Molecular Plant Breeding 2024, Vol.15, No.4, 155-166
http://genbreedpublisher.com/index.php/mpb

Review Article Open Access

Advances in Sugarcane Genomics: Navigating Through Complex Polyploid Genomes

Lijun Zhang, Xiping Yang
College of Agricultural, Guangxi University, Nanning, 530005, Guangxi, China
Corresponding email: xipingyang@gxu.edu.cn
Molecular Plant Breeding, 2024, Vol.15, No.4 doi: 10.5376/mpb.2024.15.0016
Received: 01 Jun., 2024
Accepted: 03 Jul., 2024
Published: 14 Jul., 2024

Preferred citation for this article:
Zhang L.J., and Yang X.P., 2024, Advances in sugarcane genomics: navigating through complex polyploid genomes, Molecular Plant Breeding, 15(4): 155-166 (doi: 10.5376/mpb.2024.15.0016)

Abstract This study summarizes the latest advancements in sugarcane genomics, with a particular focus on the development of emerging genome sequencing and assembly technologies and their impact on deciphering complex genetic structures. It discusses the progress in high-throughput sequencing technologies and innovative assembly strategies, which have significantly enhanced the resolution and completeness of sugarcane genomes. The study reviews functional genomics studies based on these genomic advancements, emphasizing their role in uncovering the gene functions and regulatory mechanisms associated with key traits such as disease resistance, sucrose accumulation, and environmental stress adaptation. Furthermore, it explores the implications of these genetic insights on breeding strategies, particularly through marker-assisted selection and genomic selection, to accelerate the development of high-yield and stress-resistant sugarcane varieties. Despite the significant progress made, challenges remain in fully deciphering the sugarcane genome. This study highlights the potential of the dynamic field of sugarcane genomics and its possibilities for revolutionizing sugarcane breeding and cultivation practices.
Keywords Sugarcane (*Saccharum* spp.); Complex polyploid genomes; High-throughput sequencing; Genome assembly; Breeding strategies

1 Introduction

Sugarcane (*Saccharum* spp.) is a globally significant crop, primarily cultivated for sugar production and increasingly for bioenergy. It accounts for more than 70% of the world's sugar consumption and serves as a vital source of bio-based fuels, especially in tropical and subtropical regions (Setta et al., 2014; Garsmeur et al., 2018; Yadav et al., 2020). This crop significantly contributes to the economies of numerous countries, providing raw materials for both the food and energy sectors. The demand for sugarcane is driven by its applications in the production of sugar, ethanol, and various by-products which are integral to numerous industrial processes, including the production of bioplastics and pharmaceuticals (Garsmeur et al., 2018). This multifaceted utility underscores the global reliance on sugarcane, highlighting the necessity for ongoing improvements in crop yield and processing efficiency through advanced breeding and genetic research.

However, the genetic improvement of sugarcane is challenged by its highly complex genomic structure. Sugarcane is characterized by an extreme level of polyploidy and exhibits aneuploidy within its chromosomal set, making it one of the most genetically complex crops. Its genome is a mosaic of multiple copies of each chromosome, which are contributed by its progenitor species, *Saccharum officinarum* and *Saccharum spontaneum*, which add layers of genetic redundancy (Souza et al., 2011). This complexity not only complicates genetic mapping and trait association studies but also hinders the efficient manipulation of its genome for breeding purposes. Additionally, the high genetic diversity within *Saccharum* spp. presents both a challenge and an opportunity, providing a rich reservoir of genetic traits that can be harnessed to improve stress tolerance, disease resistance, and crop yield.

In light of these challenges, this study attempts to explore the recent advancements in genomic technologies that have significantly enhanced our understanding of the sugarcane genome. Over the past decade, breakthroughs in next-generation sequencing (NGS) and bioinformatics have begun to unravel the intricacies of the sugarcane genome, providing new tools for genomic selection and genetic modification. This study will synthesize findings

from the latest research efforts in sugarcane genomics, emphasizing developments in genome sequencing, functional genomics, and the emerging applications of these technologies in sugarcane breeding and agricultural practices. By examining these advancements, the study seeks to highlight the transformative potential of genomic science in overcoming the genetic complexities of sugarcane, paving the way for more targeted and efficient breeding strategies.

2 Complexity of the Sugarcane Genome

2.1 Genetic composition

Sugarcane (*Saccharum* spp.) is an interspecific hybrid primarily derived from *Saccharum officinarum* and *Saccharum spontaneum*. The genetic composition of sugarcane is notably complex due to these interspecific hybridizations, which have endowed sugarcane with genes from both progenitor species. *Saccharum officinarum*, known for its high sugar content, and *Saccharum spontaneum*, which contributes robustness and disease resistance, combine to create the genetically diverse and highly adaptable modern sugarcane varieties. This hybrid vigor or heterosis is pivotal for the enhanced productivity and resilience seen in current sugarcane cultivars (Grivet and Arruda, 2001; Sharma et al., 2018; Thirugnanasambandam et al., 2018).

2.2 Polyploidy and aneuploidy

The sugarcane genome is characterized by a high degree of polyploidy and aneuploidy, making it one of the most complex genomes in the plant kingdom (D'Hont et al., 1996; Grivet and Arruda, 2002). Polyploidy refers to the condition of having more than two complete sets of chromosomes, which in the case of sugarcane can be as high as 12x (12 sets). Aneuploidy, the presence of an abnormal number of chromosomes in a cell, further complicates genetic studies and breeding because it leads to variable gene expression levels and phenotypic diversity. These characteristics pose significant challenges in sequencing efforts and in the assembly of a coherent genome sequence, which are critical for advanced genetic research and breeding programs. The highly polyploid and aneuploid nature of the sugarcane genome results in a massive genome size, approximately 10 Gb, filled with repetitive sequences and multiple gene copies, which complicates genetic mapping and trait association studies (Hoang et al., 2017; Riaño-Pachón and Mattiello, 2017; Yang et al., 2018).

2.3 Implications of complexity

The complexity of the sugarcane genome has profound implications on breeding and genetic research. Many important traits for sugarcane improvement are polymorphic in the progenitor species and are influenced by gene dosage in hybrid breeding programs (Healey et al., 2024). Traditional breeding methods are often insufficient to address and utilize the full genetic potential of sugarcane due to the difficulty in tracking and selecting for specific traits governed by multiple genes with variable expression. However, the advent of genomic selection and marker-assisted breeding has begun to unlock the potential for more targeted and efficient breeding strategies. Despite these advances, the intricate nature of the genome still requires sophisticated, high-throughput genotyping technologies to accurately select desirable traits. Moreover, the polyploidy and aneuploidy of sugarcane necessitate innovative approaches in genetic transformation, gene editing, and biotechnological interventions to achieve desired improvements in crop yield, disease resistance, and stress tolerance. Understanding and manipulating such a complex genetic architecture remain a central challenge and focus of contemporary genomic research in sugarcane (Wang et al., 2017).

The genomic complexity of sugarcane not only defines the current limits of genetic research and breeding but also highlights the necessity for advanced genetic tools and more refined genomic resources to improve sugarcane cultivation and productivity effectively.

3 Recent Advancements in Sugarcane Genome Sequencing and Assembly

3.1 High-throughput sequencing technologies

The advent of NGS technologies has significantly impacted sugarcane genomics, a crop known for its complex polyploid genome. High-throughput sequencing (HTS) technologies, such as Illumina and PacBio, have enabled the generation of large volumes of sequencing data, facilitating the assembly of sugarcane genomes with greater accuracy and depth (Trujillo-Montenegro et al., 2021). Additionally, the integration of PacBio Iso-Seq with

RNA-Seq has provided a comprehensive view of the sugarcane transcriptome, capturing full-length transcript isoforms and enhancing gene model predictions (Hoang et al., 2017). These advancements underscore the critical role of HTS technologies in overcoming the challenges posed by the sugarcane genome's polyploidy and heterozygosity (Manimekalai et al., 2020).

3.2 Innovations in genome assembly

Innovative genome assembly methods, including long-read sequencing and hybrid approaches, have been pivotal in addressing the complexity of the sugarcane genome. Long-read sequencing technologies, such as PacBio and Oxford Nanopore, have been instrumental in generating more contiguous and complete genome assemblies (Lang et al., 2020). For example, the assembly of the SP80-3280 sugarcane variety using PacBio technology resulted in the identification of 373 869 putative genes and their regulatory regions, providing insights into gene family evolution and functional diversity (Souza et al., 2019). Shearman et al. (2022) used the PacBio RSII and chromatin conformation capture sequencing to sequence and assemble the genome of Khon Kaen 3, and genome annotation produced 242 406 genes from 30 927 orthogroups. Hybrid assembly strategies, combining long-read and short-read sequencing data, have also proven effective. The assembly of 19 Mb of the sugarcane genome using a hybrid approach with Illumina and PacBio reads demonstrated high collinearity with the sorghum genome, highlighting the utility of hybrid methods in constructing reference scaffold maps (Okura et al., 2016). These innovations are crucial for advancing our understanding of the sugarcane genome and improving breeding programs (Mikheenko et al., 2018).

3.3 Published genomic resources

The current state of sugarcane genomic resources includes several reference sequences and databases that serve as valuable tools for researchers. A notable example is the BAC-based monoploid reference sequence for sugarcane, which was constructed by exploiting colinearity with sorghum and sequencing a minimum tiling path of 4 660 BAC clones, resulting in a SNP-based sugarcane genetic map (Figure 1) (Garsmeur et al., 2018). This comparative genomic analysis by Garsmeur et al. (2018) highlights the genetic complexity and polyploidy of sugarcane, revealing conserved synteny and evolutionary links with sorghum. These insights are crucial for understanding the genetic architecture of sugarcane, aiding in the identification of functional genes and enhancing breeding programs through marker-assisted selection. By leveraging syntenic relationships, it is possible to identify and transfer desirable traits such as disease resistance and yield improvement from sorghum to sugarcane.

Additionally, two tetraploid genomes of *S. spontaneum* clones AP85-441 and Np-X have been published, provides a foundational resource for understanding the genetic architecture of sugarcane and its progenitors (Zhang et al., 2018; Zhang et al., 2022). The representative genomic assembly of the SP80-3280 genome sequence reveals differences in promoter regions associated with distinct gene expression patterns and transposable elements (TEs), contributing to fine tuning of the sugarcane genome (Souza et al., 2019). Recent publications of the genomes of the commercial variety KK3 and the modern hybrid sugarcane ZZ1 provide a solid foundation for future research in sugarcane genomics and molecular breeding, paving the way for advancements in these fields (Shearman et al., 2022; Bao et al., 2024).

These genomic resources, along with extensive collections of expressed sequence tags (ESTs) and bacterial artificial chromosome (BAC) libraries, have opened new avenues for functional genomic analyses and the development of molecular markers for breeding (Thirugnanasambandam et al., 2018). The availability of these comprehensive genomic datasets is instrumental in facilitating comparative genomics, gene discovery, and the improvement of sugarcane cultivars.

4 Functional Genomics in Sugarcane

4.1 Gene expression profiling

Gene expression profiling through transcriptome analysis has been instrumental in linking specific genes to phenotypic traits in sugarcane. Singh and Singh (2015) discussed how transcriptome resources, encompassing both specific and overlapping gene expression patterns, are used to elucidate functions related to important traits such as sucrose accumulation and stress responses. By comparing the transcriptomic expression differences

between the SCMV-resistant genotype B-48 and the susceptible genotype Badila following infection, Akbar et al. (2020) demonstrated that the B-48 genotype enhances its resistance to SCMV infection by upregulating antioxidant defense systems and activating key transcription factors. This study provides important molecular mechanisms and potential targets for disease resistance breeding and management in sugarcane. Moreover, Ma et al. (2004) provided a foundational set of sugarcane expressed sequence tags (ESTs), facilitating the functional characterization of genes potentially linked with economic traits. These transcriptomic analyses have enabled a better understanding of the sugarcane genome, providing a pathway to discover gene functions and their regulatory mechanisms.

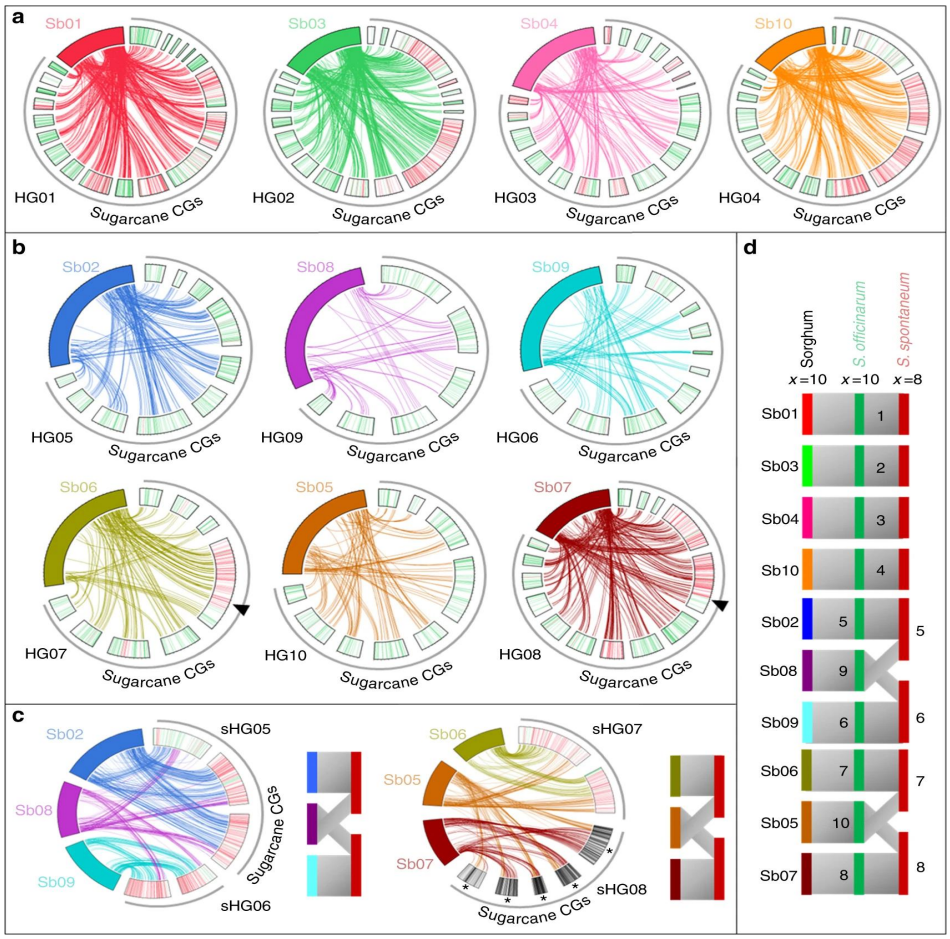

Figure 1 SNP-based sugarcane genetic map with putative origin of co-segregation groups and comparison with sorghum chromosomes (Adopted from Garsmeur et al., 2018)

Image caption: The 132 CGs of cultivar R570 are represented with SNP markers assigned to *S. officinarum* or *S. spontaneum* indicated by green and red bars, respectively. Circos represents orthologous relationships between sugarcane CGs and sorghum chromosomes (Sb1–Sb10) based on the alignment, for each CG, of a majority of the markers on one (a, b) or two (c) sorghum chromosomes (color links) (Adopted from Garsmeur et al., 2018)

4.2 Gene editing and CRISPR

Recent developments in CRISPR/Cas genome editing have opened new avenues for precise genetic modifications in sugarcane, potentially overcoming some of the limitations posed by its complex genome. The versatility of CRISPR technology allows for targeted gene modifications that can lead to enhanced trait selection and faster breeding cycles (Krishna et al., 2023). Kang (2019) highlighted the development of a web-application designed to aid researchers in finding guide RNA binding sites for CRISPR-based editing in the sugarcane genome, facilitating the precise engineering of desired traits. Recent studies have employed CRISPR/Cas9 technology to generate site-specific mutations in sugarcane. For instance, Eid et al. (2021) utilized CRISPR/Cas9 to edit multiple alleles of the magnesium chelatase subunit I (MgCh), facilitating the production of easily targetable

phenotypes in sugarcane. Similarly, Oz et al. (2021) applied CRISPR/Cas9-mediated multi-allelic targeted editing to convert inferior alleles into superior ones through targeted nucleotide replacement, thereby successfully conferring herbicide tolerance to sugarcane. These advancements contribute significantly to sugarcane improvement and present an efficient, replicable method for enhancing crops via targeted nucleotide substitutions. This technology not only enhances the efficiency of genetic modifications but also reduces the time required to develop cultivars with optimal traits.

4.3 Integrative genomics approaches

Integrative genomics, which combines genomic, transcriptomic, and metabolomic data, provides a comprehensive approach to understanding the biological functions and interactions within sugarcane. This holistic view is essential for elucidating the complex metabolic pathways and regulatory networks involved. Souza et al. (2019) demonstrated that the integration of these diverse data types could resolve the putative homo(eo)logs in the sugarcane genome, which are crucial for trait development and adaptation. Furthermore, the gene space assembly of SP80-3280 by Souza et al. (2019) provides insights into the regulatory elements involved in sucrose synthesis, showcasing the power of integrative approaches in functional genomics. By combining data from various genomic platforms, researchers can achieve a more detailed and accurate picture of the genetic underpinnings of important agronomic traits in sugarcane.

5 Genetics and Gene Mapping in Sugarcane

5.1 Genetic linkage maps

Genetic linkage maps are critical tools in understanding the genomic organization of complex polyploid organisms like sugarcane, which has a highly complicated genetic structure due to its autopolyploid nature and interspecific hybrid origins. Recent advances have significantly improved the resolution and utility of these maps for trait association studies. For instance, a comprehensive linkage map using AFLP, SSR, and TRAP markers was developed, revealing insights into the homologous chromosome groupings and their association with phenotypic traits in sugarcane cultivars (Andru et al., 2011). With the rapid development of next-generation sequencing technology, the comprehensive linkage genetic map of sugarcane developed using single nucleotide polymorphism (SNP) markers is being increasingly applied (Yadav et al., 2021). These maps facilitate the identification of linkage disequilibrium patterns and provide a foundation for marker-assisted selection and breeding strategies.

5.2 QTL mapping

Quantitative Trait Loci (QTL) mapping is a powerful genetic tool used to associate specific genomic regions with phenotypic traits. This method is particularly effective in sugarcane due to its ability to handle the complexities arising from its genome structure. For instance, multiple QTLs influencing sugar yield and related traits have been identified, demonstrating significant associations that are invaluable for breeding programs aimed at enhancing sugar production (Ming et al., 2002). Costa et al. (2016) utilized a comprehensive interval mapping approach, employing SNP markers across various ploidy levels, to develop a genetic linkage map of sugarcane that includes AFLP and SSR markers. They also identified QTLs affecting critical agronomic traits in sugarcane, thereby providing genetic information for molecular assisted selection and breeding in sugarcane. In another study, the construction of a genetic linkage map and QTL analysis identified quantitative trait loci (QTLs) associated with resistance to red rot disease in sugarcane and identified candidate genes related to plant defense responses (Banerjee et al., 2023). In recent years, many researchers have utilized QTL mapping to identify QTLs and associated candidate genes related to traits such as sugarcane yield, sugar and disease resistance (Singh et al., 2013; Ukoskit et al., 2019; Lu et al., 2023). The mapping of these QTLs helps in understanding the genetic basis of complex traits and assists in the development of sugarcane varieties with optimized traits.

5.3 Marker-assisted selection

Marker-Assisted Selection (MAS) leverages molecular markers linked to desirable traits to accelerate the breeding process. In sugarcane, MAS has been enhanced by the development and validation of markers such as EST-SSRs, which are associated with sugar-related traits. The identification and use of these markers allow for more precise

selection of phenotypes with favorable genetic profiles, significantly improving the efficiency of breeding programs (Ukoskit et al., 2019). Moreover, the integration of functional markers into linkage maps enables breeders to directly target genes involved in key metabolic pathways, thereby streamlining the development of superior sugarcane varieties.

6 Implications for Sugarcane Breeding and Agriculture

6.1 Breeding for disease resistance

Recent advancements in sugarcane genomics have provided significant insights into disease resistance, which are crucial for breeding programs. The identification of the rust resistance gene (*Bru1*) through map-based cloning techniques exemplifies the potential of genomic strategies to overcome the challenges posed by the highly polyploid nature of the sugarcane genome (Islam et al., 2021). Additionally, genomic selection has shown promise in predicting genetic values for disease resistance traits, with studies demonstrating correlations between observed and predicted values, thus validating the feasibility of genomic selection in sugarcane breeding (Islam et al., 2021). Lu et al. (2023) investigated the symptoms of sugarcane mosaic disease (SMD) in offspring through natural infection and artificial infection with a mixture of sugarcane mosaic virus (SCMV) and sorghum mosaic virus (SrMV) (Figure 2). 110 pathogen response genes and 69 transcription factors were identified in the QTL interval, and 9 key genes were predicted. Genome-wide association studies (GWAS) revealed the dominant role of alleles from the wild species *Saccharum spontaneum* in conferring resistance to sugarcane orange rust (SOR) in modern sugarcane varieties. Six quantitative trait loci (QTLs) associated with this resistance were identified, which can effectively predict disease resistance, thereby paving the way for efficient marker-assisted breeding strategies (Dijoux et al., 2024). These genetic insights enable breeders to develop disease-resistant cultivars more efficiently, ensuring sustainable crop production.

6.2 Improving yield and sugar content

Genetic discoveries aimed at improving yield and sugar content have been crucial in enhancing sugarcane productivity. GWAS have identified multiple marker-trait associations (MTAs) for key yield components such as stalk height, stalk number, and cane yield, which can be utilized in marker-assisted selection to improve these traits (Barreto et al., 2019; Meena et al., 2022; Wang et al., 2023; Saavedra-Díaz et al., 2024). Furthermore, advancements in genomic selection techniques, such as genomic estimated breeding values (GEBVs), have significantly improved the accuracy of predicting complex traits like tonnes of cane per hectare (TCH) and commercial cane sugar (CCS), potentially doubling the rate of genetic gain in breeding programs (Hayes et al., 2021; Satpathy et al., 2022). Genetic engineering and genome editing technologies, such as CRISPR/Cas9, have opened new avenues for directly manipulating genes associated with yield and sugar content (Khan et al., 2019). These genomic tools facilitate the accumulation of favorable alleles, resulting in increased yield and sucrose accumulation in sugarcane cultivars.

6.3 Adaptation to environmental stresses

The adaptation of sugarcane to abiotic stresses, such as drought and heat is critical for maintaining productivity in the face of climate change. Meena et al. (2022) have highlighted the role of next-generation sequencing and genome-editing technologies in identifying and harnessing genes associated with stress tolerance. For instance, the establishment of a monoploid reference sequence has provided a comprehensive understanding of the sugarcane genome, enabling the identification of genes involved in stress responses (Garsmeur et al., 2018). Additionally, the integration of functional genomics and gene expression profiling has resulted in the delineation of gene networks that contribute to stress tolerance, paving the way for the development of stress-resilient sugarcane varieties. These advancements ensure that sugarcane can thrive under adverse environmental conditions, securing its role as a major crop for sugar and bioenergy production.

By leveraging these genetic insights and biotechnological tools, sugarcane breeding programs can achieve significant improvements in disease resistance, yield, sugar content, and environmental stress adaptation, ultimately enhancing the sustainability and productivity of sugarcane agriculture.

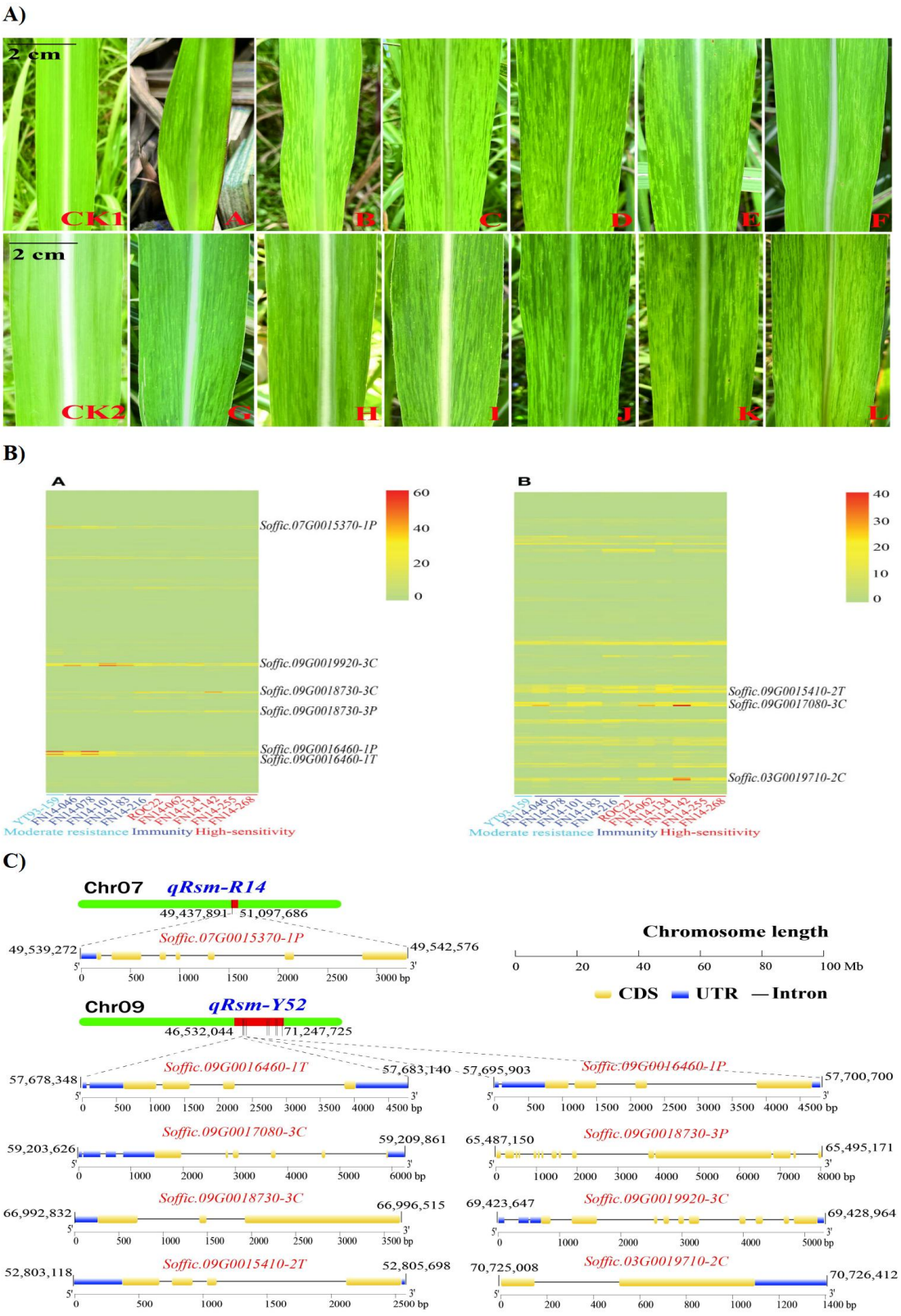

Figure 2 The SMD symptoms of a highly susceptible progeny and the expression of SMD resistance-related candidate genes (Adopted from Lu et al., 2023)

Image caption: A) SMD symptoms of a highly susceptible progeny (FN14-255) observed in different months CK1: disease free control (January); CK2: disease free control (December); (A–L): January-December, respectively; B) The gene expression levels of 110 pathogen-responsive genes and 69 transcription factors; C) The genomic positions, conserved domains and gene structures of the nine predicted genes (Adopted from Lu et al., 2023)

7 Challenges and Future Directions

7.1 Overcoming genetic complexity

Sugarcane exhibits polyploid and aneuploid genetic complexity, which poses significant challenges to genome assembly and genetic manipulation. However, recent advances in sequencing technologies have begun to alleviate some of these difficulties. For example, the use of high-throughput sequencing technologies, including long-read sequencing approaches, has enhanced the resolution of genetic information in sugarcane (Garsmeur et al., 2018; Souza et al., 2019). These methodologies enable researchers to navigate through large and repetitive genomic regions more effectively, which are prevalent in sugarcane due to its hybrid origin from *Saccharum officinarum* and *Saccharum spontaneum*. Future strategies must focus on improving the efficiency of these technologies and integrating data from different genomic platforms to build a more comprehensive and detailed structure of the sugarcane genome.

7.2 Enhancing genomic resources

Despite the advancements in sequencing and assembling the sugarcane genome, there is a crucial need for more comprehensive genomic databases and tools that can manage and analyze the vast amounts of data generated. The development of databases such as SUCEST, which facilitates access to expressed sequence tags (ESTs), represents a significant step forward (Casu et al., 2005). However, enhancing these resources to include more functional annotations and integration with phenotypic data could dramatically improve the utility of genomic information in breeding programs. Furthermore, there is a demand for tools that can effectively address polyploidy and heterozygosity in genetic analyses are needed to fully exploit the sugarcane genome for crop improvement.

7.3 Future of genomic selection

The future of genomic selection in sugarcane looks promising with the potential to revolutionize breeding strategies for this vital crop. Genomic selection, which uses genome-wide genetic markers to predict phenotypic performance, is likely to become a pivotal component of sugarcane breeding programs. This approach can be particularly effective in sugarcane, where traditional breeding is hampered by the crop's complex genetics and long breeding cycles (Souza et al., 2011). Innovations such as SNP genotyping and gene editing technologies are expected to improve the accuracy and efficiency of genomic selection, enabling the manipulation of multiple traits simultaneously, such as yield, sucrose content, and stress resistance (Manimekalai et al., 2020). As these technologies mature, the integration of genomic selection with high-throughput phenotyping and environmental modeling could lead to a new era of precision breeding in sugarcane, specifically tailored to specific agro-environmental conditions.

8 Concluding Remarks

Over the past decade, the field of sugarcane genomics has seen substantial advancements, driven by rapid technological innovations in sequencing and computational biology. The development and application of next-generation sequencing technologies have allowed researchers to delve into the highly complex and polyploid genome of sugarcane with unprecedented detail and accuracy. For example, the construction of a BAC-based monoploid reference sequence for sugarcane significantly enhances the resolution of genetic analysis in this crop. The integration of long-read sequencing platforms has facilitated the assembly of large genomic regions, which are particularly challenging in polyploid genomes like that of sugarcane. Additionally, functional genomics has progressed substantially, with extensive transcriptome analyses revealing the expression patterns and potential regulatory mechanisms of thousands of genes associated with traits such as sucrose accumulation, stress responses, and biomass production.

The insights gained from these genomic studies have profoundly transformed sugarcane breeding programs. The ability to identify and manipulate genes related to yield, sucrose content, and stress resistance directly impacts the efficiency of breeding strategies, reducing the time and resources required to develop new cultivars. Marker-assisted selection has become more targeted, with genetic markers linked to desirable traits speeding up the selection process. Moreover, the advent of genomic selection in sugarcane offers the potential to revolutionize breeding by predicting the performance of genotypes based on genomic data alone, a shift that is expected to enhance the genetic gains per unit of time significantly.

Despite these advances, significant challenges remain, and there are several key areas where future research is critically needed. First, the full assembly of the polyploid sugarcane genome remains incomplete. Continued efforts to achieve a more complete and annotated reference genome will be crucial, as this will provide the necessary foundation for all genetic and genomic studies in sugarcane. Additionally, the functional validation of candidate genes identified through genomic studies is still in its infancy. Advanced gene-editing technologies such as CRISPR/Cas systems need to be adapted and optimized for sugarcane to enable precise manipulation of genetic traits. Meanwhile, there is a need to better integrate multi-omics data (genomics, transcriptomics, proteomics, and metabolomics) to gain a holistic understanding of the biological processes underlying trait development in sugarcane. This integration will not only help in elucidating complex traits such as stress resistance and photosynthetic efficiency but also in harnessing these traits for the development of superior sugarcane varieties. By addressing these research needs, the sugarcane research community can continue to make significant contributions to global food security and sustainable bioenergy production.

Funding

This work was financially supported by the National Key Research and Development Program of China (2022YFD2301100), the Guangxi Natural Science Foundation (GK AA22117002), and the 'One Hundred Person' Project of Guangxi Province, Science.

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.

References

Akbar S., Wei Y., Yuan Y., Khan M.T., Qin L., Powell C.A., Chen B., and Zhang M., 2020, Gene expression profiling of reactive oxygen species (ROS) and antioxidant defense system following sugarcane mosaic virus (SCMV) infection, BMC Plant Biol., 20: 532.
https://doi.org/10.1186/s12870-020-02737-1
PMid:33228528 PMCid:PMC7685628

Andru S., Pan Y., Thongthawee S., Burner D., and Kimbeng C., 2011, Genetic analysis of the sugarcane (*Saccharum* spp.) cultivar 'LCP 85-384'. I. Linkage mapping using AFLP, SSR, and TRAP markers, Theoretical and Applied Genetics, 123: 77-93.
https://doi.org/10.1007/s00122-011-1568-x
PMid:21472411

Banerjee N., Khan M.S., Swapna M., Yadav S., Tiwari G.J., Jena S.N., Patel J.D., Manimekalai R., Kumar S., Dattamajuder S.K., Kapur R., Koebernick J.C., and Singh R.K., 2023, QTL mapping and identification of candidate genes linked to red rot resistance in sugarcane, 3 Biotech, 13: 82.
https://doi.org/10.1007/s13205-023-03481-7
PMid:36778768 PMCid:PMC9911584

Bao Y., Zhang Q., Huang J., Zhang S., Yao W., Yu Z., Deng Z., Yu J., Kong W., Yu X., Lu S., Wang Y., Li R., Song Y., Zou C., Xu Y., Liu Z., Yu F., Song J., Huang Y., Zhang J., Wang H., Chen B., Zhang X., and Zhang M., 2024, A chromosomal-scale genome assembly of modern cultivated hybrid sugarcane provides insights into origination and evolution, Nature Communications, 15: 3041.
https://doi.org/10.1038/s41467-024-47390-6
PMid:38589412 PMCid:PMC11001919

Barreto F., Rosa J., Balsalobre T., Pastina M., Silva R., Hoffmann H., Souza A., Garcia A., and Carneiro M., 2019, A genome-wide association study identified loci for yield component traits in sugarcane (*Saccharum* spp.), PLoS One, 14(7): e0219843.
https://doi.org/10.1371/journal.pone.0219843
PMid:31318931 PMCid:PMC6638961

Casu R., Manners J., Bonnett G., Jackson P., McIntyre C., Dunne R., Chapman S., Rae A., and Grof C., 2005, Genomics approaches for the identification of genes determining important traits in sugarcane, Field Crops Research, 92: 137-147.
https://doi.org/10.1016/j.fcr.2005.01.029

Costa E.A., Anoni C.O., Mancini M.C., Santos F.R.C., Marconi T.G., Gazaffi R., Pastina M.M., Perecin D., Mollinari M., Xavier M.A., Pinto L.R., Souza A.P., and Garcia A.A.F., 2016, QTL mapping including codominant SNP markers with ploidy level information in a sugarcane progeny, Euphytica, 211: 1-16.
https://doi.org/10.1007/s10681-016-1746-7

D'Hont A., Grivet L., Feldmann P., Rao S., Berding N., and Glaszmann J.C., 1996, Characterisation of the double genome structure of modern sugarcane cultivars (*Saccharum* spp.) by molecular cytogenetics, Molecular and General Genetics, 250: 405-413.
https://doi.org/10.1007/BF02174028
PMid:8602157

Dijoux J., Rio S., Hervouet C., Garsmeur O., Barau L., Dumont T., Rott P., D'Hont A., and Hoarau J.Y., 2024, Unveiling the predominance of *Saccharum spontaneum* alleles for resistance to orange rust in sugarcane using genome-wide association, Theor. Appl. Genet., 137: 81.
https://doi.org/10.1007/s00122-024-04583-3
PMid:38478168

Eid A., Mohan C., Sanchez S., Wang D., and Altpeter F., 2021, Targeted mutagenesis of magnesium chelatase with CRISPR/Cas9 provides a rapidly scorable phenotype in highly polyploid sugarcane, Front. Genome Ed., 3: 654996.
https://doi.org/10.3389/fgeed.2021.654996

Garsmeur O., Droc G., Antonise R., Grimwood J., Potier B., Aitken K., Jenkins J., Martin G., Charron C., Hervouet C., Costet L., Yahiaoui N., Healey A., Sims D., Cherukuri Y., Sreedasyam A., Kilian A., Chan A., Sluys M., Swaminathan K., Town C., Bergès H., Simmons B., Glaszmann J., Vossen E., Henry R., Schmutz J., and D'Hont A., 2018, A mosaic monoploid reference sequence for the highly complex genome of sugarcane, Nature Communications, 9: 2638.
https://doi.org/10.1038/s41467-018-05051-5
PMid:29980662 PMCid:PMC6035169

Grivet L., and Arruda P., 2002, Sugarcane genomics: depicting the complex genome of an important tropical crop, Current Opinion in Plant Biology, 5(2): 122-127.
https://doi.org/10.1016/S1369-5266(02)00234-0
PMid:11856607

Hayes B., Wei X., Joyce P., Atkin F., Deomano E., Yue J., Nguyen L., Ross E., Cavallaro T., Aitken K., and Voss-Fels K., 2021, Accuracy of genomic prediction of complex traits in sugarcane, Theoretical and Applied Genetics, 134: 1455-1462.
https://doi.org/10.1007/s00122-021-03782-6
PMid:33590303

Healey A.L., Garsmeur O., Lovell J.T., Shengquiang S., Sreedasyam A., Jenkins J., Plott C.B., Piperidis N., Pompidor N., Llaca V., Metcalfe C.J., Doležel J., Cápal P., Carlson J.W., Hoarau J.Y., Hervouet C., Zini C., Dievart A., Lipzen A., Williams M., Boston L.B., Webber J., Keymanesh K., Tejomurthula S., Rajasekar S., Suchecki R., Furtado A., May G., Parakkal P., Simmons B.A., Barry K., Henry R.J., Grimwood J., Aitken K.S., Schmutz J., and D'Hont A., 2024, The complex polyploid genome architecture of sugarcane, Nature, 628: 804-810.
https://doi.org/10.1038/s41586-024-07231-4
PMid:38538783 PMCid:PMC11041754

Hoang N., Furtado A., Mason P., Marquardt A., Kasirajan L., Thirugnanasambandam P., Botha F., and Henry R., 2017, A survey of the complex transcriptome from the highly polyploid sugarcane genome using full-length isoform sequencing and de novo assembly from short read sequencing, BMC Genomics, 18: 395.
https://doi.org/10.1186/s12864-017-3757-8
PMid:28532419 PMCid:PMC5440902

Islam M., McCord P., Olatoye M., Qin L., Sood S., Lipka A., and Todd J., 2021, Experimental evaluation of genomic selection prediction for rust resistance in sugarcane, The Plant Genome, 14(3): e20148.
https://doi.org/10.1002/tpg2.20148
PMid:34510803

Kang Y.J., 2019, Sugarcane ORF finder: the web-application for mining genes from sugarcane genome, Plant Biotechnology Reports, 13: 553-558.
https://doi.org/10.1007/s11816-019-00574-9

Khan M., Khan I., and Yasmeen S., 2019, Genetically modified sugarcane for biofuels production: status and perspectives of conventional transgenic approaches, RNA interference, and genome editing for improving sugarcane for biofuels, In: Khan M., and Khan I. (eds.), Sugarcane biofuels, Springer, Cham, Switzerland, pp.67-96.
https://doi.org/10.1007/978-3-030-18597-8_4

Krishna S.S., Viswanathan R., Valarmathi R., Lakshmi K., and Appunu C., 2023, CRISPR/Cas-mediated genome editing approach for improving virus resistance in sugarcane, Sugar Tech., 25: 735-750.
https://doi.org/10.1007/s12355-023-01252-5

Lang D., Zhang S., Ren P., Liang F., Sun Z., Meng G., Tan Y., Li X., Lai Q., Han L., Wang D., Hu F., Wang W., and Liu S., 2020, Comparison of the two up-to-date sequencing technologies for genome assembly: HiFi reads of Pacific Biosciences Sequel II system and ultralong reads of Oxford Nanopore, GigaScience, 9(12): giaa123.
https://doi.org/10.1093/gigascience/giaa123
PMid:33319909 PMCid:PMC7736813

Lu G., Wang Z., Pan Y., Wu Q., Cheng W., Xu F., Dai S., Li B., Que Y., and Xu L., 2023, Identification of QTLs and critical genes related to sugarcane mosaic disease resistance, Frontiers in Plant Science, 14: 1107314.
https://doi.org/10.3389/fpls.2023.1107314
PMid:36818882 PMCid:PMC9932707

Lu S., Zhang H., Guo F., Yang Y., Shen X., and Chen B., 2022, SsUbc2 a determinant of pathogenicity functions as a key coordinator controlling global transcriptomic reprogramming during mating in sugarcane smut fungus, Frontiers in Microbiology 13: 954767.
https://doi.org/10.3389/fmicb.2022.954767
PMid:36204604 PMCid:PMC9530204

Ma H., Schulze S.R., Lee S., Yang M., Mirkov T.E., Irvine J.E., Moore P.H., and Paterson A.H., 2004, An EST survey of the sugarcane transcriptome, Theoretical and Applied Genetics, 108: 851-863.
https://doi.org/10.1007/s00122-003-1510-y
PMid:14647901

Manimekalai R., Suresh G., Kurup H., Athiappan S., and Kandalam M., 2020, Role of NGS and SNP genotyping methods in sugarcane improvement programs, Critical Reviews in Biotechnology, 40: 865-880.
https://doi.org/10.1080/07388551.2020.1765730
PMid:32508157

Meena M., Appunu C., Kumar R., Manimekalai R., Vasantha S., Krishnappa G., Kumar R., Pandey S., and Hemaprabha G., 2022, Recent advances in sugarcane genomics, physiology, and phenomics for superior agronomic traits, Frontiers in Genetics, 13: 854936.
https://doi.org/10.3389/fgene.2022.854936
PMid:35991570 PMCid:PMC9382102

Mikheenko A., Prjibelski A., Saveliev V., Antipov D., and Gurevich A., 2018, Versatile genome assembly evaluation with QUAST-LG, Bioinformatics, 34: i142-i150.
https://doi.org/10.1093/bioinformatics/bty266
PMid:29949969 PMCid:PMC6022658

Ming R., Wang Y., Draye X., Moore P., Irvine J., and Paterson A., 2002, Molecular dissection of complex traits in autopolyploids: mapping QTLs affecting sugar yield and related traits in sugarcane, Theoretical and Applied Genetics, 105: 332-345.
https://doi.org/10.1007/s00122-001-0861-5
PMid:12582536

Okura V., Souza R., Tada S., and Arruda P., 2016, BAC-Pool sequencing and assembly of 19 Mb of the complex sugarcane genome, Frontiers in Plant Science, 7: 342.
https://doi.org/10.3389/fpls.2016.00342
PMid:27047520 PMCid:PMC4804495

Oz M.T., Altpeter A., Karan R., Merotto A., and Altpeter F., 2021, CRISPR/Cas9-mediated multi-allelic gene targeting in sugarcane confers herbicide tolerance, Front Genome Ed., 3: 673566.
https://doi.org/10.3389/fgeed.2021.673566
PMid:34713261 PMCid:PMC8525412

Riaño-Pachón D.M., and Mattiello L., 2017, Draft genome sequencing of the sugarcane hybrid SP80-3280, F1000Research, 6: 861.
https://doi.org/10.12688/f1000research.11859.2
PMid:28713559 PMCid:PMC5499785

Saavedra-Díaz C., Trujillo-Montenegro J.H., Jaimes H.A., Londoño A., Villareal F.A.S., López L.O., Valens C.A.V., López-Gerena J., Riascos J.J., Quevedo Y.M., and Aguilar F.S., 2024, Genetic association analysis in sugarcane (*Saccharum* spp.) for sucrose accumulation in humid environments in Colombia, BMC Plant Biol., 24: 570.
https://doi.org/10.1186/s12870-024-05233-y
PMid:38886648 PMCid:PMC11184777

Satpathy S., Shahi D., Blanchard B., Pontif M., Gravois K., Kimbeng C., Hale A., Todd J., Rao A., and Baisakh N., 2022, Evaluation of models for utilization in genomic prediction of agronomic traits in the Louisiana sugarcane breeding program, Agriculture, 12(9): 1330.
https://doi.org/10.3390/agriculture12091330

Setta N., Monteiro-Vitorello C., Metcalfe C., Cruz G., Bem L., Vicentini R., Nogueira F., Campos R., Nunes S., Turrini P., Vieira A., Cruz E., Corrêa T., Hotta C., Varani A., Vautrin S., Trindade A., Vilela M., Lembke C., Sato P., Andrade R., Nishiyama M., Cardoso-Silva C., Scortecci K., Garcia A., Carneiro M., Kim C., Paterson A., Bergès H., D'Hont A., Souza A., Souza G., Vincentz M., Kitajima J., and Sluys M., 2014, Building the sugarcane genome for biotechnology and identifying evolutionary trends, BMC Genomics, 15: 540.
https://doi.org/10.1186/1471-2164-15-540
PMid:24984568 PMCid:PMC4122759

Sharma A., Song J., Lin Q., Singh R., Ramos N., Wang K., Zhang J., Ming R., and Yu Q., 2018, Comparative analysis of homologous sequences of *Saccharum officinarum* and *Saccharum spontaneum* reveals independent polyploidization events, Frontiers in Plant Science, 9: 1414.
https://doi.org/10.3389/fpls.2018.01414
PMid:30319674 PMCid:PMC6167920

Shearman J.R., Pootakham W., Sonthirod C., Naktang C., Yoocha T., Sangsrakru D., Jomchai N., Tongsima S., Piriyapongsa J., Ngamphiw C., Wanasen N., Ukoskit K., Punpee P., Klomsa-ard P., Sriroth K., Zhang J., Zhang X., Ming R., Tragoonrung S., and Tangphatsornruang S., 2022, A draft chromosome-scale genome assembly of a commercial sugarcane, Scientific Reports, 12: 20474.
https://doi.org/10.1038/s41598-022-24823-0
PMid:36443360 PMCid:PMC9705387

Singh R.K., and Singh S.P., 2015, Prospects of functional genomics in sugarcane, In: Al-Khayri J., Jain S., and Johnson D. (eds.), Advances in plant breeding strategies: breeding, biotechnology and molecular tools, Springer, Cham, Switzerland, pp.489-511.

Singh R.K., Singh S.P., Tiwari D.K., Srivastava S., Singh S.B., Sharma M.L., Singh R., Mohapatra T., and Singh N.K., 2013, Genetic mapping and QTL analysis for sugar yield-related traits in sugarcane, Euphytica, 191: 333-353.

Souza G., Bergès H., Bocs S., Casu R., D'Hont A., Ferreira J., Henry R., Ming R., Potier B., Sluys M., Vincentz M., and Paterson A., 2011, The sugarcane genome challenge: strategies for sequencing a highly complex genome, Tropical Plant Biology, 4: 145-156.

Souza G.M., Van Sluys M.A., Lembke C.G., Lee H., Margarido G.R.A., Hotta C.T., Gaiarsa J.W., Diniz A.L., Oliveira M.M., Ferreira S.S., Nishiyama M.Y., Ten-Caten F., Ragagnin G.T., Andrade P.M., de Souza R.F., Nicastro G.G., Pandya R., Kim C., Guo H., Durham A.M., and Heckerman D., 2019, Assembly of the 373k gene space of the polyploid sugarcane genome reveals reservoirs of functional diversity in the world's leading biomass crop, GigaScience, 8(12): giz129.
https://doi.org/10.1093/gigascience/giz129

Thirugnanasambandam P., Hoang N., and Henry R., 2018, The challenge of analyzing the sugarcane genome, Frontiers in Plant Science, 9: 616.
https://doi.org/10.3389/fpls.2018.00616
PMid:29868072 PMCid:PMC5961476

Trujillo-Montenegro J., Cubillos M., Loaiza C., Quintero M., Espitia-Navarro H., Villareal F., Valens C., Barrios A., Vega J., Duitama J., and Riascos J., 2021, Unraveling the genome of a high yielding Colombian sugarcane hybrid, Frontiers in Plant Science, 12: 694859.
https://doi.org/10.3389/fpls.2021.694859
PMid:34484261 PMCid:PMC8414525

Ukoskit K., Posudsavang G., Pongsiripat N., Chatwachirawong P., Klomsa-ard P., Poomipant P., and Tragoonrung S., 2019, Detection and validation of EST-SSR markers associated with sugar-related traits in sugarcane using linkage and association mapping, Genomics, 111(1): 1-9.

Wang J., Zhao T., Yang B., Xiong G., and Zhang S., 2017, Polyploidization genetic mechanism of sugarcane genome, Asian Agricultural Research, 9(8): 84-87.

Wang L., Yeo S., Lee M., Endah S., Alhuda N.A., and Yeu G.H., 2023, Combination of GWAS and FST-based approaches identified loci associated with economic traits in sugarcane, Molecular Genetics and Genomics, 298: 1107-1120.
https://doi.org/10.1007/s00438-023-02040-2
PMid:37289230

Yadav S., Jackson P., Wei X., Ross E., Aitken K., Deomano E., Atkin F., Hayes B., and Voss-Fels K., 2020, Accelerating genetic gain in sugarcane breeding using genomic selection, Agronomy, 10(4): 585.

Yadav S., Ross E.M., Aitken K.S., Hickey L.T., Powell O., Wei X., Voss-Fels K.P., and Hayes B.J., 2021, A linkage disequilibrium-based approach to position unmapped SNPs in crop species, BMC Genomics, 22: 773.
https://doi.org/10.1186/s12864-021-08116-w
PMid:34715779 PMCid:PMC8555328

Yang X., Song J., Todd J., Peng Z., Paudel D., Luo Z., Ma X., You Q., Hanson E., Zhao Z., Zhao Y., Zhang J., Ming R., and Wang J., 2018, Target enrichment sequencing of 307 germplasm accessions identified ancestry of ancient and modern hybrids and signatures of adaptation and selection in sugarcane (*Saccharum* spp.), a 'sweet' crop with 'bitter' genomes, Plant Biotechnology Journal, 17: 488-498.
https://doi.org/10.1111/pbi.12992
PMid:30051590 PMCid:PMC6335080

Zhang J., Zhang X., Tang H., Zhang Q., Hua X., Ma X., Zhu F., Jones T., Zhu X., Bowers J., Wai C.M., Zheng C., Shi Y., Chen S., Xu X., Yue J., Nelson D.R., Huang L., Li Z., Xu H., Zhou D., Wang Y., Hu W., Lin J., Deng Y., Pandey N., Mancini M., Zerpa D., Nguyen J.K., Wang L., Yu L., Xin Y., Ge L., Arro J., Han J.O., Chakrabarty S., Pushko M., Zhang W., Ma Y., Ma P., Lv M., Chen F., Zheng G., Xu J., Yang Z., Deng F., Chen X., Liao Z., Zhang X., Lin Z., Lin H., Yan H., Kuang Z., Zhong W., Liang P., Wang G., Yuan Y., Shi J., Hou J., Lin J., Jin J., Cao P., Shen Q., Jiang Q., Zhou P., Ma Y., Zhang X., Xu R., Liu J., Zhou Y., Jia H., Ma Q., Qi R., Zhang Z., Fang J., Fang H., Song J., Wang M., Dong G., Wang G., Chen Z., Ma T., Liu H., Dhungana S.R., Huss S.E., Yang X., Sharma A., Trujillo J.H., Martinez M.C., Hudson M., Riascos J.J., Schuler M., Chen L.Q., Braun D.M., Li L., Yu Q., Wang J., Wang K., Schatz M.C., Heckerman D., Van Sluys M.A., Souza G.M., Moore P.H., Sankoff D., VanBuren R., Paterson A.H., Nagai C., and Ming R., 2018, Allele-defined genome of the autopolyploid sugarcane *Saccharum spontaneum* L., Nature Genetics, 50: 1565-1573.
https://doi.org/10.1038/s41588-018-0237-2

Zhang Q., Qi Y., Pan H., Tang H., Wang G., Hua X., Wang Y., Lin L., Li Z., Li Y., Yu F., Yu Z., Huang Y., Wang T., Ma P., Dou M., Sun Z., Wang Y., Wang H., Zhang X., Yao W., Wang Y., Liu X., Wang M., Wang J., Deng Z., Xu J., Yang Q., Liu Z.J., Chen B., Zhang M., Ming R., and Zhang J., 2022, Genomic insights into the recent chromosome reduction of autopolyploid sugarcane *Saccharum spontaneum*, Nature Genetics, 54: 885-896.
https://doi.org/10.1038/s41588-022-01084-1
PMid:35654976