency and genetic gain in sugarcane (Zan et al., 2020; Hayes et al., 2021). These modern biotechnological tools have facilitated the identification and accumulation of favorable alleles, thereby enhancing the selection efficiency in breeding programs.

3 GWAS in Sugarcane: Current Status

3.1 Summary of major GWAS studies conducted in sugarcane

Genome-wide association studies (GWAS) have been increasingly utilized to dissect the genetic basis of complex traits in sugarcane, a crop with a highly complex polyploid genome. Several significant studies have been conducted to identify marker-trait associations (MTAs) for various agronomic traits. For instance, a study on the Brazilian Panel of Sugarcane Genotypes (BPSG) identified 23 MTAs for traits such as soluble solid content, stalk height, stalk number, stalk weight, and cane yield (Barreto et al., 2019). Racedo et al. (2016) focused on a breeding population and identified 43, 42, and 41 markers associated with cane yield (CY) across three successive crop cycles, respectively, and 38, 34, and 47 markers associated with sugar content (SC). Additionally, research on the Louisiana sugarcane core collection identified MTAs for 11 cane yield and sucrose traits using SNP and Indel markers (Fickett et al., 2019).

3.2 Key findings from these studies

The key findings from these GWAS studies highlight the potential of GWAS in identifying significant genetic markers associated with important agronomic traits in sugarcane. For example, the study on the BPSG revealed that the broad-sense heritability values for yield traits were above 0.48 and 0.49 for the first and second harvests, respectively, and identified 23 MTAs (Barreto et al., 2019). The breeding population study demonstrated the effectiveness of a novel mixed-model framework in identifying consistent markers across multiple years and locations, with 20 markers associated with CY and 12 with SC over two years (Racedo et al., 2016). The Louisiana sugarcane core collection study found high correlations between sucrose traits and identified 56 markers consistent across multiple traits, explaining up to 15% of the phenotypic variation (Fickett et al., 2019).

3.3 Identified genetic markers associated with important traits

Several genetic markers have been identified as being associated with key agronomic traits in sugarcane. In the BPSG study, 23 MTAs were identified, including markers for soluble solid content, stalk height, stalk number, stalk weight, and cane yield (Barreto et al., 2019). The breeding population study identified 43, 42, and 41 markers associated with CY across three crop cycles, respectively, and 38, 34, and 47 markers associated with SC (Racedo et al., 2016). The Louisiana sugarcane core collection study identified 56 markers consistent across multiple sucrose traits, which could be used in marker-assisted selection (MAS) for breeding programs (Fickett et al., 2019). Additionally, a study on a diversity panel of polyploid sugarcane identified 217 nonredundant markers and 225 candidate genes associated with yield traits, providing a comprehensive genetic resource for future breeding efforts (Yang et al., 2020). These findings underscore the importance of GWAS in uncovering the genetic basis of yield and agronomic traits in sugarcane, facilitating the development of superior cultivars through marker-assisted selection and genomic prediction.

4 Functional Genomics and Candidate Gene Validation

4.1 Approaches for validating GWAS findings

Genome-wide association studies (GWAS) have become a pivotal tool in identifying genetic loci associated with important agronomic traits in sugarcane. However, validating these findings is crucial to ensure their reliability and applicability in breeding programs. One common approach is to replicate the GWAS in different populations or environments to confirm the marker-trait associations (MTAs) (Racedo et al., 2016; Barreto et al., 2019; Fickett et al., 2019). Additionally, integrating GWAS with other genomic tools such as transcriptomics and proteomics can help in identifying candidate genes and understanding their functional roles (Khanbo et al., 2020). For instance, candidate gene association mapping using gene expression data can validate the functional significance of identified loci.

4.2 Role of functional genomics in understanding gene function

Functional genomics plays a critical role in elucidating the biological mechanisms underlying the genetic associations identified by GWAS. By studying gene expression patterns, protein interactions, and metabolic pathways, researchers can gain insights into how specific genes influence phenotypic traits. For example, the integration of transcriptome and proteome data with GWAS findings can help in pinpointing the exact genes involved in sucrose metabolism and other yield-related traits in sugarcane (Khanbo et al., 2020). This comprehensive approach not only validates the GWAS findings but also enhances our understanding of the genetic architecture of complex traits (Liu and Yan, 2018).

4.3 Techniques for candidate gene validation

Several techniques are employed to validate candidate genes identified through GWAS. Gene editing technologies such as CRISPR/Cas9 allow for precise modifications of target genes to study their effects on phenotypic traits. Overexpression studies, where candidate genes are introduced and expressed at higher levels in model organisms or crop plants, can also provide valuable insights into gene function (Liu and Yan, 2018). Additionally, RNA interference (RNAi) can be used to knock down the expression of candidate genes to observe resultant phenotypic changes. These techniques, combined with traditional breeding methods, can significantly accelerate the validation and utilization of candidate genes in sugarcane improvement programs.

5 Case Study: Detailed Analysis of a Specific GWAS in Sugarcane

5.1 Example: Brazilian Panel of Sugarcane Genotypes (BPSG) study

The Brazilian Panel of Sugarcane Genotypes (BPSG) study aimed to dissect the genetic basis of yield traits in sugarcane through a comprehensive genome-wide association study (GWAS). The specific objectives were to estimate adjusted means and genetic parameters for ten traits over three harvest years using a mixed model, and to estimate genotypic correlation among those traits (Figure 1) (Barreto et al., 2021).

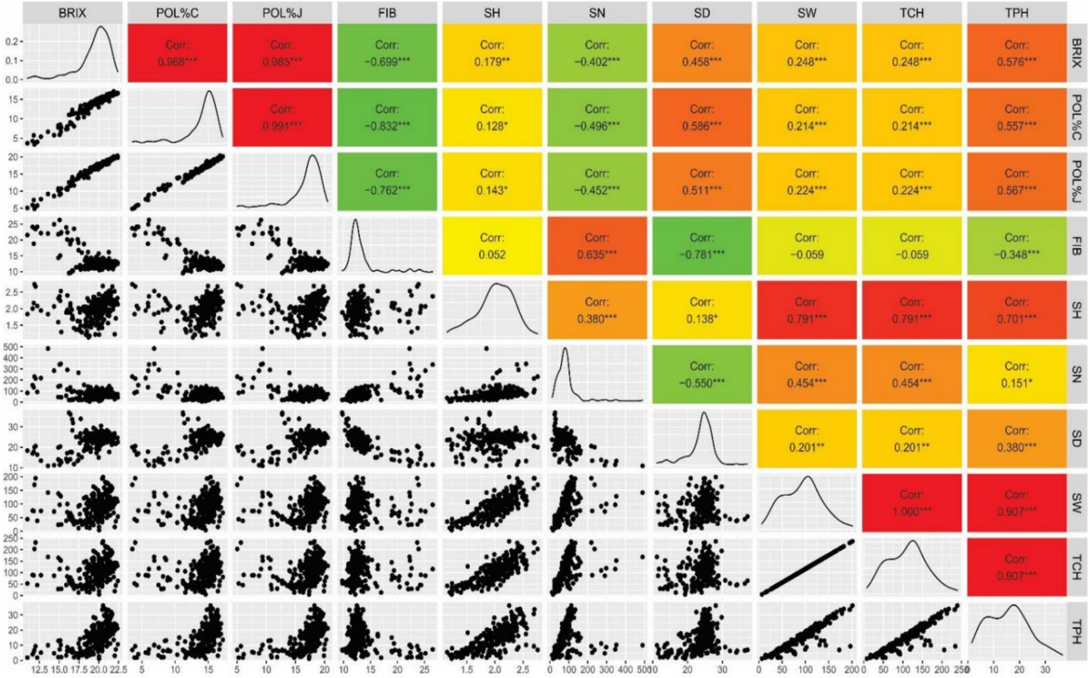

Figure 1 Genotypic correlation between yield traits evaluated in the Brazilian Panel of Sugarcane Genotypes (BPSG) (Adopted from Barreto et al., 2021)

Image caption: BRIX (in Brix), sucrose content of the cane (POL%C, in %), sucrose content of the juice (POL%J, in %), fiber content (FIB, in %), stalk height (SH, in m), stalk number (SN), stalk diameter (SD, in mm), stalk weight of the plot (SW, in kg), cane yield (TCH, in t/ha) and sucrose yield (TPH, in t/ha); For each trait, the density plots of the adjusted means (diagonal), scatterplots (below diagonal), and values of the genotypic correlation (above diagonal) between pairs of traits are shown; * Significant at the 5% global level ($p<0.05$). ** Significant at the 1% global level ($p<0.01$). *** Significant at the 0.1% global level ($p<0.001$) (Adopted from Barreto et al., 2021)

The study by Barreto et al. (2021) showed high positive correlations between BRIX, POL%C, and POL%J (all > 0.98), indicating strong relationships among these sucrose-related traits, positive correlations of TCH and TPH with most traits, suggesting these are key yield determinants. SH and SW show moderate to strong correlations with yield traits. Conversely, FIB has a negative correlation with sucrose-related traits (BRIX, POL%C, POL%J), highlighting a trade-off between fiber content and sugar yield. This analysis highlights the interconnected nature of sugarcane yield components, crucial for breeding programs aimed at enhancing yield and sucrose content.

Barreto et al. (2019) also utilized a diversity panel of sugarcane genotypes and employed SSR markers to analyze genetic diversity and population structure in 2019. The phenotypic data analysis revealed broad-sense heritability values above 0.48 and 0.49 for the first and second harvests, respectively. The SSR markers produced 1 483 fragments, with 99.5% being polymorphic, which helped estimate the number of subpopulations and the extent of LD. Meanwhile, the GWAS identified 23 MTAs for traits such as soluble solid content, stalk height, stalk number, stalk weight, and cane yield.

5.2 Implications for breeding programs and future research directions

The findings from the BPSG study have significant implications for sugarcane breeding programs. The genotype correlation of major agronomic traits provides a basis for future association map research. And the identification of MTAs provides valuable markers that can be used for marker-assisted selection (MAS) to introgress favorable alleles into breeding populations. This can enhance the efficiency of selecting superior genotypes with desirable yield traits. Additionally, the study’ s methodology and results can serve as a reference for future research aiming to validate these MTAs in other populations and environments. Future research should focus on fine-mapping the identified loci and exploring the functional roles of the candidate genes to better understand the genetic mechanisms underlying yield traits in sugarcane (Racedo et al., 2016; Barreto et al., 2019; Fickett et al., 2019).

5.3 Impact of these findings on sugarcane breeding programs

The impact of the BPSG study on sugarcane breeding programs is profound. By providing a set of validated markers associated with key traits, researchers can more effectively manage crosses and select superior genotypes, thereby accelerating the development of high-yielding sugarcane varieties. The study's approach to using a diverse panel and robust statistical models ensures that the identified markers are reliable and applicable across different breeding contexts. This can lead to more targeted and efficient breeding strategies, ultimately contributing to increased sugarcane productivity and sustainability (Barreto et al., 2019; Yang et al., 2020).

6 Integrating GWAS Findings into Breeding Programs

6.1 Strategies for incorporating GWAS results into practical breeding

Incorporating GWAS findings into practical breeding programs involves several strategic steps. Firstly, the identification of significant marker-trait associations (MTAs) through GWAS provides a foundation for selecting desirable traits. For instance, studies have identified numerous MTAs for cane yield and sucrose traits in sugarcane, which can be validated and utilized in breeding programs (Racedo et al., 2016; Barreto et al., 2019). The integration process begins with the validation of these markers in diverse populations to ensure their reliability and effectiveness across different genetic backgrounds and environmental conditions (Fickett et al., 2019).

Once validated, these markers can be used to develop marker-assisted selection (MAS) protocols. This involves genotyping breeding populations for the presence of favorable alleles and selecting individuals that carry these alleles for further breeding (Barreto et al., 2019; Fickett et al., 2019). Additionally, the use of genomic selection (GS) models, which incorporate genome-wide marker data to predict the breeding values of individuals, can enhance the selection process by providing more accurate predictions of genetic potential (Hayes et al., 2021; Ravelombola et al., 2021).

6.2 Marker-assisted selection (MAS) and genomic selection (GS)

Marker-assisted selection (MAS) and genomic selection (GS) are two pivotal approaches for integrating GWAS findings into breeding programs. MAS focuses on the use of specific markers associated with desirable traits to guide the selection of breeding candidates. For example, significant markers identified for cane yield and sucrose traits in sugarcane can be used in MAS to select high-yielding and high-sucrose clones (Barreto et al., 2019; Fickett et al., 2019). This approach has been shown to be effective in improving traits such as disease resistance and yield components in various crops (Ravelombola et al., 2021).

On the other hand, GS utilizes genome-wide marker data to predict the genetic potential of individuals. This method has been demonstrated to improve the accuracy of selection and accelerate the breeding process. In sugarcane, GS models have been developed to predict traits such as tonnes of cane per hectare (TCH), commercial cane sugar (CCS), and fiber content, achieving high prediction accuracies (Hayes et al., 2021). The combination of MAS and GS can provide a comprehensive strategy for enhancing breeding efficiency and achieving genetic gains in sugarcane (Ravelombola et al., 2021).

6.3 Examples of successful integration in sugarcane breeding

Several studies have demonstrated the successful integration of GWAS findings into sugarcane breeding programs. For instance, a study conducted on the Louisiana sugarcane core collection identified significant MTAs for cane yield and sucrose traits, which were subsequently validated and used in MAS to select superior clones. Fickett et al. (2019) formed the Louisiana sugarcane core collection using 97 clones. The heat map and dendrogram generated from the IBS K-matrix showed strong differentiation between ten clones and the rest of the collection that was divided into two main groups (Figure 2). Similarly, another study on a Brazilian panel of sugarcane genotypes identified MTAs for various yield traits, which were used to guide the selection of high-performing genotypes (Barreto et al., 2019).

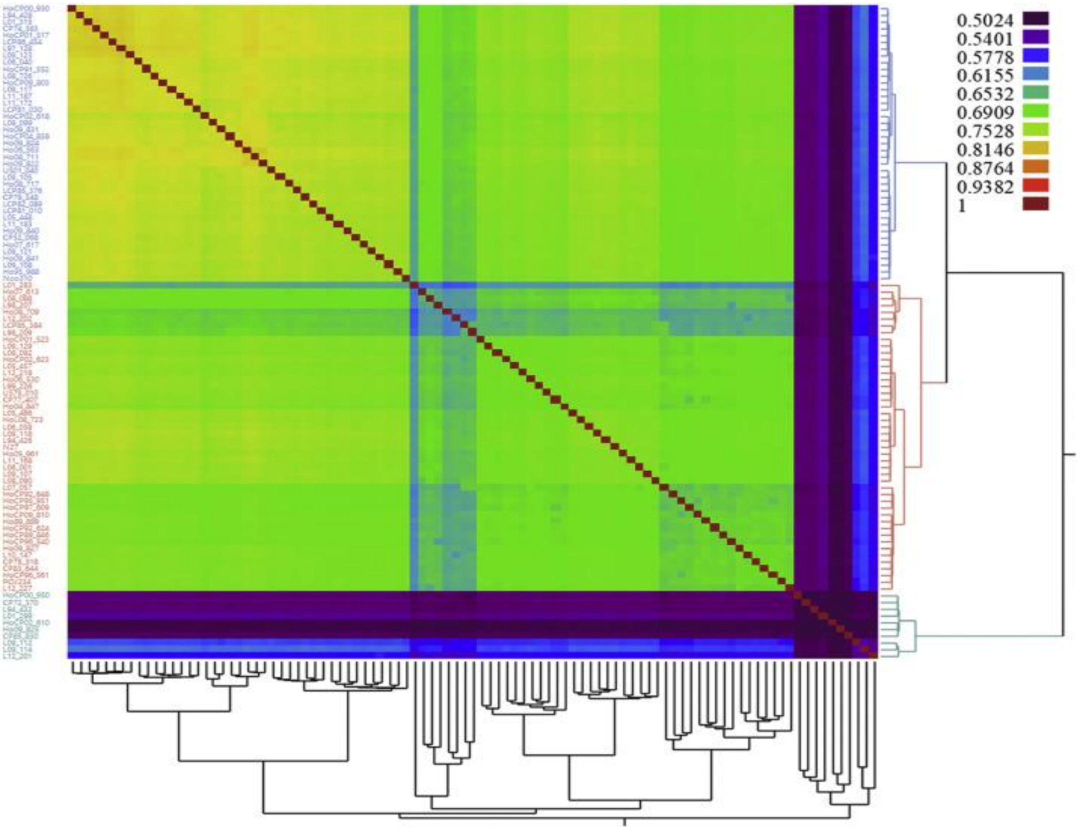

Figure 2 Heat map and dendrogram generated with the kinship matrix (K) (Adopted from Fickett et al., 2019)

Image caption: The K-matrix is an identity by state matrix of the 97 clones using 6 534 SNP and InDel markers in sugarcane (Adopted from Fickett et al., 2019)

Fickett et al. (2019) highlights the genetic diversity within the studied sugarcane population. High similarity clusters suggest close genetic relationships, useful for identifying potential parent pairs in breeding programs to enhance desired traits. Conversely, areas of low similarity indicate genetic diversity, which is crucial for maintaining a robust breeding pool. The kinship matrix aids in selecting genetically diverse parents to avoid inbreeding and maximize heterosis in offspring, contributing to improved sugarcane breeding strategies.

Moreover, the application of GS in sugarcane breeding has also shown promising results. Islam et al. (2022) studied the sugar and yield-related trait data from 432 sugarcane clones and 10 435 single nucleotide polymorphisms (SNPs) by using seven different GS models (Figure 3). These examples highlight the potential of integrating GWAS findings into practical breeding strategies to improve yield and agronomic traits in sugarcane.

Islam et al. (2022) highlights the potential of the GS methods to predict breeding values and select superior sugarcane genotypes effectively. Panel A shows that prediction accuracy varies among the traits and methods, with values generally ranging between 0.1 and 0.3. Stalk weight (SW) demonstrates slightly higher prediction accuracy across methods, while other traits show similar moderate accuracy. Panel B presents the coincidence index, which measures the proportion of top individuals correctly identified by the models. The index is relatively consistent across traits and methods, typically around 0.2 to 0.3, indicating moderate model performance in identifying top performers.

7 Future Prospects and Challenges

7.1 Emerging technologies and their potential impact on GWAS

The field of genome-wide association studies (GWAS) in sugarcane is poised for significant advancements with the integration of emerging technologies. The advent of next-generation sequencing (NGS) and high-throughput genotyping platforms has already revolutionized GWAS by enabling the rapid and cost-effective identification of genetic variants across the genome. Whole-genome sequencing, in particular, has shown promise in identifying novel genes associated with agronomic traits that were previously undetectable using standard SNP analysis (Yano et al., 2016). Additionally, the development of more sophisticated statistical models and computational tools has enhanced the accuracy and speed of GWAS, allowing for the detection of rare variants and synthetic associations (Liu et al., 2018; Cortes et al., 2021). These technological advancements are expected to further refine the resolution of GWAS, thereby facilitating the discovery of key genetic loci that can be targeted for crop improvement.

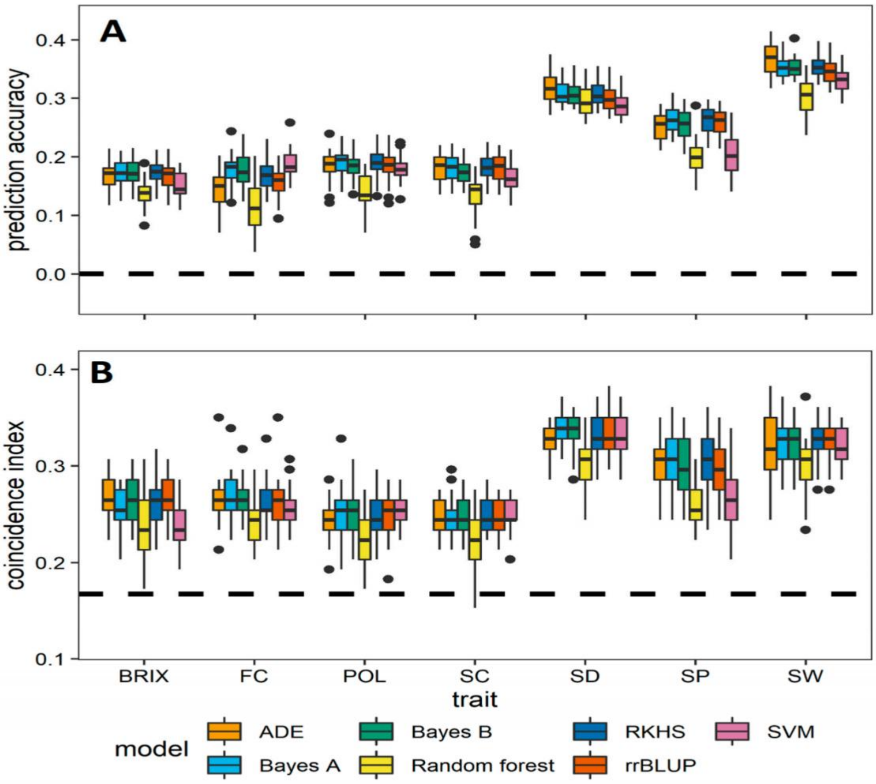

Figure 3 Prediction accuracy (A) and coincidence index (B) of the genomic estimated breeding estimated value (GEBV) of seven yield- and sugar-related traits for fivefold cross-validation (fivefold CV) of seven genomic selection (GS) methods (Adopted from Islam et al., 2022)

Image caption: The fivefold CV was performed by randomly selecting four-fifths of the individuals for training and reaming a fifth as the validation population for the plant cane. The seven traits were Brix, fiber content (FC), pol, sucrose content (SC), stalk diameter (SD), stalk population (SP), and stalk weight (SW) (Adopted from Islam et al., 2022)

7.2 Challenges in translating GWAS findings to field applications

Despite the progress in GWAS, several challenges remain in translating these findings into practical applications in the field. One major hurdle is the complex polyploid genome of sugarcane, which complicates the identification of marker-trait associations (MTAs) and the subsequent validation of these markers in diverse populations (Barreto et al., 2019). The large extent of linkage disequilibrium (LD) in sugarcane also poses a challenge, as it can lead to the identification of false positives and obscure true associations (Yano et al., 2016). Moreover, the genetic diversity and population structure within sugarcane breeding populations can affect the reproducibility of GWAS results, making it difficult to apply these findings universally (Racedo et al., 2016). Another significant challenge is the integration of GWAS data with phenotypic data from field trials, which is essential for the effective implementation of marker-assisted selection (MAS) and genetic engineering (Fickett et al., 2019). Addressing these challenges requires a concerted effort to develop more robust and scalable GWAS methodologies that can account for the unique genetic architecture of sugarcane.

7.3 Future research directions to overcome current limitations

To overcome the current limitations in GWAS for sugarcane, future research should focus on several key areas. First, there is a need for larger and more diverse breeding populations to increase the statistical power of GWAS and improve the accuracy of MTA detection. The use of multi-environment trials and longitudinal studies can also help in identifying stable and consistent genetic markers across different growing conditions and crop cycles (Racedo et al., 2016; Fickett et al., 2019). Meanwhile, integrating multi-omics approaches, such as transcriptomics, proteomics, and metabolomics, with GWAS can provide a more comprehensive understanding of the genetic basis of complex traits and facilitate the identification of candidate genes (Liu et al., 2018; Cortes et al., 2021). Advances in genome-editing technologies, such as CRISPR/Cas9, offer exciting opportunities for validating GWAS findings and directly manipulating target genes to enhance desirable traits. Additionally, fostering collaborations between geneticists, breeders, and computational biologists will be crucial in translating GWAS discoveries into tangible benefits for sugarcane breeding programs.

By addressing these future prospects and challenges, the potential of GWAS to unlock the genetic basis of yield and agronomic traits in sugarcane can be fully realized, paving the way for the development of superior sugarcane varieties that meet the growing demands of the food and biofuel industries.

8 Concluding Remarks

Genome-wide association studies (GWAS) have emerged as a pivotal tool in sugarcane research, primarily due to the crop's complex polyploid genome and the significant economic importance of sugarcane for both sugar and biofuel industries. The ability of GWAS to identify marker-trait associations (MTAs) has revolutionized the understanding of the genetic basis of yield and agronomic traits in sugarcane. By leveraging GWAS, researchers can dissect the genetic architecture of complex traits, facilitating the identification of favorable alleles that can be introgressed into breeding programs to develop superior sugarcane cultivars.

The application of GWAS in sugarcane has yielded several important insights. Firstly, numerous genetic markers associated with critical traits such as high sucrose content, overall yield, disease resistance, and abiotic stress tolerance have been identified, providing valuable targets for breeding programs. Additionally, GWAS has shed light on the heritability of various agronomic traits, helping to clarify the genetic architecture underlying these traits and aiding in the selection of desirable phenotypes. The integration of GWAS findings into marker-assisted selection (MAS) and genomic selection (GS) has further advanced breeding strategies, enhancing the precision and efficiency of sugarcane breeding. These approaches enable breeders to make more informed decisions, leading to the development of high-performing varieties. Moreover, detailed analyses, such as the Brazilian Panel of Sugarcane Genotypes (BPSG) study, exemplify the practical applications of GWAS. The BPSG study highlighted significant genetic regions associated with yield and disease resistance, demonstrating the potential of GWAS to accelerate genetic improvements.

The future of sugarcane genetics and breeding looks promising with the continued application and advancement of GWAS. The integration of GWAS with other genomic tools, such as genomic prediction and marker-assisted selection (MAS), will accelerate the development of high-yielding and resilient sugarcane cultivars. Additionally, the incorporation of whole-genome sequencing and advanced bioinformatics approaches will enhance the resolution of GWAS, enabling the discovery of rare variants and epistatic interactions that contribute to complex traits.

The establishment of comprehensive genetic resource databases and the validation of identified MTAs in diverse populations will also further strengthen breeding programs. Collaborative efforts across research institutions and the adoption of cutting-edge technologies will be essential to meet the growing global demand for sugar and biofuels, ensuring sustainable sugarcane production in the face of environmental challenges.

In conclusion, GWAS has proven to be a transformative tool in sugarcane research, and it has unlocked new avenues for understanding the genetic basis of yield and agronomic traits in sugarcane, paving the way for innovative breeding strategies that will shape the future of sugarcane cultivation.

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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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