

Genetic Characterization of Benin's Bambara Groundnut (*Vigna subterranea* (L.) Verdc.) Germplasm using Molecular Markers

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Abstract

Bambara groundnut (*Vigna subterranean* L.), a leguminous crop native to Africa, is of paramount importance to food security as it represents one of the protein source to poor farmers in rural area. However, its genetic diversity and population structure remain poorly understood, especially among the diverse germplasm available in Benin. This study was directed towards genetic characterization of Bambara groundnut population in Benin using single nucleotide polymorphism (SNP) markers. A population of 90 Bambara groundnut accessions were genotyped with SNP markers and analyzed for genetic diversity and population structure. With the population structured into 9 sub-populations, the analysis revealed a higher diversity within the collected germplasm. The results showed a higher observed heterozygosity compared to expected heterozygosity. Population structure analysis demonstrated significant differentiation among accessions from distinct geographical regions, suggesting the influence of environmental factors on genetic variation. Clustering analysis showed that some accessions shared genetic similarities, indicating a common ancestry or gene flow between populations. Results from this research highlights the importance of conservation efforts and the need for targeted breeding strategies that leverage the genetic diversity available in local populations. This study contributes to the understanding of the genetic basis of Bambara groundnut in Benin and provides essential information for future breeding programs and sustainable agricultural practices aimed at improving this underutilized crop. Acquiring knowledge on genetic characteristics of this crop will aid in its conservation and genetic improvement to meet the challenges of food security in a changing climate.

Introduction

Bambara groundnut [*Vigna subterranea* (L) Verdc.] belongs to Fabaceae family, and is widely grown as a plant protein source for human especially in sub-Saharan Africa (Brough and Azamm, 1992; Brough et al. 1993). The Bambara groundnut has 11 pairs of chromosomes ($2n = 22$), is cleistogamous, and is 96% self-pollinated (Forni-Martins, 1986). In addition to being drought-tolerant, the crop can supply nitrogen to agricultural systems and can withstand low fertility soils (Azam et al., 2001). The crop's growth cycle lasts 90–170 days, and in ideal circumstances, it lasts 120–150 days. The crop is high in protein (18–26%) and has a lipid content that is lower than groundnut (45.3–47.7%) but comparable to that of cowpeas (1–1.6%) and pigeon peas (1.2–1.5%) (Azam-Ali et al., 2001). According to Oyeyinka et al. (2017) and Akintayo et al. (2021), the two noteworthy characteristics of Bambara groundnut grain are: i) it is hard-to-cook, and ii) it has resistant starch.

In tropical Africa, Bambara groundnut falls in the third rank of the most significant grain legume (Olanrewaju et al., 2021). It is distinguished by a high nutritional composition, resilience to drought, and high temperatures. Since the seventeenth century, this crop has been native to Africa (Olanrewaju et al., 2021). Bambara groundnut is a potential food security and income generation crop in Sub-Saharan Africa due to its widespread adoption. Annually, 0.3 million tons of this crop is produced in Africa, with an average yield of 0.85 tons per hectare. Previous reports show that Nigeria, Burkina Faso, and Niger are Africa's major producers, respectively producing 100,000 tons, 44,712 tons, and 30,000 tons (Hillocks et

al., 2012). Cameroon is currently one of the top producers, with a global production of 74% (Majola et al., 2021). According to Azam-Ali et al. (2001), the crop's anticipated production in Africa varies from a minimum of 300 kg/ha to a maximum of 3,000 kg/ha. The authors reports that of this poduction, the bulk will come from West African nations with production ranging between 300 and 1,000 kg/ha whereas Southern African countries production ranges from 1,000 to 3,000 kg/ha. As a result, the crop is produced most efficiently in the continent's south. Majola et al. (2021) validated this perspective by noting that the most suited region on the continent for Bambara groundnut production is in the southern African.

One of the main characteristics of legumes is biological nitrogen (N) fixation, which is a natural process that is important to enhancing agricultural productivity (Herridge, Peoples, and Boddey 2008; Unkovich et al. 2008). It has been reported that legumes have a nitrogen fixing capacity of 20–100 kg N per hectare (Linnemann 1991). According to reports, the crop performs well on marginal soils where it is not cost-effective to grow other legume crops like cowpea, common bean, mungbean and groundnut. As a result, it is a preferred crop for low-income farmers who cannot afford all required farm inputs (Roskoski, Pepper, and Pardo 1986; Yakubu, Kwari, and Sandaba 2010). Small-scale farmers grow it mostly throughout semi-arid regions of Africa, where the crop is ranked third among other legumes in terms of cultivation after cowpea and groundnut (Linnemann 1991; Toungos, Sajo, and Gungula 2009). Indeed, this crop can be grown in drier regions where other pulse crops cannot thrive. If used effectively, the crop's extraordinary capacity to flourish in a variety of agroecologies indicates its greater versatility and could make it a viable alternative food legume across the globe.

The low yield of Bambara groundnuts, despite its claimed virtues, is one of the major obstacles to their production (Sidibé et al., 2020; Temegne et al., 2020). Genetic analysis and other strategic technology developments in Bambara groundnut production might yield crucial information for breeding initiatives that will maximize the crop's potential to improve food and nutritional availability when water supplies are limited.

Determination the level of genetic diversity in the study population is fundamental in improvement of the crop. Indeed, among the factors that greatly contribute in enhancing the rate of genetic gain is the existence of high genetic diversity in a breeding population. High diversity presents superior alleles in the population, providing breeders with opportunity to select and develop superior individuals (Swarup et al., 2021). High genetic diversity ensures that breeding programs have resources to help the in adapting to future challenges and this ensures sustainable food security. Analysis of opulation strustructure is a fundamental aspect in all breeding programs. It provides breeders with information on genetic differentiation and diversity between and within subpopulations (Govindaraj et al., 2015). With this information, breeders are able to identify progenitors that are divergent for desirable traits leading to development of varieties that are superior and well adapted to an ecosystem. Identification of structure in a breeding population is fundamental in the development of molecular breeding tools through association studies. In the process of identification of quantitative nucleotides (QTNs), population structure is accounted for in order to counter spurious associations (Uffelman et al., 2021). Therefore,

determination of population structure enhances the reliability of QTNs detected through association studies.

Benin Bambara groundnut germplasm has not yet been the subject of any documented genetic diversity and population structure studies (Ho et al., 2017; Olanrewaju et al., 2022). Therefore, this research was directed towards genetic characterization of Benin's Bambara groundnut germplasm through genetic diversity and population structure studies.

Material and Methods

Materials

The genetic resources used in this study comprised of 90 Bambara groundnut accessions from Benin, Mali, and IITA. This represents Benin's core collection conserved at the Laboratory of Applied Ecology, University of Abomey-Calavi, Benin.

Sample collection and genotyping

The seeds of the accessions were planted in pots at Montpellier, France. Two weeks after planting, the young leaves were collected into a properly labelled 96-well sample collection plate. The samples were sent to SEQART AFRICA, ILRI Campus, Nairobi, Kenya for genotyping. DNA from the leaf tissue samples was extracted using Nucleomag Plant Genomic DNA extraction kit (Macherey-Nagel), and 0.8% agarose was used for quality control. Genome by sequencing technologies (DArT sequencing) were used for genotyping. Using genomic complexity reduction technologies, the genomic DNA library was created (Kilian et al., 2012). The automated clonal amplification system (cBOT Illumina) was used to purify and quantify the library in order to generate clusters. Next-generation sequencing was then carried out with the Illumina HiSeq 2500 sequencer. The readings were compared to the publically available reference genome of *Vigna* on Phytozome 13 (Goodstein et al., 2012) (Lonardi et al., 2019).

Genetic diversity analysis

SNP marker quality control was carried out using *snpReady* package in R statistical software (R) where markers with $MAF < 0.01$ and SNP call rate of 0.80 were filtered out. Population diversity analysis was carried out using *popgen* function of *snpReady* package in R. The computed marker quality statistics included allele frequencies, minor alleles frequency (MAF) and polymorphism information content (PIC). The population's genetic diversity statistics included expected heterozygosity (H_e) also known as gene diversity (GD), observed heterozygosity (H_o), coefficient of inbreeding (F_{IS}), additive variance (V_a) and dominance variance (V_d)

Population structure analysis

Filtered SNP marker data was used to determine population structure within the study population. The number of optimum ancestral populations (K) was identified through *snmf* and *lfmm* algorithms in *LEA* package in R. The identified clusters were visualized in a dendrogram generated using *dendextend* and *circlize* packages. Each accessions was allocated into a cluster group based on values from coefficient of ancestry that were produced in the population structure analysis. It was assumed that an individual truly belonged into a particular cluster when its value of the coefficient of ancestry was above 0.52. in a cluster (Basak et al., 2019).

Genetic relationship and diversity analysis

Diversity statistics within each population and across the subpopulations were carried out in *dartR* package in R. The *NAM* package was used to generate an identity-by-state distance matrix in R in order to verify the number of clusters and look into the evolutionary links between accessions. The neighbor-joining (NJ) approach was used to create a phylogenetic tree in R, with the *Dendextend* package. The genetic diversity parameters including expected heterozygosity (H_e) also known as gene diversity, observed heterozygosity (H_o), coefficient of inbreeding (F_{IS}), and fixation index (F_{ST}) of the identified subpopulations were computed using *snpReady* package in R. Analysis of molecular variance (AMOVA) was implemented using *poppr* package in R.

Results

The population MAF ranged between 0.01 and 0.5 with a mean of 0.15. The mean genetic diversity (GD) /expected heterozygosity (H_e) was 0.22 and this was higher than the means of observed heterozygosity (H_o) that stood at 0.02. The mean polymorphic information content (PIC) was 0.18 ranging from 0.02 to 0.38. The population has a mean coefficient of inbreeding (F_{IS}) of 0.81 and this ranged from 0.05 to 1.0. Additive genetic variance (V_a) was high (1162.27) compared to dominance variance (V_d) which stood at 405.33 (Table 1).

Table 1
Diversity statistics of the population

	Mean	Lower	Upper
GD/He	0.22	0.02	0.5
PIC	0.18	0.02	0.38
MAF	0.15	0.01	0.5
Ho	0.02	0	0.21
F _{IS}	0.89	0.05	1
Va	1162.27		
Vd	405.33		

The population was structured into 9 sub-populations (Fig. 2). This was revealed through *snmf* model which indicated 9 ancestral populations having the lowest cross-entropy value. Similarly, eigenvalues of principal components' scree plot from *lmm* model showed an elbow at the 9th principal component (Fig. 1). As shown in Fig. 2, the 9 ancestral clustered were visualized in a dendrogram.

The AMOVA revealed that there was 24.68% variation between the nine differentiated populations. The results indicated that within variation was high (75.32%) compared with between variation (Table 2).

Table 2
Analysis of molecular variance

	Df.	Mean Square	Percent
Variation between clusters	8	3999.92	24.68
Variation within clusters	81	1000.64	75.32
Total variations	89	1270.24	100.00
Df. = degree of freedom			

The nine population clusters arising from population structure results had different number of individuals with the highest subpopulation having 31 individuals while the smallest having 3 individuals. In all subpopulations, observed heterozygosity was higher compared to expected heterozygosity. Each of the nine subpopulations had observed heterozygosity of 0.38 or 0.39 whereas expected heterozygosity across the population ranged between 0.21 to 0.23. All the sub populations had negative inbreeding coefficient (F_{IS}) ranging from - 0.46 to -0.66 (Table 3).

Table 3
Cluster diversity statistics

Pop.	nInd	polyLoc	monoLoc	Ho	He	F _{IS}
5	31	4052	1250	0.38	0.23	-0.63
3	11	3575	1727	0.39	0.23	-0.62
6	4	2606	2696	0.39	0.21	-0.60
8	5	2853	2449	0.39	0.22	-0.56
1	7	2808	2494	0.39	0.22	-0.65
2	14	3242	2060	0.38	0.22	-0.66
4	11	3146	2156	0.39	0.22	-0.66
9	4	3029	2273	0.39	0.23	-0.46
7	3	2691	2611	0.39	0.22	-0.47
Pop. = Population, nInd = number of individuals, polyLoc = polymorphic loci, monoLoc = monomorphic loci						

The inter-population fixation index (F_{ST}) across the nine subpopulations were near zero and this ranged between 0.02 and 0.13 (Table 4). Results from admixture analysis showed that the nine subpopulations were sharing their genetic materials (interbreeding) freely as indicated in Fig. 3.

Table 4
Fixation indices (F_{ST}) across the nine sub populations

	Pop. 5	Pop. 3	Pop. 6	Pop. 8	Pop.1	Pop.2	Pop.4	Pop.9
Pop.3	0.02	NA						
Pop.6	0.09	0.10	NA					
Pop.8	0.04	0.06	0.08	NA				
Pop.1	0.04	0.06	0.13	0.09	NA			
Pop.2	0.03	0.05	0.11	0.08	0.03	NA		
Pop.4	0.02	0.04	0.12	0.07	0.06	0.06	NA	
Pop.9	0.05	0.06	0.09	0.05	0.08	0.07	0.07	NA
Pop.7	0.06	0.08	0.13	0.08	0.08	0.08	0.08	0.06

Discussion

This research aimed at identifying the extent of genetic diversity and population structure in the Bambara groundnuts population. Genetic diversity is important in the initial stage of breeding because it provides access to novel alleles for use in crop improvement. Crop diversity provides scientists with resources to use in improving crops against unforeseen crop production constraints. The study population markers had a mean PIC of 0.18 and this polymorphism level had been classified to have medium informativeness while PIC of 0.30–0.4 is high and 0.4–0.5 is very high (Serrote et al., 2020). Nevertheless, the marker data had SNPs that having PIC of up to 0.38 which is considered to be highly informative. Heterozygosity is associated with the presence of genetic diversity in a population. The study population exhibited a moderate diversity levels with mean $H_e = 0.22$ whereas mean $H_o = 0.02$. In population genetics, the use of H_e is more reliable compared to H_o because unlike H_o , H_e is not dependent of sample size. (Mukhopadhyay & Bhattacharjee, 2016; Serrote et al., 2020). The entire population showed a significantly high H_e compared to H_o and this could suggests that this population is generally inbreeding (Mukhopadhyay & Bhattacharjee, 2016). This is further validated by the population having a high F_{IS} of 0.89 ranging from 0.05 to 1.0 among population individuals. A high F_{IS} indicates a considerable degree of inbreeding in a population.

The population was structured into nine subpopulations based on *snmf* function of LEA package. The *snmf* function employs sparse Non-Negative Matrix Factorization (sNMF) to compute admixture coefficients, which gives an output similar to that of STRUCTURE. The variability within the subpopulation was higher (75.32%) than between the subpopulations (24.68%) as revealed by AMOVA. The implication of this result is that selection can be carried out reliably within subpopulations compared to between populations. There was genetic diversity in each of the subpopulation where H_e ranged between 0.21 and 0.23 while H_o ranged between 38 and 39. Presence of heterozygosity is an indication of genetic diversity. Therefore, each of the sub population had diverse genotypes. Unlike the overall population, in each subpopulation H_o was greater than H_e , which indicates the population was being crossed so as to avoiding inbreeding (Mukhopadhyay & Bhattacharjee, 2016). Furthermore, the F_{IS} ranged between – 0.46 and – 0.66; an indication that the subpopulations had excess heterozygotes. The inter-population fixation index (F_{ST}) was below 0.15 across the subpopulations. This implies that the population was into panmixia and thus, the subpopulations shares the genetic diversity. Indeed, the admixture proportion revealed that some individuals in a subpopulation shared some genetic proportion of another subpopulation.

In comparing our results with previous studies, there was both similarities and differences in the genetic characteristics of the crop. Our findings of moderate genetic diversity align with those reported by Mayes et al. (2019) whose study was based on West African Bambara groundnut accessions. However, we observed higher levels of diversity compared to the study by Molosiwa et al. (2015) on Southern African landraces, which may be attributed to the broader geographical range of our Benin germplasm. The genetic diversity observed in our study ($H_e = 0.22$) indicates a moderate level of variation within the Benin Bambara groundnut population. This diversity is crucial for breeding programs and adaptation to various environmental conditions (Aliyu et al., 2016). The diversity levels are comparable to those found

in other legume species such as cowpea (*Vigna unguiculata*) by Xiong et al. (2018), suggesting similar evolutionary pressures on these crops. Based on population structure, our analysis revealed nine distinct genetic clusters within the Benin germplasm. This structure is more complex than that reported by Oyeyinka et al. (2015) for Nigerian Bambara groundnut, which identified two main clusters. The observed structure in our study may reflect the diverse agroecological zones in Benin and the influence of farmers' selection practices (Gbaguidi et al., 2018). Understanding this population structure is essential for developing effective conservation strategies and tailoring breeding programs to specific eco-geographical regions.

DArT SNP markers used in this study offer several advantages, including high throughput, genome-wide coverage, and cost-effectiveness compared to traditional markers (Kilian et al., 2012). In this work, DArT SNP markers revealed significant genetic diversity among the Bambara groundnut accessions in Benin, allowing for the identification of distinct genetic clusters and potential geographic patterns of diversity. However, as limitations, the DArT SNP markers are typically dominant, which can limit the detection of heterozygotes (Wenzl et al., 2004). This may affect the accuracy of genetic diversity estimates, particularly in highly heterozygous populations. Additionally, the genome coverage of DArT markers may not be uniform across all chromosomes, potentially leading to bias in diversity assessments (Cruz et al., 2013). Despite these limitations, these markers have demonstrated their utility in characterizing genetic diversity in various crop species, including orphan crops like Bambara groundnut (Olukolu et al., 2012). The high number of polymorphic markers obtained in this study suggests that DArT SNP markers are well-suited for genetic diversity analysis in Bambara groundnut, providing valuable insights into the population structure and genetic relationships among Benin accessions.

The findings of this study highlight that the current germplasm collection represents a valuable reservoir of diverse alleles. This diversity can be exploited for crop improvement programs, particularly for developing of genetically superior varieties that can withstand the prevailing challenges (Mayes et al., 2019). Grouping the population into distinct genetic clusters within the Bambara groundnut germplasm implies the existence of potentially adapted gene pools. This information can guide breeding strategies, allowing for the development of heterotic groups and the exploitation of hybrid vigor in future breeding programs (Aliyu et al., 2016). Moreover, the genetic structure revealed by this study can inform conservation strategies, ensuring that the full spectrum of genetic diversity is preserved in ex situ collections and in situ conservation efforts.

Future research on the genetic diversity of Bambara groundnut (*Vigna subterranea*) should focus on extensive sampling across varied agro-ecological zones to capture a broader range of genetic variability. Incorporating advanced genomic techniques such as whole-genome sequencing could unravel deeper insights into polymorphisms that contribute to preferred agronomics traits such as drought tolerance and pest or disease resistance (Kumar et al., 2021). Moreover, studies exploring the functional genomics of identified SNP markers may help elucidate the underlying genetic mechanisms influencing phenotypic traits (Li et al., 2022). Integration of molecular data with phenotypic assessments under varying environmental conditions could enhance our understanding of genotype-by-environment interactions,

aiding in the development of climate-resilient varieties. Furthermore, comparative studies across other leguminous crops could offer contextual knowledge on evolutionary adaptations and farming strategies (Tivana et al., 2020). Such directions not only augment current genetic resources but also ascertain food security initiatives in the region.

Genetic diversity serves as a reservoir for traits critical to adaptation and resilience, especially in the context of climate change (FAO, 2020). The findings of this study demonstrate substantial variation within Benin's populations, providing opportunity to breeders aiming at selecting individuals with superior alleles (Chijioke et al., 2023). Such diversity is essential for sustaining agro-biodiversity, which is vital for long-term food security and development of superior varieties that are resilient to stresses (World Bank, 2019). Thus, the conservation and utilization of the genetic diversity in Bambara groundnut not only support local agricultural systems but also promote ecosystem health and sustainability.

The results indicated considerable genetic variation among the assessed accessions, suggesting the presence of diverse genotypes that are pivotal to breeding programs. The high genetic diversity identified is vital as it points toward a broad potential for improvement in traits such as yield, pest resistance, and drought tolerance (Foyer et al., 2016). Moreover, the population structure analysis dissected more into the genetic relationships across the accessions, which is essential for strategic conservation and utilization of this underutilized legume (Vernays et al., 2018). Overall, this study lays the groundwork for future research aimed at enhancing the value and adaptability of Bambara groundnut through effective conservation and robust breeding strategies.

Conclusion

This study investigated the genetic characteristics of Bambara groundnut germplasm in Benin through genetic diversity and population structure analysis. The results revealed a moderate genetic diversity within the germplasm, indicating a modest range of genetic variation for potential improvement programs. The population structure analysis revealed distinct genetic groups, suggesting potential geographic and historical influences on the germplasm's genetic of Bambara groundnut. The identified genetic clusters give useful information for targeted breeding techniques towards the improvement of particular traits in the crop. The high level of genetic diversity observed in this study underscores the importance of preserving this valuable germplasm for future generations. Furthermore, the identification of distinct genetic groups provides opportunities for developing new varieties with desirable traits. The study provides a solid foundation for future research focused on understanding the genetic basis of key agronomic traits, thereby facilitating the development of improved Bambara groundnut varieties with enhanced yield, resilience to biotic and abiotic stresses and nutritional value as well. This research serves as a valuable resource for breeders and researchers working to improve Bambara groundnut production in Benin and beyond.

Declarations

Competing interest

All authors declare that they have no competing interest

Author Contribution

S. A. contributed to the conceptualization of ideas, project administration, investigation, mobilization of resources, and supervision. W. A. contributed to formal data analysis, designing research methodology, and review. J.B. B. contributed to writing, supervision, and review. D. K. contributed in writing, supervision, and review. S. B contributed in writing, supervision, and review

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Data Availability

The data generated in this research is available upon request

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Figures

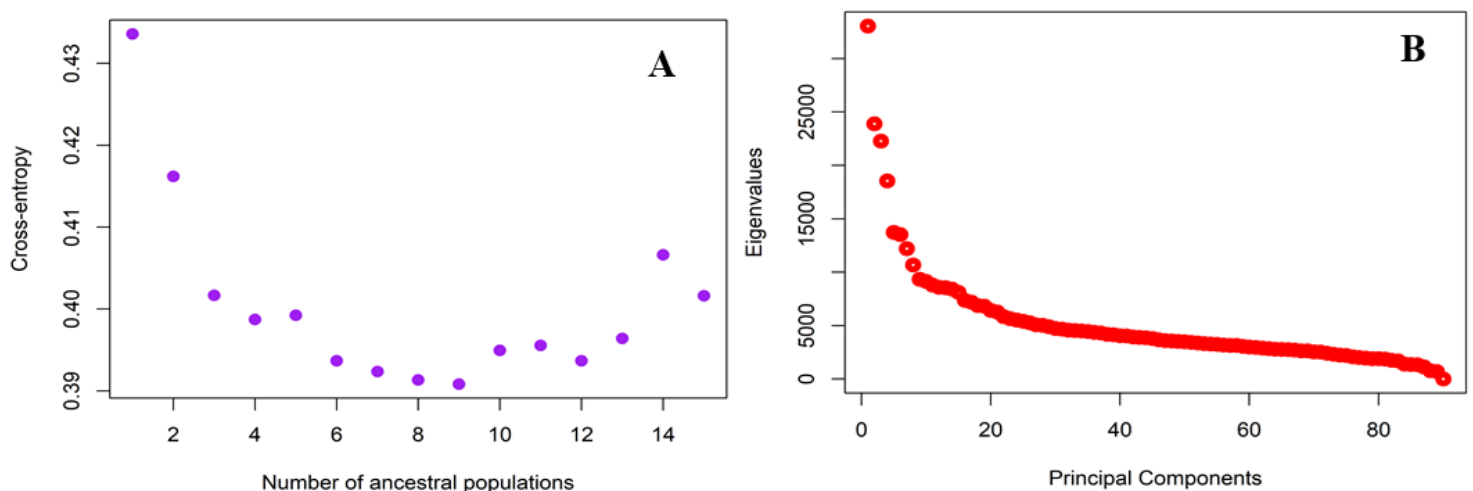


Figure 1

Identification of optimal ancestral clusters (K) using A= snmf and B= lfmm models

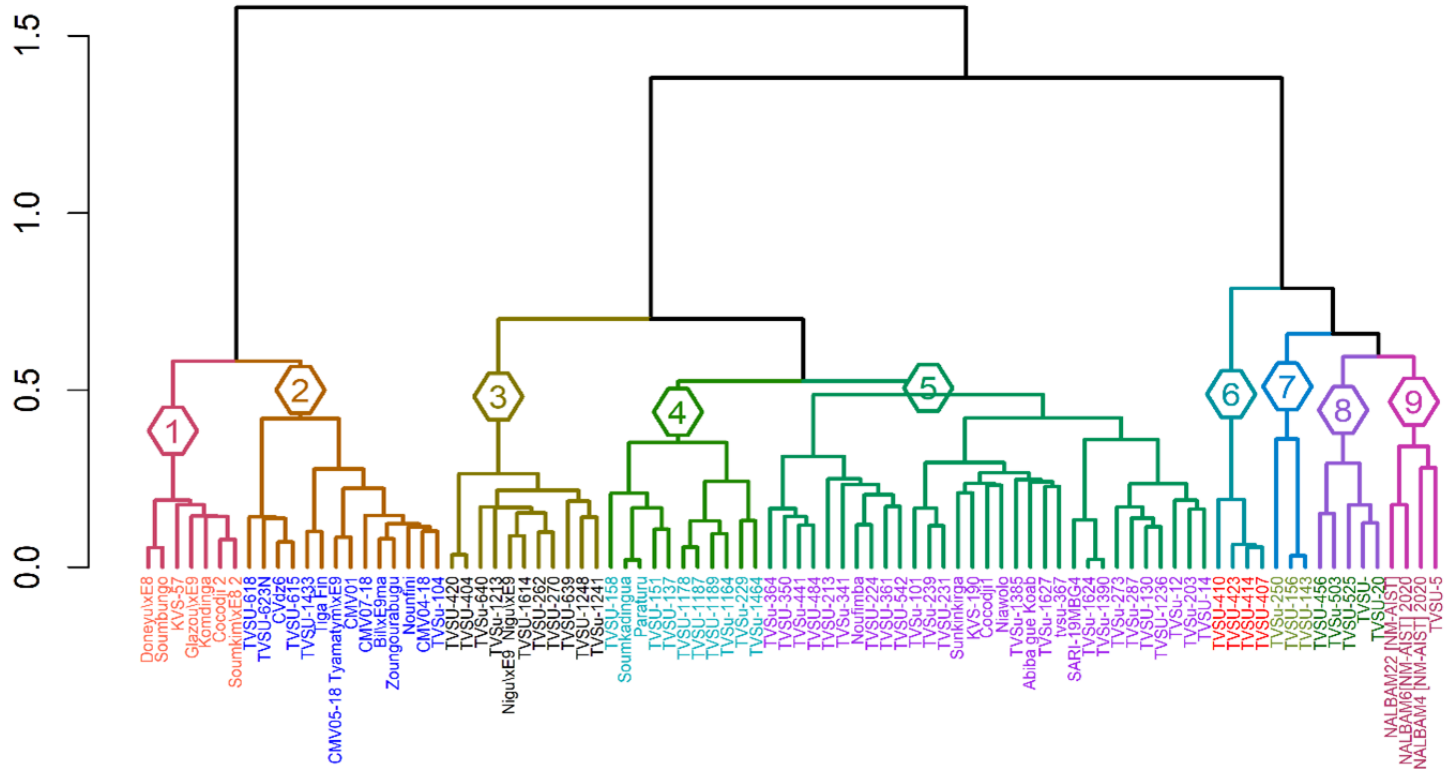


Figure 2

Dendrogram showing the 9 subpopulations

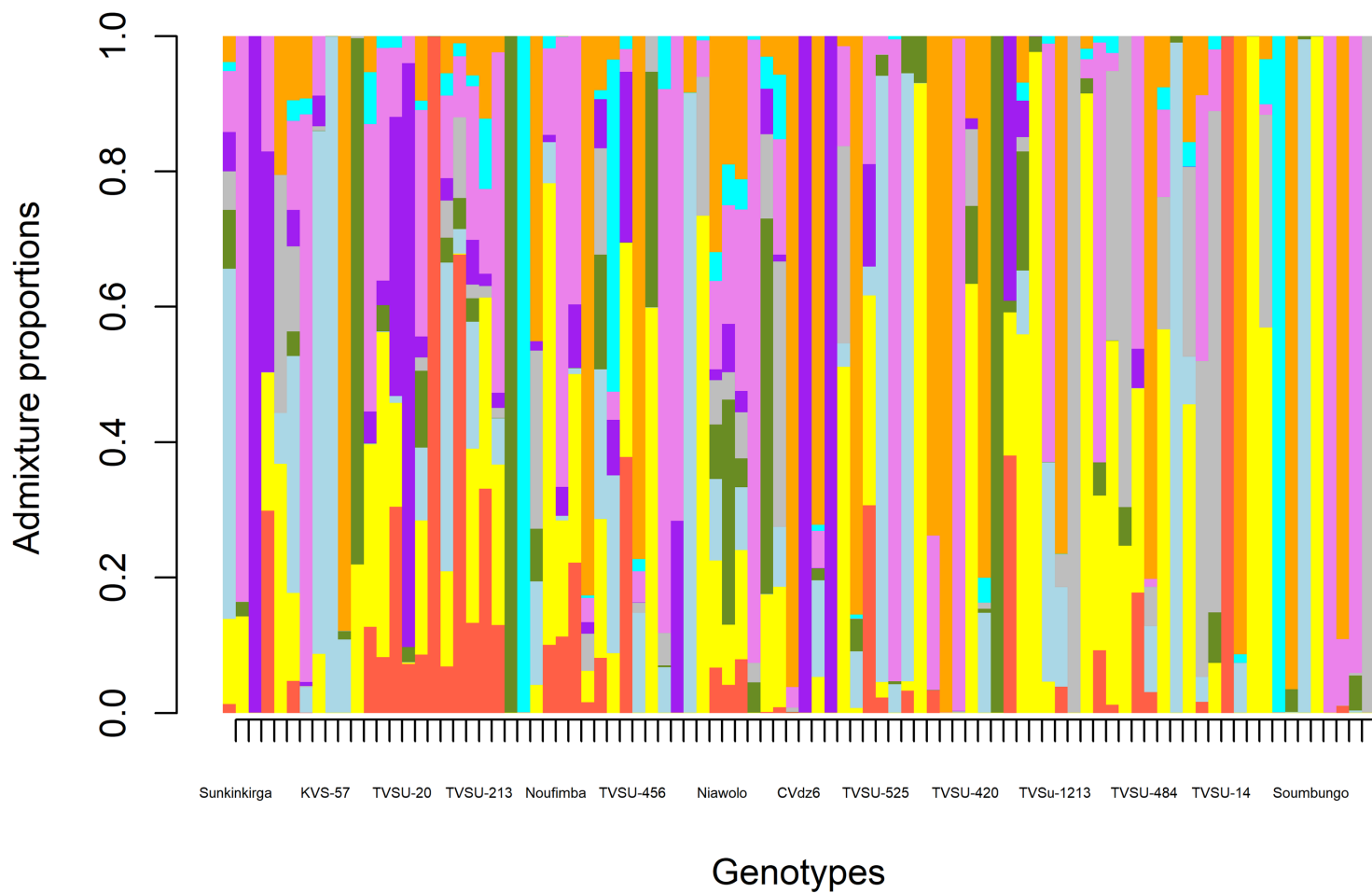


Figure 3

Genetic admixture proportions across nine sub populations