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Genetic Relationship between Sweet Grain Sorghum and the Other Sorghum Types Cultivated in Burkina Faso Assessed with Nuclear Microsatellite Markers SSRs

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Abstract

In Burkina Faso, sweet grain sorghum [*Sorghum bicolor* (L.) Moench] is generally cultivated in association with several other types of sorghum. However, the lack of information on the genetic relationship between this sorghum and grain sorghum as well as sweet stalk sorghum hinders the efficient management of its genetic resources. Thus, 34 sorghum accessions consisting of 14-grain sorghum, 10-sweet stalk sorghum, and 10 sweet grain sorghum were evaluated using 15 nuclear microsatellites markers (SSRs) to determine their genetic relationship. Results revealed significant genetic diversity within each sorghum type and a significant index of genetic differentiation per pair of sorghum types (0.017) between sweet grain sorghum and sweet stalk sorghum. The minimum Nei distance was also high (0.12) between these two sorghum types. Sweet grain sorghum indeed showed the lowest values of theoretical heterozygosity (0.35), of observed heterozygosity (0.13). Structuring of the accessions of the three types of sorghum cultivated in two distinct groups, one of grain sorghum and sweet stalk sorghum and another consisting of accessions of grain sorghum and sweet grain sorghum was also obtained. The low differentiation observed would suggest greater genetic proximity between the three types of sorghum. The differences observed would be more of a physiological and biochemical nature. These results could contribute to better management of the genetic resources of sweet grain sorghum.

Keywords

Sorghum, Markers, Genetic Diversity, Phylogeny, Burkina Faso

1. Introduction

Sorghum is a very diverse species. In Burkina Faso, different types of sorghum (grain sorghum, sweet grain sorghum, sweet stalk sorghum, dyer sorghum.) are cultivated with associated agricultural practices. Several studies conducted on grain sorghum [1] [2] [3], sweet stalk sorghum [4], and sweet grain sorghum [5] [6], respectively, revealed the existence of genetic diversity within these sorghums. The co-evolution of crop diversity and local agricultural practices ensure their maintenance in agroecosystems [7] [8] [9]. In fact, multiple cropping of sorghum in the same field is a common agricultural practice in our countries, especially with the reduction of arable land. Sweet grain sorghum is generally cultivated in hut fields and sometimes in bush fields in association with other types of sorghum or cereals such as corn. This farmer management method ensures the maintenance of genetic variability in the cultivated plants, but also promotes significant gene flow between local cultivars and their close relatives [10]. Moreover, the different types of sorghum present significant inter-fertilization possibilities due to allogamy, which can reach 30% [11], and to their evolution often in the same geographical areas and in the same environments. Inter- and intra-fertilization of sorghum types in the context of selection and development of sweet grain sorghum raises the problem of its conservation and stability in its environment.

However, the genetic relationship between grain sorghum, sweet grain sorghum, and sweet stalk sorghum is not well known, which could constitute a constraint to the rational exploitation of the potential of each type of sorghum. Good knowledge of the relationships between the different sorghum cultivated would make it possible to consider improving one type of sorghum with another type while maintaining the characteristics of interest of the latter. Thus, the present study aims to further knowledge of the specific relationships among these sorghum. This includes 1) assessing the genetic diversity of each type of sorghum and 2) determining the genetic relationship between sweet grain sorghum and the other types of sorghum grown in Burkina Faso precisely grain sorghum and sweet stalk sorghum using microsatellite markers.

2. Material and Methods

2.1. Plant Material

The plant material consists of 34 sorghum accessions including 10-sweet grain sorghum, 10-sweet stalk sorghum, and 14-grain sorghum. Twenty-four accessions were obtained from the genebank of the "Laboratoire Biosciences" of "Université Joseph KI-ZERBO" and 10-grain sorghum accessions were received from the INERA Saria genebank (Burkina Faso).

2.2. Methods

2.2.1. DNA Extraction

Seeds of the 34 sorghum accessions were sown in pots in September 2018. These pots were stored in the experimental garden of our research Institute "Unité de

Formation et de Recherche en Sciences de la Vie et de la Terre" of "Université Joseph KI-ZERBO". For each accession, 100 mg of young fresh leaves (14-days-old) were collected and finely ground in 750 µl of pure water using a mortar. The grindings of each sample obtained were centrifuged at 10,000 RPM (rotations per minute) for 10 mins. At the end of this operation, the supernatant was removed and 200 µl of DNAzol was added to the pellet. The tubes containing the DNAzol and the pellet were then shaken to completely recover the pellet in the lysis buffer. The collected extracts were then, incubated at 65˚C in a water bath for 2 h. At the end of the incubation, the obtained extracts were cooled for a few minutes at room temperature of the laboratory and then centrifuged at 10,000 RPM for 15 mins. The supernatant was collected in eppendorf tubes and stored at −20˚C.

2.2.2. Characteristics of the SSR Markers Used

Fifteen microsatellite markers were used in this study. The distribution of these markers covers seven of the 10 chromosomes of the sorghum genome. These markers were chosen for their polymorphism revealed in previous studies of sorghum genetic diversity in Niger [12] [13], Mali [14], Burkina Faso [15] [16] [17], and from a global collection [18]. The characteristics of the molecular markers are presented in **Table 1**.

2.2.3. Amplification PCR

PCRs were performed in a final volume of 20 µl containing 1 µl of 3' primer (forward primer) at 0.2 µM, 1 µl of 5' primer at 0.2 µM (reverse primer), 9 µl of ultrapure water, 4 µl of PCR premix, and 5 µl of accession DNA. The PCR premix consisted of 0.4 µl of 10 mM concentration dNTPs, 2 µl of 10 X Buffer, and 0.4 µl of Taq polymerase containing 2U.

PCR amplification was performed following a program consisting of an initial denaturation phase at 94˚C for 4 mins, followed by a series of 35 cycles and a final extension at 72˚C for 4 mins. Each cycle included a denaturation phase at 94˚C for 45 s, a hybridization phase at the temperature (T m˚C) of each primer for 1 min, and an extension at 72˚C for 1 min 30 s.

2.2.4. Electrophoretic Migration and Band Reading

The amplification products were then subjected to electrophoresis at 100 V on a 2% agarose gel prepared with a 1x TBE solution. The migration time was 2 h in 0.5x Tris Borate EDTA buffer (TBE). Deposits were made in the presence of a molecular weight marker ranging in size from 50 bp to 1500 bp. The gel was then immersed in a 5% Bromide Ethidium (BET) solution used as a fluorescent developer for 15 mins. It was then rinsed with distilled water for 3 mins before being read under ultraviolet light from a model UVDI-254 trans-illuminator topped with a 10 mega pixel camera. Bands were identified on the basis of their position on the gel. Thus, a binary coding was used with 1 in case of presence and 0 in case of absence of band for each individual and for each primer tested.

Table 1. List of microsatellite primers used and loci revealed.

N°	Marker_Name	Motive	Forward_Primer	Reverse_Primer	T (°C)	Size_Range	Chromosom
1	gpsb123	(CA)7 + (GA)5	ATAGATGTTGACGAAGCA	GTGGTATGGGACTGGA	50	288-296	SBI08
2	Sb6-84	(AG)14	CGCTCTCGGGATGAATGA	TAACGGACCACTAACAAATGATT	55	32	SBI02
3	SbAGB02	(AG)35	CTCTGATATGTCGTTGTGCT	ATAGAGAGGATAGCTTATAGCTCA	55	96-154	SBI07
4	Xcup02	(GCA)6	GACGCAGCTTTGCTCCTATC	GTCCAACCAACCCACGTATC	54	192-204	SBI09
5	Xcup11	(GCTA)4	TACCGCCATGTCATCATCAG	CGTATCGCAAGCTGTGTTTG	54	165-172	SBI03
6	Xcup14	(AG)10	TACATCACAGCAGGGACAGG	CTGGAAAGCCGAGCAGTATG	54	211-225	SBI03
7	Xcup53	(TTTA)5	GCAGGAGTATAGGCAGAGGC	CGACATGACAAGCTCAAACG	54	186-198	SBI01
8	Xcup62	(GAA)6	CGAGAAGATCGAGAGAACCC	TGAAGACGACGACGACAGAC	54	190-193	SBI01
9	Xcup63	(GGATGC)4	GTAAAGGGCAAGGCAACAAG	GCCCTACAAAATCTGCAAGC	54	133-145	SBI02
10	Xtxp010	(CT)14	ATACTATCAAGAGGGGAGC	AGTACTAGCCACACGTCAC	50	135-151	SBI09
11	Xtxp040	(GGA)7	CAGCAACTTGCACTTGTC	GGGAGCAATTTGGCACTAG	55	129-141	SBI07
12	Xtxp057	(GT)21	GGAACTTTTGACGGGTAGTGC	CGATCGTGATGTCCCAATC	55	223-257	SBI06
13	Xtxp114	(AGG)8	CGTCTTCTACCGCGTCCT	CATAATCCCACTCAACAATCC	50	211-217	SBI03
14	Xtxp145	(AG)22	GTTCCTCCTGCCATTACT	CTTCCGCACATCCAC	55	208-244	SBI06
15	Xtxp295	(TC)19	AAATCATGCATCCATGTTCGTCTTC	CTCCCGCTACAAGAGTACATTCATAGCTTA	55	153-183	SBI07

Tm: Hybridization Temperature, Repeated motive: G: Guanine, C: Cytosine, A: Adénine; T: Thymine.

3. Statistical Analysis of Molecular Data

The assessment of genetic diversity using microsatellite markers (SSR) was carried out at three levels: intra-population diversity, inter-population diversity and the general structure of the collection.

Analysis intra-type genetic diversity of sorghum

To assess genetic diversity within each sorghum type, the Genalex software was used to estimate genetic diversity parameters such as the polymorphism rate (**P**), the average number of alleles per locus (**A**), total number of alleles per sorghum type (**At**), the number of effective alleles (**Ae**), the number of distinct or private alleles ($\mathbf{A^P}$), the expected heterozygosity (**He**) or Nei's gene diversity index (**D**), the observed heterozygosity (**Ho**), the Shannon diversity index (**I**) [19], and polymorphic information content (**PIC**) [20].

Analysis inter-type genetic diversity of sorghum

For the comparison of subpopulations defined according to sorghum types, the index of genetic differentiation between subpopulations (**Fst**) and the minimum Nei distance between pairs of genetic groups were calculated using Genetix software and Fstat software. Structuring was also obtained using the same software. The genetic similarity between sorghum types was tested by correspondence factor analysis (**AFC**).

4. Results

4.1. Level of Diversity of Nuclear SSR Markers Tested

The results of the genetic diversity assessment of the three cultivated sorghum types using the 15 polymorphic microsatellite markers are reported in **Table 2**.

A total of 43 alleles were identified with numbers ranging from 2 (Xtxp40, Xcup02, Xcup11, Xcup63, Xcup62) to 3 (Xtxp145, Xtxp295, SbAGB02, Xtxp114, gpsb1123, Xtxp10, Xcup14, Xtxp57, Sb6-84, Xcup53) per locus. The number of effective alleles ranged from 2.68 (Xtxp295) to 1.13 (Xtxp114) with an average of 1.63 alleles. The expected unbiased heterozygosity (He) ranged from 0.20 for the sb6-84 locus to 0.50 for the SBAGB02 locus with an average of 0.43. As for the observed heterozygosity (Ho), its value ranged from 0 to 0.53 with an average of 0.14. Seven loci namely Xtxp40, Xtxp145, Xcup02, Xcup11, Xcup63, Xtxp114, Xcup62 showed zero observed heterozygosity values. The Shannon diversity index (I) ranged from 0.26 for the Xtxp114 primer to 0.98 for Xtxp295 with an average of 0.61. The potential for polymorphism information (PIC) ranged from 0.12 (Xtxp114) to 0.63 (Xtxp295). Figure 1 shows the migration profile obtained with the Xcup14 marker for 34 individuals

Table 2. Diversity parameters of the 15 tested nuclear markers.

General population	N	A	Ae	I	PIC	Ho	He	P (95%)
Xtxp40	34	2	1.99	0.69	0.50	0	0.51	Yes
Xtxp145	34	3	1.76	0.70	0.43	0	0.44	Yes
Xtxp295	34	3	2.68	0.98	0.63	0.03	0.65	Yes
SbAGB02	34	3	1.90	0.79	0.47	0.15	0.49	Yes
Xcup02	34	2	1.56	0.55	0.36	0	0.37	Yes
Xcup11	34	2	1.99	0.69	0.49	0	0.51	Yes
Xcup63	34	2	1.78	0.63	0.44	0	0.45	Yes
Xtxp114	34	3	1.13	0.26	0.12	0	0.12	Yes
Xcup62	34	2	1.90	0.67	0.47	0	0.49	Yes
gpsb1123	34	3	1.50	0.55	0.33	0.03	0.34	Yes
Xtxp10	34	3	1.90	0.70	0.42	0.53	0.43	Yes
Xcup14	34	3	1.36	0.51	0.26	0.53	0.27	Yes
Xtxp57	34	3	2.16	0.80	0.50	0.29	0.51	Yes
Sb6-84	34	3	2.12	0.78	0.53	0.06	0.54	Yes
Xcup53	34	3	2.17	0.82	0.53	0.50	0.55	Yes
Mean	34	3	1,61	0,68	0,43	0,14	0,45	100%

A: number of alleles per locus; Ae: effective number of alleles; Ho: observed heterozygosity; He: expected heterozygosity; PIC: Polymorphism Information Content; P: polymorphism rate; I: allelic Shannon diversity index.

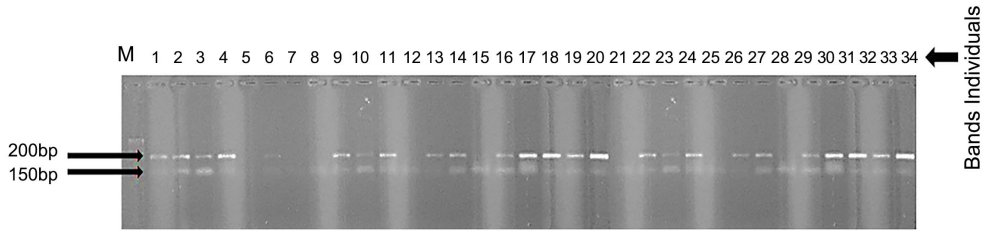

Figure 1. Migration profile obtained with the Xcup14 marker for 34 individuals. Legend: M: DNA Marker.

4.2. Genetic Diversity of Sorghum Accessions

4.2.1. Comparison of Genetic Diversity Parameters of Sorghum Types

The results in Table 3 revealed a low number of private alleles for sweet grain sorghum, sweet stalk sorghum and grain sorghum of 0.06 and 0.13, respectively. The level of diversity was significant within the different sorghum types with a total of 18 alleles detected for sweet grain sorghum and 22 alleles for sweet stalk sorghum and grain sorghum, respectively. All sorghum types showed higher expected heterozygosity (**He**) than observed. However, sweet grain sorghum had the lowest values of observed heterozygosity (Ho = 0.17), expected heterozygosity (He = 0.35), Shannon diversity index (0.5), and marker PIC (Polymorphism Information Content) (PIC = 0.31). Sweet stalk sorghum and grain sorghum on the other hand expressed similar or close values for the same diversity parameters.

4.2.2. Differentiation and Genetic Distance among Sorghum Types

The minimum Nei distance results (Table 4) showed a low level of differentiation among the three sorghum types studied. The highest Nei distance was observed between sweet grain sorghum and sweet stalk sorghum (0.12). For the genetic differentiation index by sorghum type pair, it was significant only between sweet grain sorghum and sweet stalk sorghum.

4.2.3. Structuring of the Diversity of All Accessions

The results of the spatial representation of the accessions structure through Correspondence Factorial Analysis (Figure 2) revealed a distribution of the accessions of the three types of sorghum into two large groups according to their genetic similarity in orthogonal space and according to the alleles present. Thus, a weak differentiation is observed between grain sorghum and the two other types of sorghum. The first group (G1) is made up of grain sorghum and sweet stalk sorghum accessions and the second group (G2) of grain and sweet grain sorghums.

Table 3. Intra-type diversity level of sorghum using SSR microsatellite markers.

Types	N	At	Ae	A^P	I	PIC	Ho	He	P (95%)
Sweet grain sorghum	10	18	1.61	0.06	0.50	0.31	0.13	0.35	75.00%
Sweet stalk sorghum	10	22	1.74	0.13	0.61	0.39	0.17	0.44	93.75%
Grain sorghum	14	22	1.83	0.13	0.64	0.41	0.14	0.45	93.75%

At: total number of alleles per sorghum type; Ae: effective number of alleles; Ho: observed heterozygosity; A^P: number of private alleles; He: expected heterozygosity; PIC: Polymorphism Information Content; I: allelic Shannon diversity index; P: polymorphism rate.

Table 4. Inter-type genetic differentiation of sorghum using SSRs.

Types of sorghum	Sweet grain sorghum	Sweet stalk sorghum	Grain sorghum
Sweet grain sorghum	0	**0.017***	**0.033^{ns}**
Sweet stalk sorghum	0.12	0	**0.27^{ns}**
Grain sorghum	0.08	0.02	0

Legend: The upper diagonal in bold is the comparison of Fst by pair of sorghum types and the lower diagonal is the minimum distance of Nei; ns: not significant.

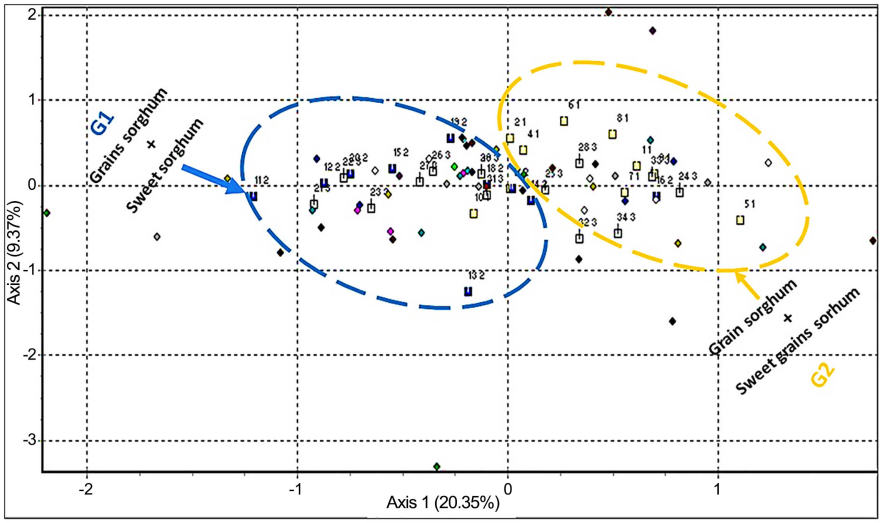

Figure 2. Spatial representation of the structuring of sorghum accessions in a 1/2 factorial design. Legend: Sweet stalk sorghum accessions, Sweet grain sorghum accessions, Grain sorghum accessions.

5. Discussion

The low number of private alleles identified could be related to the gene flow that exists between these sorghum types because despite its preferentially self-pollinated mode of reproduction, sorghum has a relatively high rate of outcrossing ranging from 3% to 31% [11]. Indeed, all five races of the bicolor subspecies can easily cross with each other as well as with wild sorghums of the bicolor species and have fertile hybrids [21]. The three types of sorghum could thus share a common genetic heritage. Similar results were also reported by [22].

The different sorghum variants encountered are thought to be the result of spontaneous mutations in sorghum. Indeed, the mutation occurs approximately every hundred million base pairs in every generation regardless of the living organism especially in eukaryotes [23]. Thus, these mutations have contributed significantly to the processes of evolution, speciation, domestication, and adaptation to environments and agricultural practices of cultivated plant species. These mutations may have been selected naturally or by man according to the objectives sought, which leads to a slow evolution of the genome over time. The genetic diversity of sorghum is therefore the result of a long process of evolution and previous selection within the species.

Sweet grain sorghum showed the lowest expected and observed heterozygosity values. This could be explained by the spatial isolation practiced by the farmers. Indeed, sweet grain sorghum is mostly cultivated in the hut fields, unlike grain sorghum cultivation in the bush fields. This farmer management method would result in a lower intra-type genetic diversity, resulting in a higher homozygosity compared to sorghum grown in bush fields where several types coexist. Previous studies by [24] on early maize varieties in Burkina Faso and [25] on late and early millet varieties in Niger reported similar results.

The low genetic differentiation observed between sweet grain sorghum and grain sorghum would suggest a greater closeness between these two types of sorghum due to their selection criterion based mainly on grain. Thus, sweet grain sorghum would be grain sorghum selected for the taste quality of the grain at a doughty stage of their development and for the earliness of their cycle. Indeed, at the dough stage, sugar is present in the form of fructose, glucose, sucrose etc [26]. These sugars are converted during maturation into starch which is the main reserve form of sugar in grains in cereals [27] [28]. The accumulated starch retains very little sweetness in mature grain. Work on sweet corn or maize has shown that the recessive *su* allele is responsible for the sweetness trait in homozygotes of the *susu* genotype. This allele would allow an accumulation of phytoglycogen instead of the traditional starch [29] [30]. This could be the case for sweet grain sorghum. Therefore, the sweet grain trait is due to the expression of the recessive *su* allele carried on chromosome 4 and results in high sugar production. The gene flow between grain sorghum and sweet grain sorghum could then evolve towards a loss of the sweetness of the grain in the latter.

The significant differentiation index recorded between sweet grain sorghum and sweet stalk sorghum would be of genetic origin. Indeed, these two types of sorghum express the very sweet character but in different accumulation organs. In sweet grain sorghum, the starch biomass is accumulated in the grains and in sweet stalk sorghum, and the saccharide biomass is located in the stem. This divergence of accumulation organs would be closely related to the expression of genes on the morphology of conductive tissues, which is expressed by a better development of the xylem in sweet stalk sorghum than in the other types of sorghum. Similar observations were reported by [31] on two sorghum varieties (grain sorghum and sweet stalk sorghum). A process of change in expression of genes responsible for the sweetness trait could be responsible for this divergence in sugar accumulation in these sorghum. This phenomenon would be common in eukaryotic organisms and would often give rise to new phenotypes. These changes have been frequently used as indirect indicators of functional gene divergence. [32] previously reported this divergence process in plants.

Moreover, this differentiation could be due to cultivation practices associated with the peasant management of sorghum cultivation. Indeed, it is very frequent and even common to encounter grain sorghum-sweet grain sorghum or grain sorghum-sweet stalk sorghum associations in the farming environment. This is not the case for the sweet grain sorghum-sweet stalk sorghum association. Thus, the latter, which could share few genes with each other, would have a common gene pool with grain sorghum, hence the structuring of the 34 accessions into two groups, the first consisting of grain sorghum and sweet grain sorghum, and the second consisting of grain sorghum and sweet stalk sorghum. These results could be explained by the fact that when two groups of initially identical individuals are isolated and maintained in isolation for a sufficient time, differences will develop and accumulate over time between the two groups. If no homoge-

nization process between the two groups is present (exchange of alleles), after a certain time, the differences will be sufficient for the two groups to be no longer compatible or interbreeding [33].

The three sorghum types are thus not well individualized genetic entities despite their distinct names, morphological differences, and differences in organs of interest for each cultivated type. Similar results were reported by [34] on rainfed and transplanted sorghum in the Lake Chad basin. In addition, some authors have shown that differences within a species can also be due to the influence of the environment [35].

The genetic proximity of the crops has led to the possibility of gene flow between sorghums. In the case of related species, management of gene flow is important for maintaining stability, production potential, and even quality of crop products. Management of crops with cross-fertilization potential involves space-time methods such as staggered sowing dates, crop separation, or choice of associations

6. Conclusion

The nuclear microsatellite markers used in this study were quite informative and revealed a little divergence between sorghum types within the collection. Thus, despite belonging to three morphologically well-differentiated sorghum groups, sweet grain sorghum and grain sorghum remain very similar genetically. The sorghum type factor is therefore not a very reliable criterion for characterizing genetic diversity. Differentiation between sorghum types could also be due to physiological or biochemical factors. The results obtained show the need for further study by sequencing the genome of the different types of sorghum cultivated.

Data Availability

The data supporting the findings of this study are available on request from the corresponding author.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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