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Phylogenetic Analysis of Sugarcane for Sugar Production: Population Structure and Adaptive Evolution Based on Whole-Genome Data

Mengting Luo [1,2] ✉
1 Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China
2 Hainan Institute of Tropical Agricultural Resources, Sanya, 572000, Hainan, China
✉ Corresponding email: mengting.luo@jicat.org

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Abstract Based on genome-wide data, the phylogenetic relationships, population structure and adaptive evolution characteristics of *Saccharum* spp. were analyzed. The results showed that there was high genetic diversity between species and species, and the modern cultivated species was derived from multiple interspecific hybridization and polyploidy events, especially the genes of *S. officinarum* and *S. spontaneum*. This study revealed the genetic basis and evolutionary process of sugar yield traits such as sucrose content, stem weight and stem yield, and determined the genetic relationships among different varieties through phylogenetic and population structure analysis. This study provided a scientific basis for the genetic improvement of important agronomic traits of sugarcane, the formulation of precise breeding strategies and the efficient use of diverse germplasm resources.

Keywords Sugarcane; Phylogenetic analysis; Population structure; Adaptive evolution; Whole-genome data

1 Introduction

Sugarcane (*Saccharum* spp.) is the main source of sugar and also plays an important role in the production of bioethanol. Garsmeur et al. (2018), Guo (2024) and Li et al. (2024) found that sugarcane accounts for about 80% of the global sugar supply, indicating that the economic value of sugarcane is great. Yadav et al. (2020) and Xiong et al. (2022) argue that the advantages of sugarcane, such as its adaptability to tropical and subtropical climates, sugar supply, and feedstock for bioenergy and other by-product industries, make it a major crop in the agricultural economy in some regions.

Sugarcane has a complex polyploid genome made up of the genetic components of multiple species, such as *Saccharum officinarum* and *S. spontaneum* (Jannoo et al., 2007; Thirugnanasambandam et al., 2018; Zhang and Yang, 2024). Because of the complexity of this genome, advanced genetic and genomic approaches are needed to enhance the agronomic traits of sugarcane, such as sucrose content, sugarcane resistance to environmental stress, etc. (Mahadevaiah et al., 2021; Li et al., 2024). Yang et al. (2018) and Xiong et al. (2022) demonstrated that phylogenetic analysis is very helpful in revealing the genetic diversity and evolutionary history of sugarcane, and thus in formulating efficient breeding strategies. Relevant studies have proved that researchers can identify genetic markers and key traits helpful for variety improvement by analyzing the population structure and adaptive evolution of sugarcane through whole-genome data (Grivet and Arruda, 2002; Ngaklunchon et al., 2023).

Through phylogenetic analysis of sugarcane with whole genome data, this study elaborated the population structure and adaptive evolution of sugarcane, more clearly understood the genetic basis of sugarcane sugar production traits, and provided a scientific basis for identifying potential genetic resources in breeding. The aim of this study is to improve the efficiency of sugarcane breeding, promote the increase of sugarcane sugar yield and the sustainability of related industries.

2 Taxonomy and Origin of Sugarcane

2.1 Classification within the *Saccharum* genus

Sugarcane belongs to genus Saccharum of Poaceae family. *Saccharum* is noted for complex hybridization characteristics involving *Saccharum officinarum* and *Saccharum spontaneum*, as well as several other species.

(Jackson et al., 2014; Mahadevaiah et al., 2021; Cursi et al., 2022). Sugarcane species have high polyploidy and rich genetic diversity, so the classification of sugarcane is complicated. Mahadevaiah et al. ’s study in 2021 showed that sugarcane hybrids (e.g. *Saccharum* spp. hybrids) were mostly formed by interspecific or intergeneric hybrids, and wild relatives also contributed. Xiong et al. ’s study in 2022 found that phylogenetic analysis divided several sugarcane species into different taxa, such as *S. barberi* and *S. sinense*, while modern sugarcane hybrids were mainly composed of *S. officinarum* and *S. spontaneum*.

2.2 Evolutionary origin and domestication history

The studies of Yang et al. (2018), Pompidor et al. (2021) and Li et al. (2024) showed that the hybridization process of *S. officinarum* and *S. spontaneum* realized the development of modern sugarcane varieties, and sugarcane was used by people to produce sugar and bioethanol. Babu et al. ’s study in 2022 found that the domestication history of sugarcane is related to long-term selection for good traits such as high sucrose content and environmental adaptability (Figure 1). Yang et al. (2018) argued that genomic studies have found differences in the genetic composition of ancient and modern sugarcane hybrids, highlighting the importance of hybridization and artificial selection in the process of sugarcane domestication. Medeiros et al. (2020) and Xiong et al. (2022) found that genetic diversity and population structure analysis illustrated the evolutionary path and domestication process of sugarcane, and revealed the contribution of different sugarcane species to the genetic background of modern cultivated species.

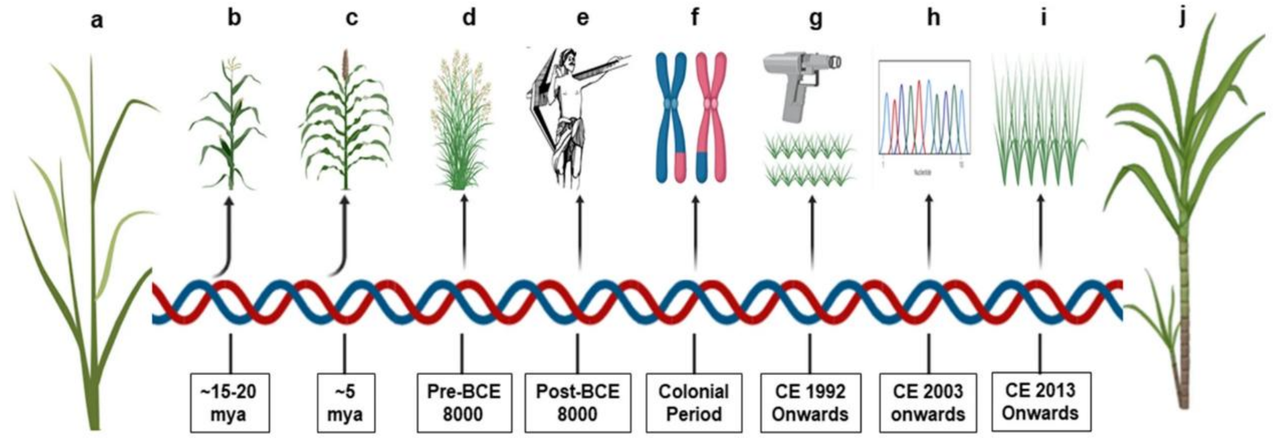

Figure 1 Timeline of sugarcane (Adopted from Babu et al., 2022)

Image caption: a: Progenitor grass species; B: Evolutionary split of maize; C: Evolutionary split of sorghum; D: Genus Saccharum pre-domestication; E: Selection and domestication; F: Breeding and improvement; G: Transgenic development; H: Omics research; I: market release of transgenic sugarcane; J: sugarcane with better traits (Adopted from Babu et al., 2022)

2.3 Polyploidy and its implications

Polyploidy is an important genetic feature of sugarcane, and it is also the main reason for the complexity and adaptability of sugarcane genome. Most of the modern sugarcane varieties have high polyploidy and complex nuclear genome background (Vilela et al., 2017; Zhou et al., 2022). Polyploidy increases the genetic variation of sugarcane and also provides the possibility for new trait combinations, which promotes the evolution and breeding of sugarcane. Vilela et al. (2017) showed that the multiploidy events of *S. officinarum* and *S. spontaneum* may have occurred independently, which promoted the diversification of sugarcane. Vilela et al. (2017) suggested that the presence of multiple haplotypes and the expression of homologous/homologous genes under purification selection indicated the functional importance of polyploidy in sugarcane adaptation and evolution.

3 Sugar Yield Traits and Their Genetic Background

3.1 Key traits related to sugar content

Sugar yield of sugarcane is mainly determined by sucrose content, stem weight and stem yield per unit area, which are the core of many genetic studies. Ngaklunchon et al. (2023) and Rakesh et al. (2023) in the same year found that highly inherited traits such as sucrose content were suitable for selection at the early stage of breeding.

Ming et al. (2002) and Barreto et al. (2019) argued that stem weight and stem yield are controlled by multiple quantitative trait loci located in specific genomic regions, which is helpful for researchers to find favorable alleles to improve sugar yield.

3.2 Molecular basis of sugar accumulation

Sun et al. (2022) and Ren et al. (2023) found that the molecular mechanism of sugar accumulation is related to multiple genes and their complex interactions with environmental factors. Yang et al. (2020) and Li et al. (2024) identified a large number of single nucleotide polymorphism loci significantly associated with sugar-related traits through GWAS, revealing the genetic architecture of sugar accumulation. A recent study by Chen et al. (2025) found that genes related to lignin synthesis were negatively correlated with sugar content, indicating that there is a complex regulatory balance between metabolic pathways. Earlier studies by Casu et al. (2005) showed that candidate genes identified by transcriptome analysis can help to resolve key molecular mechanisms controlling sugar accumulation.

3.3 Trait heritability and genetic architecture

Ngaklunchon et al. (2023) and Rakesh et al. (2023) found in the same year that sucrose content had relatively high heritability and stem yield had moderate heritability, indicating that some sugarcane sugar yield traits were suitable for selection in the early stage of breeding, while others required more complex selection strategies. According to Ming et al. (2002) and Barreto et al. (2019), the genetic framework of these traits is related to multiple quantitative trait loci, and some loci are clustered in the genome, which indicates that the genetic framework of these traits may have pleiotrophy effects or genetic linkage. Hayes et al. (2021) believe that genomic prediction models have shown potential in improving the accuracy of breeding value estimation in recent years, which is expected to further improve the efficiency of sugarcane breeding.

4 Phylogenetic Relationships among Sugarcane Accessions

4.1 Interspecific relationships and lineage divergence

Vilela et al. (2017) and Meng et al. (2019) found that sugarcane, as a complex polyploid hybrid crop, experienced many polyploidy events in its evolution, especially the hybridization between *Saccharum officinarum* and *S. spontaneum*. Vilela et al. 's 2017 study found that the divergence time between *Saccharum officinarum* and *S. spontaneum* was estimated to be 2.5 million to 3.5 million years ago, indicating that their ancient evolutionary paths are very important for the genome composition of modern sugarcane. Meng et al. (2019) found a new tetraploid *S. spontaneum* in their study with a basic chromosome number of x=10, which more clearly revealed the existence of parallel evolutionary paths between *Saccharum* species.

4.2 Insights from phylogenetics into sugar yield evolution

Li et al. (2024) used whole genome sequencing and genome-wide association analysis to find multiple single nucleotide polymorphisms associated with key agronomic traits, which are helpful for revealing the genetic basis of sugar yield traits in sugarcane and identifying selective imprinting occurring in the history of sugarcane breeding. The results of Medeiros et al. (2020) and Xiong et al. (2022) demonstrated that genetic diversity and population structure analysis supported the phylogenetic differentiation of sugarcane germplasm materials, which was closely related to the variation of sugar yield traits.

4.3 Phylogenomic support for breeding group classification

Evans et al. (2019) and Zhou et al. (2022) used mitochondrial and nuclear genome data to distinguish closely related sugarcane varieties and trace their ancestral lineages. Evans et al. (2019) and Medeiros et al. (2020) found that the phylogenetic tree constructed based on genomic data was consistent with the clustering model of known breeding populations, providing a theoretical basis for the classification and management of sugarcane germplasm resources. Mahadevaiah et al. (2021) believe that this systematic genomic approach is helpful for accurately partitioning breeding populations and understanding the genetic relationships and evolutionary history of sugarcane.

5 Population Structure and Evolutionary Dynamics

5.1 Genetic clustering of germplasm

Some studies have shown that sugarcane materials can be divided into several independent subpopulations based on genetic diversity analysis. Xiong et al. 's 2022 study of 196 *Saccharum* materials showed that the researchers could identify 3 to 8 genetic subgroups through model clustering, principal component analysis and phylogenetic analysis. This clustering is helpful for understanding the genetic relationship and diversity of *S. officinarum*, *S. spontaneum* and their hybrids. Xiong et al. (2022) demonstrated that the results of this study could not only be used in the management of germplasm resources, but also in breeding, especially in the identification of species-specific alleles for species identification and breeding selection.

5.2 Historical gene flow and hybridization patterns

Mahadevaiah et al. (2021) demonstrated that the complex hybridization nature of sugarcane mainly stems from the interspecific and intergenus hybridization between *S. officinarum* and *S. spontaneum*, and these hybridization events formed modern sugarcane varieties with highly diverse genetic background. Gene penetration analysis showed that the contribution of *S. spontaneum* chromosome fragment was decreasing in modern sugarcane varieties, while the proportion of *S. officinarum* was increasing, reflecting the breeding trend of improving target traits through artificial selection (Li et al., 2024). Meng et al. 's study in 2019 found a new tetraploid *S. spontaneum* with a basic chromosome number of x=10, which provided a new perspective on the genome evolution and polyploidy event of Saccharum.

5.3 Adaptive evolution in cultivated sugarcane

The whole genome sequencing of sugarcane varieties by Li et al. (2024) has identified several SNP markers related to important agronomic traits. These genetic variations are important factors for sugarcane to adapt to different environmental conditions and increase yield. Yang et al. 's study in 2018 identified selective sweep regions and candidate genes related to environmental factors, suggesting that adaptive evolution played a key role in the domestication and improvement of sugarcane.

6 Case Study: Phylogenetic Analysis of Sugar-Rich Cultivars

6.1 Study context and sample description

This case study focused on sugar-rich sugarcane varieties, and selected relevant cases of diverse sugarcane germplasm resources for analysis. Yang et al. (2018) and Xiong et al. (2022) believed that sugarcane was a polyploid crop with complex genetic structure. A 2018 study by Yang et al. sequenced 307 sugarcane germplasm material and revealed nearly 5 million sequence variants, a finding that is helpful in understanding the genetic makeup of sugar-rich varieties (Figure 2). Xiong et al. 's 2022 study analyzed 196 *Saccharum* materials, including multiple species and hybrids, to assess the genetic diversity and population structure of sugarcane.

6.2 Methodology and tree construction

Li et al. (2024) believe that whole genome sequencing and SNP detection are important techniques for identifying genetic variation associated with sugar content and other agronomic traits. In related studies, researchers often use model-based cluster analysis, principal component analysis and phylogenetic tree construction. Xiong et al. (2022) also used these methods to analyze the genetic structure and diversity of sugarcane. Evans et al. (2019) and Zhou et al. (2022) used mitochondrial sequencing to study sugarcane phylogeny because the mitochondrial genome structure was simple and easy to handle.

6.3 Key findings and breeding implications

Vilela et al. (2017) and Yang et al. (2018) found that ancient and modern sugarcane hybrids had different genetic compositions and hybridization processes, reflecting the genetic contributions of different ancestral species. Xiong et al. (2022) and Li et al. (2024) identified specific SSR alleles and SNP markers related to traits such as sucrose content, which provided important molecular tools for sugarcane breeding. According to the study of Mahadevaiah et al. (2021) and Li et al. (2024), these findings illustrate that modern sugarcane varieties have undergone significant genetic differentiation. Mahadevaiah et al. (2021) believe that combining genome selection with phylogenetic analysis can improve the precision introduction efficiency of good alleles and accelerate the speed of breeding.

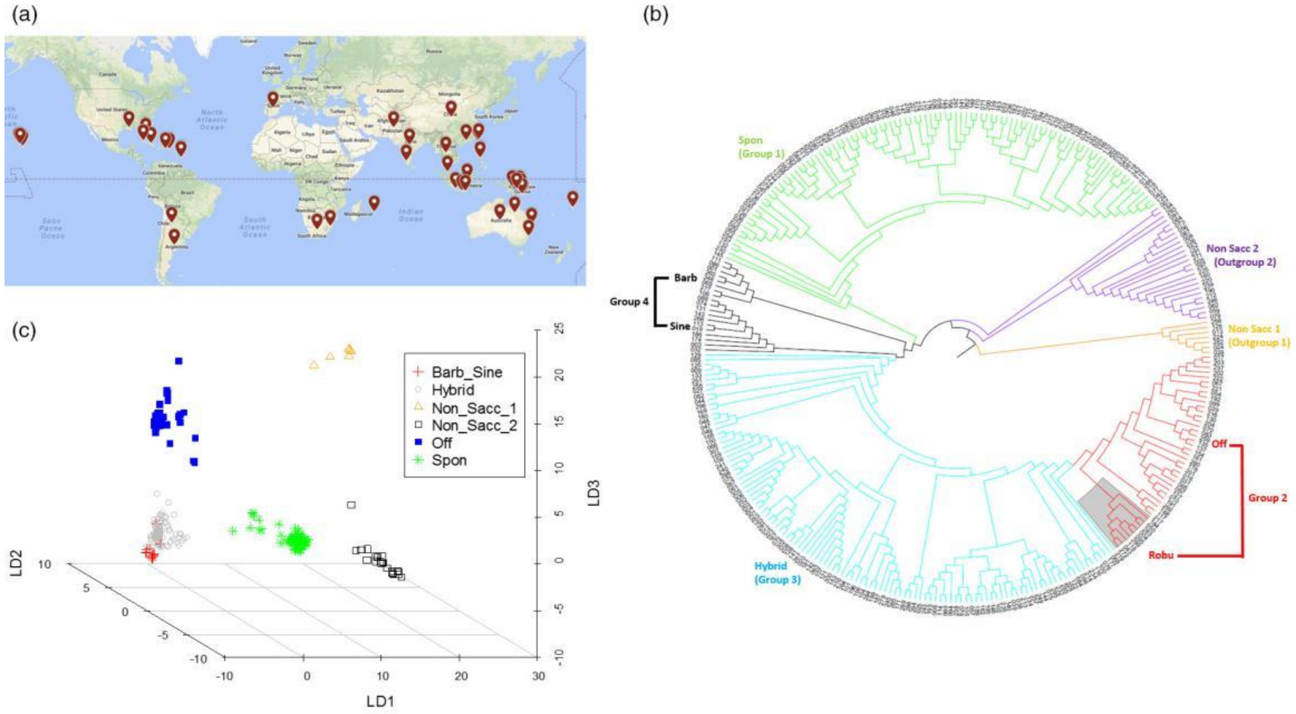

Figure 2 An overview of the diversity of the sugarcane accessions (Adopted from Yang et al., 2018)

Image caption: a: Geographical distribution of the 299 accessions selected from the World Collection of Sugarcane and Related Grasses. B: Phylogenetic tree of the 307 accessions. C: Discriminant analysis of principal components analysis of the 307 sugarcane accessions. Robu=*S. robustum*; Spon=*S. spontaneum*; Off=*S. officinarum*; Hybrid=modern *S.* hybrids; Barb=*S. barberi*, Sine=*S. sinence*; Non sacc=Non saccharum (Adopted from Yang et al., 2018)

7 Applications and Future Prospects

7.1 Phylogenetic data in breeding programs

Phylogenetic data revealed the genetic diversity and evolutionary history of different species and hybrids of sugarcane. Xiong et al. 's study in 2022 showed that selection efficiency could be improved and hybrid combinations optimized by identifying specific alleles in *Saccharum* species. Medeiros et al. (2020) found that understanding population structure and genetic diversity is beneficial to germplasm resource management and the development of new varieties. Mahadevaiah et al. (2021) believe that integrating phylogenetic data into the breeding process can improve the efficient utilization of germplasm resources and accelerate the improvement of varieties.

7.2 Integrating phylogeny with functional genomics

Li et al. 's study in 2024 showed that phylogenetic relationships can be correlated with functional traits based on whole genome sequencing and identification of SNPS associated with traits. Vilela et al. (2017) suggested that this combination could make it possible to identify candidate genes and key gene regions, and help breeders achieve trait oriented precision breeding. Evans et al. (2019) found that the application of mitochondrial and chloroplast genomes in phylogenetic studies can provide additional information for research and help researchers identify closely related varieties and analyze the evolutionary origin of sugarcane.

7.3 Prospects for evolution-informed genome editing

Yang et al. 's research in 2018 showed that key genes and pathways affected by natural selection and adaptive evolution can be identified through phylogenetic and genomic studies. This information can be used to guide genome editing techniques such as CRISPR/Cas9 to improve traits such as stress resistance, disease resistance, and biomass yield. Thirugnanasambandam et al. (2018) believe that this kind of technology is expected to achieve precise improvement, shorten the breeding cycle, and improve the production efficiency of sugarcane.

8 Conclusion

Phylogenetic analysis is helpful to reveal the genetic diversity and evolutionary history of sugarcane and improve the productivity of sugarcane. By analyzing the genetic structure and diversity of sugarcane and its relatives, the researchers distinguished different genetic lineages and evolutionary patterns. Some studies have found that ancient hybrids such as *S. barberi* and *S. sinense* differ greatly from modern hybrids in genome composition and hybridization process, which has provided new directions for understanding the origin and adaptive evolution of sugarcane. Phylogenetic studies based on mitochondrial genomes enable researchers to more clearly elucidate the evolutionary relationships among sugarcane species.

Breeders address the genetic basis of important agronomic traits by identifying species-specific alleles and optimize the management of genetic resources to improve breeding efficiency. The identification of genes related to environmental adaptation and selective clearing provided a new idea for the breeding of sugarcane varieties with high yield and stress resistance. Genome selection and association analysis have become important methods for researchers to achieve more accurate breeding strategies and screen for good alleles such as sucrose content and stalk yield. These results are useful for breeders to introduce good genes and enhance the genetic diversity of breeding populations.

The phylogenetic and genomic studies of sugarcane will provide theoretical support for further analysis of the complex genome characteristics of sugarcane and improvement of cultivation level. The development of whole genome sequencing and reference genome construction technology can help us to understand polyploid traits and genetic structure of sugarcane more comprehensively. By combining genomic data with environmental variables, breeders can predict the performance of sugarcane varieties in different ecological climate zones and optimize breeding programs under specific conditions. Exploring the role of mitochondrial and chloroplast genomes in sugarcane evolution and adaptation may open up new ways for sugarcane variety improvement. With the progress of genomic technology, researchers will continue to enhance the ability to regulate the genetic traits of sugarcane, and it is expected to cultivate new varieties with more stress resistance and high yield potential in the future, and accelerate the development of the global sugar industry and bioenergy industry.

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Conflict of Interest Disclosure

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

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