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Polyploidy and Genetic Base of Sugarcane (*Saccharum officinarum* L.) and Its Implications for Varietal Improvement: a Review Article

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Abstract: Increasing sugar productivity is the main concern of sugarcane (*Saccharum officinarum* L.) breeding programs. The choice of parents and better understanding of genetic diversity among the available parental genotypes would help the breeder to make better crosses. Thus, genetic bases of genotypes used as a tool to assist sugarcane breeders with selecting the most divergent parents to maximize heterosis and transgressive segregation in the progeny population; individual sugarcane varieties contain a very considerable store of genetic variability because of their hybrid nature, heterozygosity and high polyploidy. However, most commercial varieties of sugarcane exhibited narrow genetic base since these varieties are becoming increasingly similar to each other time to time due to commonness of one or more parents in their ancestry and/or repeated backcrossing with *S. officinarum* as recurrent parent as well as selection pressure during domestication for high sucrose types and the vegetative mode of propagation of the crop has been suggested as the major reason for the low genetic diversity within the *S. officinarum* species. Thus, this review attempts to assess nature of the existing genetic base of sugarcane and evidence that this genetic base may need to be widened to enable continued improvement and conscious efforts are to be made to diversify the parental genetic base to ensure high genetic variability among the cultivated varieties. Further, new sources from the interspecific and/or intergeneric hybrid gene pool need to be used along with proven parents to generate the variability that will be both commercially viable and genetically diverse.

Key words: Genetic Base · Genetic Distance · Polyploidy · Sugarcane · Varietal Improvement

INTRODUCTION

Sugarcane (*Saccharum officinarum* L.) is an economically important commercial crop that accounts for 70% of the world's sugar production [1]. It recently has gained increased attention because of the potential of its by-products; ethanol, molasses and bagasse, as important renewable biofuel sources. It has also been reported that sugarcane has a C_4 carbohydrate metabolism which allied with its perennial nature, makes it one of the most productive cultivated plants [1]. However, sugarcane probably the most complex of all crop genomes is studied to date, mainly due to its very high degree of polyploidy and interspecific origin [2] and it thus represents a major challenge for genetic improvement in sugarcane.

Improvement of sugarcane for increased sugar yield through classical hybridization and selection has been a directed, ongoing process since 1888, following the observation in 1858 that sugarcane produced viable seed [3]. However, modern sugarcane cultivars are hybrids derived from interspecific crosses between *S. officinarum* and *S. spontaneum* and result in a high degree of polyploidy and frequent aneuploidy [4], making the construction of genetic maps by conventional methods difficult. *S. officinarum* is the high sugar content species and *S. spontaneum* provides stress and disease tolerance and high fiber for biomass.

The genetic variability of the breeding populations used to produce new varieties of a crop is termed its genetic base [5]. It sets the limit of improvement of that crop through breeding. Individual sugarcane varieties contain a very considerable store of genetic variability because of their hybrid nature, heterozygosity and high polyploidy [5] since commercial sugarcane varieties are interspecific hybrids. The number of parental clones involved in these crosses is limited [6, 7] and the

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commercial varieties of sugarcane are becoming increasingly similar to each other time to time due to commonness of one or more parents in their ancestry and/or repeated backcrossing with *S. officinarum* as recurrent parent.

Consequently, the genetic base of the modern varieties appears to be very narrow and this is reflected in the slow progress in sugarcane breeding at present [4]. Overall, genetic base of sugarcane is said to be already exhausted or the proper characterization and evaluation is limited. The lack of universal, standard and systematic characterization and evaluation procedures of sugarcane germplasm is a big reason for the limited use of readily available germplasm. In this context, information on the genetic base of available sugarcane germplasm is essential for the identification of potential germplasm groups and for optimizing hybridization and selection procedures.

The main reason for characterizing and evaluating of genetic resources are: (i) To study genetic variability of certain characters in relation to their geographical distribution in order to develop new and more adequate collecting strategies for further collection of useful germplasm in the same or similar areas, (ii) To study genetic variability present in the germplasm, especially within samples and develop the most appropriate technique and strategies for maintaining the genetic integrity of such diversity; studies on genetic drift and the physiology of seed aging are the most appropriate, (iii) To widen genetic diversity of crop through intraspecific and intergeneric hybridization and mutation; other genetic engineering technique may be of interest and (iv) To screen the germplasm for traits which from time to time are considered important for breeding programs aiming to improve agriculture in a given country, regions or geographical area; this include studies on seed quality, resistant to diseases and pest and adaptation to adverse soil conditions. Therefore, this review is initiated with the aim of assessing nature of the existing genetic base of sugarcane and evidence that this genetic base may need to be widened to enable continued sugarcane improvement.

Sugarcane Evolution and Domestication: According to Acquaah [8], domestication described as the process by which genetic changes in wild plants are brought about through a selection process imposed by humans and/or it is an evolutionary process in which selection (both natural and artificial) operates to change plants genetically. For the last century, exhaustive investigation was carried out for the domestication and the early evolution of sugarcane since centers of crop domestication are of interest to researchers from various disciplines particularly; plant breeders are interested in centers of crop domestication as regions of genetic diversity and variability are critical to the success of crop improvement [8]. Thus, the most popular scenario has been developed by Artschwager and Brandes; sugarcane (*S. officinarum*) was domesticated from the wild species of *S. robustum* in New Guinea and was then dispersed in the Pacific and mainland Asia during human migrations. In mainland Asia, they hybridized with local *S. spontaneum* giving rise to North Indian (*S. barberi*) and Chinese (*S. sinense*) cultivars. The direct emergence of sugarcane (*S. officinarum*) from *S. robustum* is now generally accepted and it has been hypothesized that *S. robustum* was the result of complex introgressions between *S. spontaneum* and other related genera, particularly *Erianthus* and *Miscanthus* [9]. However, the emergence of sugarcane from a wild species other than *S. robustum* was considered a minor hypothesis [10].

The genus *Saccharum* is a well-defined lineage that diverged over a long evolutionary period from the lineages leading to the *Erianthus* and *Miscanthus* genera [10]. The implication of this is that cultivated sugarcane species most likely emerged from wild *Saccharum* species [10]. The members of the *Saccharum* clade therefore, contributed directly to sugarcane cultivars through allopatric speciation of *S. spontaneum* and *S. robustum* [11]. *Miscanthus* and *Erianthus*, previously proposed as contributing to sugarcane, are recognized as sharing common ancestors. Following *Saccharum* speciation, *S. robustum* contributed to cultivars of *S. officinarum* for sugar, *S. edule* for vegetables and *S. robustum* used for fencing and construction purpose [11] (Fig. 1).

Polyploidy and Genetic Base of Sugarcane

Polyploidy in Sugarcane: As stated by Premachandran *et al*. [12], polyploids are organisms having more than two genomes in their nucleus and are widespread in wild as well as cultivated plants. Autopolyploids have three or more homologous chromosome sets derived from a single species and are usually characterized by fully homologous chromosomes. The autopolyploids are intraspecific polyploids, having monophyletic origin. However, allopolyploids contain two or more sets of homologous chromosomes and they were derived as a result of interspecific or intergeneric hybridization between species with diverged genomes.

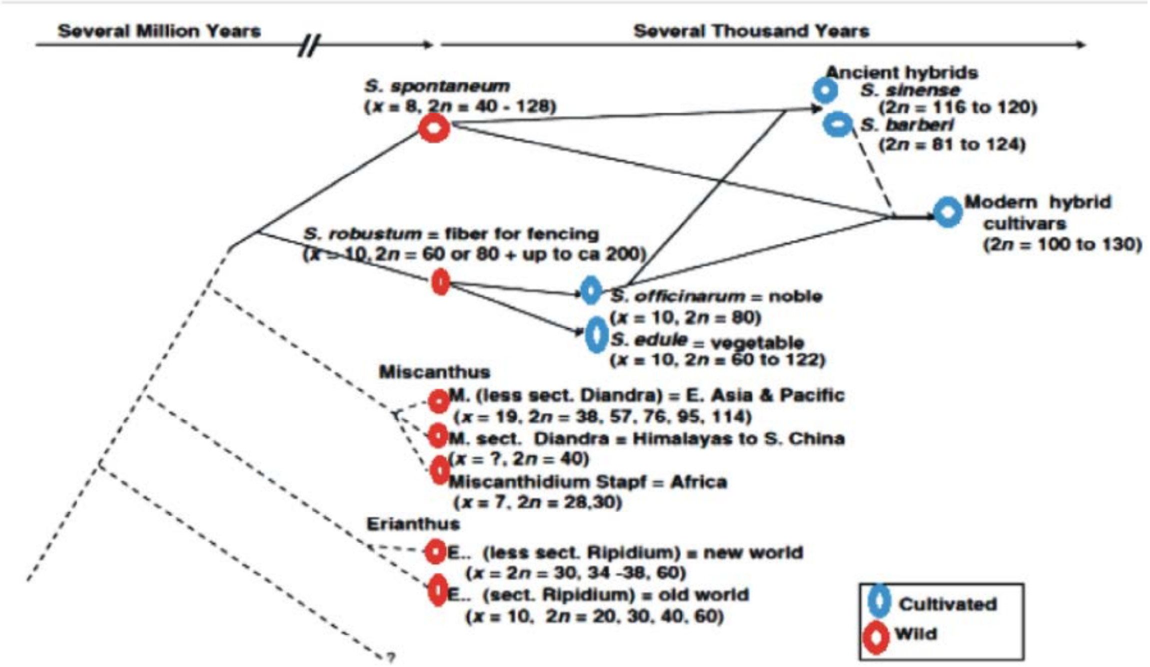

Fig. 1: Hypothetical pathway for sugarcane evolution and domestication*: strongest evidence for the evolution and domestication are indicated with solid lines; weaker evidence is indicated with dashed lines*. Source: [11]

Commercial sugarcane varieties, which is an allopolyploid with genome contributions from *S. officinarum* and *S. spontaneum*, is having high chromosome number of 2n = 100 to 130 in different varieties. *Saccharum officinarum* is an octoploid, having 80 chromosomes with a base chromosome number of x = 10, while *S. spontaneum* forms a polyploid series from 5 to 16 ploid number, with a base chromosome number of x = 8 [13]. However, polyploidy is regarded as an important mechanism of speciation and adaptation [12] and there are documented advantages in sugarcane such as (i) heterosis that provides increased vigour, (ii) gene redundancy as a result of gene duplication and (iii) asexual reproduction that enables the polyploids to reproduce efficiently [14] which are present in allopolyploid sugarcane. Moreover, polyploids are more vigorous due to heterosis and gene redundancy protects polyploids from the deleterious effects of mutations. Another advantage of gene redundancy is the ability to diversify gene function by altering redundant copies of important or essential genes (neofunctionalization). In polyploids all genes have a duplicated copy that is available for evolutionary experimentation [14]. They also have greater chances of acquiring new beneficial alleles and are better poised to evolve novel functions. Premachandran *et al.* [12] reported that gene redundancy due to polyploidy provides a selective advantage for a wider geographical adaptation, increased vigour, sucrose and fiber content of sugarcane crop.

Sugarcane Genetic Base: In the case of genetic base, however most commercial varieties exhibited narrow genetic base and this prompted sugarcane researchers and breeders to be more conscious of the role of sugarcane germplasm in increasing the variability since the commercial varieties of sugarcane are becoming increasingly similar to each other due to commonness of one or more parents in their ancestry. This has led to the narrowing down of the genetic base of these varieties which eventually creates genetic vulnerability; which refers to the susceptibility of most of the cultivated varieties of sugarcane to disease, insect or some other stress due to similarity in their genotype [5].

In general, the sugarcane genetic base is said to be already exhausted or the proper characterization and evaluation is limited. The lack of universal, standard and systematic characterization and evaluation procedures of sugarcane germplasm is a big reason for the limited use of readily available germplasm. Furthermore, the lack of it is a setback in the assessment of level of the genetic diversity present in the sugarcane germplasm.

Genetic Diversity Analysis for Varietal Improvement: Genetic diversity is the total of heritable variation present within and among populations of organisms that serves an important role in evolution by allowing a species to adapt to a new environment [15]. The ultimate source of genetic diversity is gene mutation which is a permanent change in the DNA sequence, molded and shaped by selection, recombination, gene flow, genetic drift and migration in heterogeneous environments in space and time [16]. Natural selection chooses the best fit among and within a population, thus there can be no adaptive evolution without genetic variation. Hence, genetic diversity is an essential raw material for evolution, which enables populations of the crop species to survive, adapt to new circumstances and evolve to produce new genetic variants, where some of them may become the fit variants that meet long-term changes in the environment [17].

Analysis of the extent and distribution of genetic variation in a crop species is also essential in understanding the evolutionary relationships between cultivars and to sample genetic resources in a more systematic fashion for breeding and conservation purposes [18]. Thus, accurate assessment of the levels and patterns of genetic diversity can be invaluable in plant breeding for diverse applications including (i) analysis of genetic variability in cultivars, (ii) identifying diverse parental combinations to create segregating progenies with maximum genetic variability for further selection and (iii) introgressing desirable genes from diverse germplasm into the available genetic base [19]. To achieve the above, genetically diverse germplasm is selected in breeding programs to enhance the productivity and diversity of cultivars. Therefore, a major focus of research in genetics has been to determine the amount of genetic variation in both natural and domestic populations and describing the possible mechanisms of maintaining such variability in meeting new environmental challenges [20].

According to the heterosis theory, parental lines with wider genetic bases must be selected for crossing during variety development on the premise that the main attributes of the parental lines are complementary [21]. However, in terms of genetic diversity within the *Saccharum* genus, numerous studies have shown that sugarcane appears to be the least variable species than other *Saccharum* species [22-24]. Selection pressure during domestication for high sucrose types (i.e. severely erodes the genetic variability created from recombination among selected parental clones) and the vegetative mode of propagation of the crop has been suggested as the major reason for the low genetic diversity within the *S. officinarum* species [23, 25].

However, there is molecular evidence that due to its polyploid nature, interspecific origin and vegetative mode of propagation (i.e., maintenance of hybrid vigour), high levels of heterozygosity exist among modern sugarcane cultivars using RFLP markers [22, 26]. The major part of diversity was contributed to the 15-25 % chromosome complement that was inherited from *S. spontaneum* by random assortment of half its chromosomes which has the greatest intraspecific diversity [4]. Similar patterns of molecular diversity were also detected using AFLP [27] and SSR markers [28].

In general, genetic diversity information that can be derived from molecular analyses of sugarcane germplasm will help to identify outstanding morphological and agronomic characters present in the germplasm, determine the degree of relationships of the different germplasm within and among breeding populations and design collection and conservation strategies. Also, this will provide benchmark data for the effective utilization of the germplasm in sugarcane breeding programs and pre-breeding activities.

Genetic Distance and Similarity in Sugarcane Varieties: Genetic distance is a measure of the average genetic divergence between two species or between populations within a species or taxa [29, 30] and/or it is the extent of gene differences between cultivars, as measured by allele frequencies at a sample of loci. On the other hand, genetic similarity is the extent of gene similarities among cultivars [29]. However, the distance in gene frequency between the parent genotypes is important because the higher the difference in gene frequency, the higher the amount of heterosis, which indicated that a more distant genetic relationship [31]. Information concerning genetic relatedness is crucial, for it indicates the rate of adaptive evolution and the extent of response in crop improvement. Furthermore, it is essential as a guideline in the choice of parents for breeding programs and implementing an effective genetic conservation program [32].

In most instances, modern sugarcane varieties are interspecific hybrids mostly derived from crosses involving *S. officinarum* and *S. spontaneum* [4] but the genetic base of the modern varieties appears to be narrow and this is reflected in the slow progress in sugarcane breeding at present. This could be associated with the limited number of parental clones involved in the primary crosses and/or their parental breeding lines, used to develop these varieties, are the same or are very close to each other, or use repeated backcrosses with *S. officinarum* and clonal way of propagation [33-35]. Therefore, conscious efforts are to be made to diversify the parental genetic base to ensure high genetic variability among the cultivated varieties. Moreover, new sources from the interspecific/intergeneric hybrid gene pool need to be used along with proven parents to generate the variability that will be both commercially viable and genetically diverse. Thus, information on the genetic divergence/similarity of available germplasm is essential for the identification of potential germplasm groups and for optimizing hybridization and selection procedures in sugarcane improvement [33, 34].

CONCLUSION

The current hybrid sugarcane varieties on which present day sugar industries are based have been derived from a very limited sample of the naturally occurring forms of *Saccharum*. Many sugarcane breeders have been content to capitalize on the initial gains from interspecific hybridization by intercrossing the original hybrids and their derivatives and success is still being achieved by this process. In recent years, a number of sugarcane breeders have become aware of the limited genetic base of their material and the possibility that the wide array of unused forms of *Saccharum* and its relatives may be important for future progress. Breeders have attempted to transmit specific desirable characters from naturally occurring clones to commercial hybrids and have incorporated new genetic material into their breeding program with the general aim of improving sugar yield. For the development of improved varieties, genotypic studies of sugarcane are required. Described as an allopolyploid, modern cultivated sugarcane have approximately 80-140 chromosomes with 8-18 copies of a basic set ($x = 8$ or $x = 10$ haploid chromosome number).

Continuous selection for the same traits may narrow genetic diversity to the extent that it may be difficult to predict diversity based on pedigree history alone. However, with the advent of molecular markers, it is now possible to make direct comparison of genetic diversity at the DNA level without some of the over simplifying assumptions associated with calculating genetic diversity based on pedigree history. Rapid advances in the field of molecular biology and its allied sciences made the use of molecular markers a routine practice providing plant breeders a precise tool in analyzing genetic diversity for sugarcane improvement. This will be contributed for future breeding efforts involving crosses between and within breeding populations and may provide useful strategies for combining beneficial genes and alleles in developing new sugarcane varieties while maintaining genetic diversity.

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