

Genotyping, distribution and structure of Benin's rice germplasm using Infinium 7k SNP array

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Research Article

Keywords: Rice, 7K SNP, Structure, Farmer preferences, Benin

Posted Date: September 10th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10892690/v1>

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Additional Declarations: No competing interests reported.

Abstract

Rice (*Oryza* spp.) cultivation has expanded considerably in West Africa over the past two decades, becoming a major staple crop, particularly in Benin. This expansion has been driven by the introduction of improved interspecific varieties such as NERICA and IR841, which are well adapted to local agroecological conditions. However, the coexistence of Asian rice and African rice in traditional farming systems promotes seed exchange and natural hybridization, leading to morphologically similar phenotypes that complicate varietal identification and management. This study combines molecular and socioeconomic approaches to investigate the genetic diversity and structure of rice germplasm, assess interspecific introgression, and relate genetic patterns to farmers' selection criteria. A total of 79 rice accessions, including 7 reference varieties (TOG5681, TO5307, CG14, Azucena, Moroberekan, IR64 and IR841), were genotyped using a 7K SNP array. After quality filtering, 5,526 SNPs were retained for downstream analysis. The genetic diversity indexes showed that there was moderate variability, with an average PIC of 0.27 and a low heterozygosity ($H_e = 0.06$). Multivariate, phylogenetic, and structure analyses consistently revealed a strong population structure, with four main genetic groups. Most accessions clustered within the indica group, while others were assigned to aus, tropical japonica, or *O. glaberrima*, with evidence of admixture and introgression. Farmers' preference analysis identified productivity, vegetative cycle, and disease resistance as the most important selection criteria. These findings provide insights into the structure and evolution of rice germplasm in Benin and support the development of breeding strategies that integrate both genetic diversity and farmers' needs.

1 Introduction

Rice cultivation (*Oryza* spp) has experienced a remarkable expansion over the past two decades in West Africa, becoming one of the region's major staple crops with production accounting for about 65% of the total rice output in sub-Saharan Africa (Soullier et al. 2020).

In Benin, in particular, rice contributes significantly to food security and poverty reduction and ranks second, after maize, in both national production and consumption (Ndindeng et al. 2021). Rice production in Benin has increased substantially over the last decade, reaching approximately 5,966.84 tons of paddy rice cultivated on a total area of 1,267.48 hectares (Faostat, 2021). This improvement is largely attributed to the introduction of improved interspecific varieties derived from crosses between *O. glaberrima* and *O. sativa*, notably the NERICA (New Rice for Africa) and IR841 varieties (Sanni et al. 2008). Indeed these improved rice varieties are better adapted to local agroecological conditions (Sedah et al. 2023). Although progress has been made, national production is only covering approximately 25% of domestic consumption, resulting in a strong reliance on imports (Houngue and Nonvid, 2021).

Beyond productivity concerns, the massive introduction of the improved rice varieties raises questions regarding their effects on the conservation and dynamics of genetic diversity among local rice varieties. In many smallholder farms across Benin, Asian rice (*O. sativa*) and African rice (*O. glaberrima*) are grown side by side within the same agroecological zones (Loko et al. 2021). This coexistence promotes seed

exchange among farmers, which may lead to the substitution of varieties exhibiting morphologically similar phenotypes. These dynamics can hinder the accurate distinction between *O. glaberrima* and *O. sativa* in germplasm collections and breeding programs, partly due to the variability and convergence of certain morphological traits, particularly those related to panicle architecture, as reported in several studies on rice diversity and domestication (Wang et al. 2014; Meyer et al. 2016; Ntakirutimana et al. 2023)

Such dynamics may lead to the emergence of morphologically similar phenotypes, making it sometimes difficult to distinguish between *O. glaberrima* and *O. sativa* varieties in germplasm collections and breeding programs. Breeders face significant practical and scientific challenges due to this morphological distinction, which complicates the reliable identification of lines and the management of target traits. It also raises concerns about the preservation of specific and varietal diversity for conservation purposes. For farmers, it affects their seed choices, cultivation practices, and the transmission of local knowledge. In areas of co-cultivation and seed exchange, these social dynamics interact with biological processes, reinforcing the need for an integrated approach. In this context, it is essential to combine molecular analyses with socio-economic surveys to: (i) characterize the actual genetic structure of local rice germplasm; (ii) determine the spatial distribution and frequency of introgressions between *O. sativa* and *O. glaberrima*; and (iii) link genetic data with farmers' preference and selection criteria. The present study addresses these needs by genotyping a representative set of cultivars, analyzing their distribution and genetic relationships, and assessing farmers' perceptions and motivations for variety selection. The purpose is to provide guidance for conservation strategies, breeding programs, and participatory seed management frameworks.

2 Materials and methods

2.1 Materials

Rice varieties were collected from the JEAI-GRAB/Benin project upon a survey carried out from the North to the South of Benin in the various rice-producing areas (Loko et al. 2021). A group survey was organized in each selected village, bringing together the identified rice producers with the help of local officials. An inventory of the rice varieties grown was set up, followed by a socio-demographic characterization of the producers from whom the seed accessions were collected. The final collection was composed of 79 samples, 72 of which are paddy rice cultivars from 22 villages in Benin (Table S1). In addition, 07 other pure line rice varieties, including 05 (TOG5681, TOG5307, CG14, Azucena and Moroberekan) from the genebank of the "Institut National de Recherche pour le Développement Durable (IRD)" in Montpellier/France and 02 other ecotypes (IR841 and IR64) from the genebank of the "Institut National de la Recherche Agricole Béninoise" were collected for the experimentation.

2.2 DNA extraction and SNP genotyping with 7K SNP Illumina Infinium

The collection was purified by phenotypic evaluation of accessions to eliminate off-types and duplicates in the collection (Sedah et al. 2023a). After sowing 10 seeds from each accession in soil-filled pots, seedlings were established. At 21 days after sowing (DAS), three leaves were sampled from a single seedling per accession. The leaves had an average length of 15.6 cm and a width of 0.6 cm, and were subsequently oven-dried at 45°C for 72 hours. They were sent for genotyping at the Genotyping Services Laboratory of the International Rice Research Institute (IRRI), Los Baños, Philippines. DNA extraction was performed from leaf samples using CTAB according to the protocol of the IRRI Genotyping Services Laboratory and genotyping was performed using the SNP 7K Infinium array for Rice (C7AIR) with Illumina technology (Morales et al. 2020).

2.3 Data analysis

Genotype data from the rice whole genome were filtered according to (i) $\leq 5\%$ heterozygosity (he) and (ii) $\geq 1\%$ minor allele frequency (MAF) as described by Ndjioudjop et al. (2017). Benin genotypes were compared to genotypes from around the world using sequence data from the 3,000 accessions genotyped by Wang et al. (2018) using the same procedures adopted by Barro et al. (2021) and Sedah et al. (2023). Briefly, data were filtered using R v4.1.2 by the R Core Team (2021) based on the number of the common SNP markers between the sequencing data from the Benin samples and those from Wang et al. (2018). After performing a principal component analysis, the results were projected onto the PCA axes (XYZ). The DaPC (Discriminant Analysis of PCA) package from adegenet (<http://adegenet.r-forge.r-project.org/>) was used to identify the discriminant functions and applied to the Benin samples to assign genetic groups that represent of the global diversity of rice.

For the phylogenetic analysis, each dataset was converted to 'interleaved' phylo format and imported into R v4.0.335 using the ape version 5.4-1 package (Paradis et al. 2004). The Neighbors John (NJ) trees were constructed using a maximum-likelihood approach and bootstrap analysis methods with 200 replicates using version 2.5.5 of the R/phangorn package (Schliep 2011). The 'Newick' format of the trees was exported and refined using the online program iTOL v5 (Letunic and Bork 2021).

Heterozygosity, IBS-based genetic distance matrices and Principal Component Analysis (PCA) were calculated using TASSEL v.5.2.58 (Bradbury et al. 2007). The first three principal components of the PCA were plotted for visual inspection in CurlyWhirly based on the method of performing a Classical Multidimensional Approach (MDS) using GLAND v.5.2.58 (Gouda et al. 2021). The R/poppr package version 2.9.3 (Kamvar et al. 2014) was used to perform Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992) to detect genetic variance within and between populations using the PhiPT value (analogue of the F_{ST} fixation index) (Holsinger and Weir 2009).

The HapMap format of each dataset was exported in PHYLIP interleaved format using TASSEL v.5.2.57, which was then converted to MEGA X (Kumar et al. 2018) and formats using PGDSpider v.2.1.1.3 (Pritchard et al. 2000). MEGA X was used to determine the number of segregating sites (S), calculate the proportion of polymorphic sites (Ps), estimate diversity parameters (θ) based on the number of segregating sites in the samples and estimate the average number of pairwise nucleotide difference

between two sequences (π). A site (SNP) was considered to be segregating if it had two or more nucleotides at that site.

Population structure was analyzed using the model-based method implemented in STRUCTURE v.2.3.4 software (Pritchard et al. 2000). Accessions with membership probabilities > 60% were assigned to the same clusters (group), while those with probabilities < 60% in any group were assigned to a 'mixed' group (Gouda et al. 2020; Ndjioudjop et al. 2017).

The major agronomic parameters (Cycle, drought resistance, productivity, disease resistance, processing and cooking speed, and Taste) in the farmer's production system were assessed using descriptive statistics computed on scores obtained from the pairwise ranking (Tchokponhoué et al. 2021).

3 Results

3.1 Characterization of the rice collection using SNPs based on the infinium 7k chip

After cleaning and filtering, 5,526 SNPs were extracted from the 7,098 SNPs generated by the 7k Rice SNP chip to estimate the diversity and determine the structure of the benign rice germplasm. However, 5,170 SNPs were retained from the 7,098 starting SNPs for genotyping accessions. The SNPs were distributed across the rice genomes ranging from 362 SNPs (6%) on chromosome 9 to 657 SNPs (14%) on chromosome 1. The average map length per SNP ranged from 56 kb (chromosome 11) to 78 kb (chromosome 5) (Figure S1).

Polymorphism Information Content (PIC), Major Allele Frequency (MAF) and Heterozygous Proportion (He), as well as Genetic Distance were calculated to assess the global genetic diversity within the Benin rice collection. From the 5,526 SNPs in the 79 accessions, the PIC ranged from 0.02 to 0.69 with an average of 0.27. The heterozygosity ranged from 0 to 0.49 with an average of 0.06 (Figure S2), and the frequency of Major Alleles at each locus varied from 0.34 to 0.99 with an average of 0.82 (Figure S3). Finally, the genetic distance calculated between accessions taken in pairs varied between 0.004 and 0.645 with an overall mean of 0.263.

3.2 Genotypic diversity of Beninese rice accessions in relation to global rice diversity

Principal Component Analysis (PCA) based on the filtered complete dataset (7k Benin + 3k RGP) resulted in a good predictor for group membership (over 90% correct posterior assignment compared with prior information), particularly for the *indica*, *aus* and aromatic groups. The vast majority of Benin genotypes were classified as *indica*, two belonging to the *aus* group and two to the tropical *japonica* group, while a five were classified as intermediate between the *aus* and tropical *japonica* groups, being probably hybrids (Fig. 1). Discriminant analysis of the PCA (DAPC) showed that the genotypes cover some of the different clusters of the *indica* subspecies, but with the majority belonging to the *indx* cluster (Figure S4).

3.3 Phylogenetic relationship and population structure

Based on the 5,526 SNPs, phylogenetic clustering revealed 6 genetic groups (G1, G2, G3, G4, G5 and G6) using the Neighbor-joining (NJ) method (Fig. 2). On the other hand, projection of the accessions onto the first three axes revealed 4 major groups, such as the G1 group, the grouping of the G3, G4 and G6 groups, the G2 group and the G5 group (Fig. 3).

Group I (G1) contained 17 accessions with 9 local varieties, including IR841, R8, Essai, Moii Poua, Bériss21, Yayi Boni4, Inaris, Moii laque and NERICAL41, including the control IR841. Samples in this group came from the North, Center and South departments of the country.

Group II (G2) contained 14 accessions, including 9 local varieties (Burkina, Yayi Boni2, IR841, Wondia, Bakilafema, NERICAL20, Pointinini, Moii nihoun) and the control IR64. This group is characterized as 'lowland rice', with samples coming solely from the department of Atacora in northern Benin.

Group V (G5) is a mixed group containing both *O. sativa* controls (the varieties Azucena and Moréberékan) and *O. glaberrima* controls (the varieties TOG5681, TOG5307 and CG14).

This group is made up of 13 accessions with the local varieties Yoncomon, Takomorri, Degaule, Gbega1 and 2, Antonoumon, Moii doenoun and Bakikrouma. Group VI (G6), containing 16 accessions, is made up entirely of local varieties and is essentially represented by samples from the Atacora Department.

Analysis of the genetic structure of the collection of 79 accessions using the STRUCTURE Bayesian clustering algorithm with different levels of K (number of subpopulations) revealed significant levels of variation. Optimal structuring of the collection was observed for maximum likelihood with ΔK , $K = 4$ (Fig. 4a), suggesting the presence of four primary rice populations in the Benin collection (Fig. 4b). These populations present a grouping that corresponds logically with the expected taxonomic and phylogenetic relationships, and adequately matches the groups obtained with the trees described by the NJ method.

The population 1 (Pop1) is the largest one and contains 47 (59.49%) accessions of improved elite varieties with high yields and long aromatic grains (IR841, IR64, and NERICA 20), including the controls IR841 and IR64, and nine local varieties. This population includes all genetic groups (G1, G2, G3, G4 and G5) except for group G6. The population 2 (Pop2) contains 18 (22.78%) accessions, mainly local varieties with two improved varieties (possibly due to naming errors). The population 3 (Pop3) represents the *O. glaberrima* controls (TOG5681, TOG5307 and CG14) and two other accessions, Bagou17 and Tchaka39B (possibly *O. glaberrima*). Finally, the population 4 (Pop4) contains the *O. sativa japonica* controls (Azucena and Moroberekan) with the Bagou22 accession.

3.4 Selection criteria for producers

Out of the nine selection criteria evaluated, farmers found productivity, vegetative cycle, and disease resistance to be the most significant. Productivity ranked first with a score of 2.259, reflecting producers’ strong preference for high-yielding varieties capable of improving production and income. The vegetative cycle came in second place with a score of 2.631, which shows how important it is for farmers to choose varieties that have an appropriate growth duration for better adaptation to seasonal conditions and cropping calendars. Disease resistance ranked third with a score of 2.504, highlighting farmers’ concern for varieties that can reduce yield losses and ensure more stable production under field conditions. Overall, these results suggest that farmers prioritize traits that directly influence productivity, crop adaptation and resilience to biotic stresses (Table 1).

Table 1
Order of importance of selection criteria

Parameters	Importance Score (IS)	Rank N
Cycle	2.631	2nd
Drought	2.646	7th
Productivity	2.259	1st
Diseases	2.504	3rd
Transformation	2.346	4th
Cooking	2.335	5th
Taste	2.331	6th

4 Discussion

Maintaining and managing varietal diversity in crops such as cereals (maize, rice), legumes (cowpea) and certain tubers and roots (cassava) requires frequent evaluation of germplasm (Ademilola et al. 2024). These germplasm are subject to change and are not under the control of researchers and breeders due to the introduction of certain farm-preferred cultivars for their performance (Gatto et al. 2021; Thiele et al. 2021).

PCA analysis showed that out of the five existing rice phylogenetic groups identified on the basis of SNPs, namely *indica*, *aus*, aromatic, temperate *japonica* and tropical *japonica* (Garris et al. 2005; McNally et al. 2009; Wang et al. 2018 and Fuentes et al. 2019), only three (*indica*, *aus* and tropical *japonica*) are present in Benin, with the majority of samples (82.19%) classified in the *indica* group. These results are consistent with those observed by Sedah et al. (2023b) using phenotypic descriptors and made are similar to those observed by Kam et al. (2017) and Barro et al. (2021) on rice germplasm in Burkina Faso, also dominated by *O. sativa ssp indica*. These results are also concordant with previous studies on the good adaptation of the Asian species to the hot and humid climate in Africa in general, and particularly in West Africa, including Benin (Chevalier, 1937; Sarla and Swamy 2005). In fact, the Beninese rice-growing

system is dominated by lowland rice cultivation (Dansou et al. 2016), thus *indica* varieties suit better than their *japonica* counterpart, which are adapted to cooler and drier ecological environments.

Diversity in terms of species (*O. sativa* and *O. glaberrima*) is low, as expected, but very pronounced in terms of sub-populations, as revealed by the DAPC, indicating that a good proportion of the global *indica* diversity is present in Benin. The structural analysis is consistent with the DAPC suggesting that the germplasm can be subdivided into four primary groups. Population 1 (59.49% of samples) containing elite varieties such as IR841, IR64 and NERICA-L confirming the phenotypic trends observed in our previous work on the agromorphic characterization of cultivars in the Beninese rice germplasm (Sedah et al. 2023b). The dominance of improved cultivars in the Beninese rice germplasm can be explained by the varietal selection criteria of producers and consumers (long grain and aromatic, high yield, short or medium growing cycle, and disease resistance). Producers therefore prefer short-cycle varieties with higher yields and disease resistance, as shown by the pairwise scores. This contrasts with the low rate of *japonica* (Population 4 = 5.06%) whose grains are more often short, round and sticky when cooked. In fact, IR841 is a popular long grain rice variety widely grown in West Africa for its high yield potential, early maturity and disease resistance. In Benin, it is by far the most widely grown (Loko et al. 2021, 2022), known as AGRA in Ghana (TAAT 2021), exported and marketed in the USA as Jasmine 85 (Adjah et al. 2022). Similarly, IR64 is another high quality, high yielding, disease resistant, long fine grain, lowland reference *indica* variety that was first released in the Philippines in 1985 and grown in West Africa, including Burkina Faso, Gambia, Togo and Benin (Mackill and Khush, 2018; Melandri et al. 2021; Adjah et al. 2022). NERICA-L (New Rice for Africa, Nassirou and He 2011), on the other hand, is a cross between *O. glaberrima* and *O. sativa ssp indica* that combines the advantages of both species. More than 80 improved *indica* varieties, including 60 lowland varieties (NERICA-L), have been developed and disseminated in West Africa, including Benin (Ndjiondjop et al. 2008).

The low rate (Population 3 = 6.32%) of cultivars of African species (*O. glaberrima*) observed testifies to the popularity of Asian rice in the germplasm and corroborates the observations made by Odjo et al. (2017) about the abandonment of African rice by Beninese producers. The high yields and resistance to certain diseases such as the rice yellow mottle virus of improved varieties, combined with adaptation to climatic conditions, have led to the gradual abandonment of African rice (*O. glaberrima*) in favor of Asian rice (*O. sativa*), which has become a popular choice for rice-growing systems in Africa since the 1990s (Sié et al. 1998; Barry et al. 2007).

Previous studies by Loko et al. (2021) on the management of diversity in rice systems in Benin have shown that northern Benin, including the Atacora department, contains the greatest diversity of local rice cultivars in the country. This observation is consistent with the results of the structural analysis using SNPs in this study. Indeed, the presence of local *indica* cultivars (Population 2 = 22.78%), all mainly dependent on the Atacora Department, raises hypotheses and explanations. The first probable explanation is that the populations of northern Benin are, especially those of the Atacora and Donga departments, never depart from their traditional agriculture. There, religious practices are linked to the cultivation of cereals such as sorghum (*Sorghum bicolor*), millet (*Pennisetum glaucum*), fonio (*Digitaria*

exilis) and rice (*Oryza* sp.) (Missihoun et al. 2012; Dagba et al. 2014; Loko et al. 2021). These producers have not only adopted the improved varieties (such as IR841 or NERICA) for their yield and marketing but also kept the local varieties (especially African varieties) for their grain organoleptic character and their importance in the different rituals (Gnacadja et al. 2017; Loko et al. 2021). Added to this is the probable confusion made between the local varieties of the *O. sativa* species and the African rice varieties by the producers given the distant introduction of the Asian varieties (Loko et al. 2021). Another hypothesis is that the presence of these cultivars only in the Atacora Department could be due to the adaptation of these rice cultivars to an ecological niche specific to the area. Indeed, the Atacora Department, located in the northwest of Benin, is rich in cultivable lowlands and with rugged reliefs rich in mountain ranges (The Atacora range) with altitudes ranging from 200 to 400 m (Adomou et al. 2006; Abdoulaye 2016), suggesting the presence of a complex climate system unique to Benin generated by the mountain range belt. Thus, the cultivars have adapted to the climates prevailing in the lowlands and have been conserved by the Atacora producers. Similar observations have already been reported by Barry et al. (2007) on rice diversity in Guinea. According to Orozco-Ramírez et al. (2014), cultivating both improved and local varieties allows producers to maintain their socio-cultural habits while meeting market demands.

The Beninese rice germplasm is dominated by improved varieties, which makes this unexpected result highly important for breeding and conservation. It is therefore imperative to implement in-situ and ex-situ conservation strategies for these cultivars to maximize their use. Indeed, the structural diversity observed in rice germplasm reflects the multiplicity of selection processes carried out over time by producers and local ecological conditions. This diversity, both genetic and phenotypic, is a strategic resource for varietal improvement and food security (Sanni et al. 2012; Ndjiondjop et al. 2018). However, to be truly effective and sustainable, policies for the management and development of rice germplasm should adopt a differentiated approach that takes into account farmers' preferences, culinary uses and production constraints, which strongly influence varietal adoption and management of rice genetic resources (Arouna et al. 2024). In Benin, as in several West African countries, producers have varying expectations depending on the agroecological context: some favour early maturity and drought tolerance, while others emphasize taste quality, amylose content or productivity in flooded areas (Fatondji et al. 2020). These local preferences, often passed down from generation to generation, reflect a detailed empirical knowledge of the environment and the potential of the varieties grown. Ignoring them would compromise the adoption and sustainability of varietal innovations, as shown by studies on the low uptake of certain improved varieties that are not aligned with consumer tastes and needs (Saito et al. 2019). Thus, the implementation of an integrated and differentiated rice policy should combine participatory breeding approaches, molecular genetics tools and agroecological mapping in order to identify, conserve and promote genotypes adapted to different production environments (Palanog et al. 2023; Yadav et al. 2026). Such a strategy would not only strengthen the resilience of rice systems to climate change, but also promote inclusive and sustainable agriculture, aligned with the real socio-economic needs of rural communities and the ecological specificities of the country (FAO 2023).

Declarations

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Supplementary data associated with this article can be found in the online version of this manuscript.

ETHICS STATEMENT

Research conducted for this manuscript complies with the ethical rules applicable to this journal, as stated in the Instructions for authors.

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Author Contribution

PS: Formal analysis, methodology, writing-original draft, writing - review and editing; AO: Formal analysis, Germplasm collection, Methodology and provided phenotypic information; MG: Resources, investigation and Writing-review and editing; ACG: Data curation, Methodology and software; SB: Resources, visualization and Writing-review and editing; PC: Data curation, Methodology and validation; LGD: Conceptualization, supervision, validation and writing - review and editing; LYEL: Supervision, project Administrator, visualization and writing - review and editing; FS: Conceptualization, supervision, validation, methodology, writing-review and editing. All authors contributed to the study and conception and design

Acknowledgement

This study was supported by the French National Research Institute for Sustainable Development (IRD) through the GRAB project under the Jeune Equipe Associée à l'IRD (JEAI-GRAB) program in Bénin

Data Availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request

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Figures

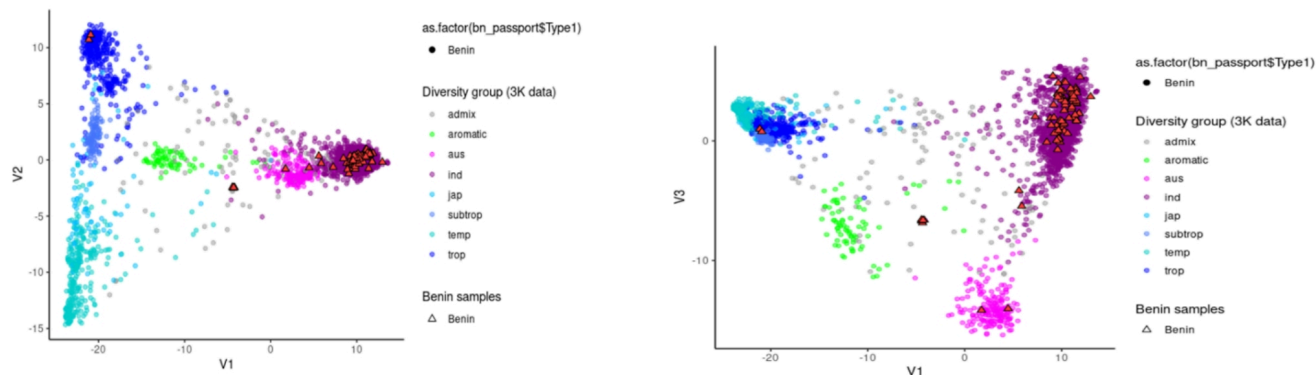


Figure 1

Organization of Beninese rice accessions compared to the 3K RGP data through PCA based on common SNP. Colors represent genetic groups while triangle symbolized data from Beninese rice.

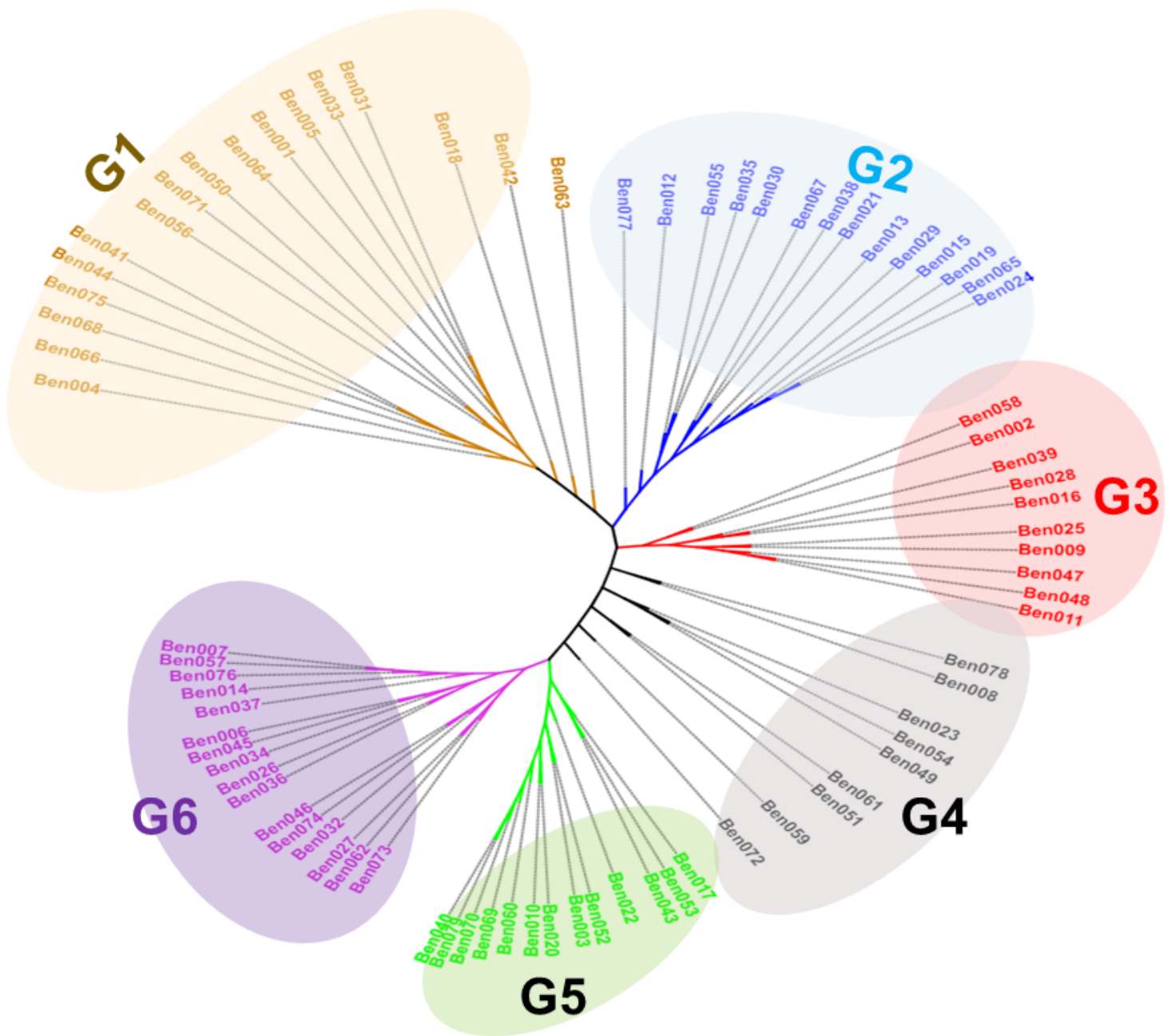


Figure 2

Neighbor joining tree of 79 Beninese *Oryzasp* samples computed with 5,564 polymorphic SNPs. Group III (G3) contains 10 accessions and 7 local varieties (IR841, Bérés21, NERICAL19, Toyéta, Mori Poua, IR15 and Tricos), with characteristics similar to those of G2. Group IV (G4) contained 9 accessions including 7 local varieties (R8, Yayi Boni3, Moii Touanja, Fondia Kéno, Gbega2, Fondi Ibéro and NERICAL56), with samples from the Departments of Borgou, Alibori, Collines and Atacora. Groups G3 and G4 had no reference controls.

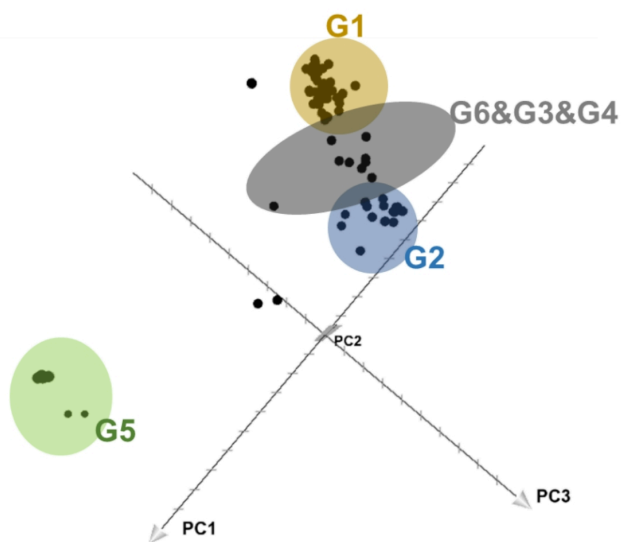
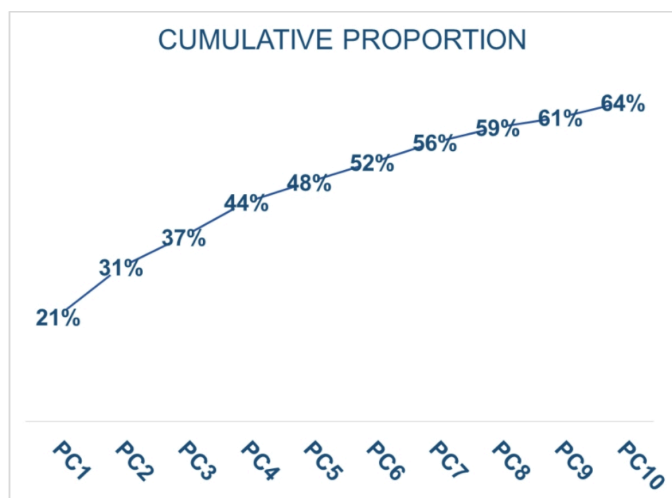
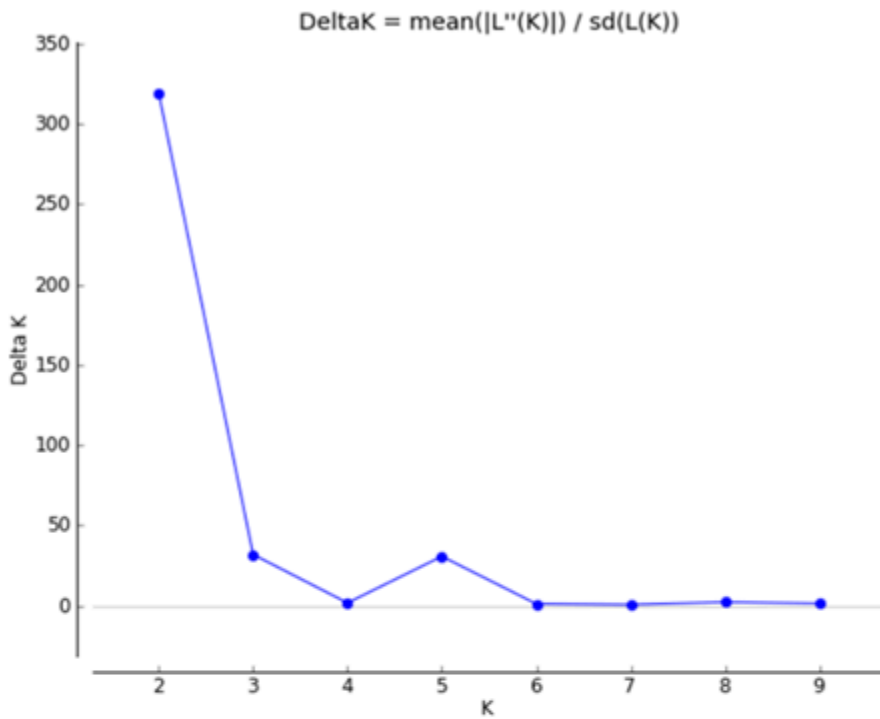
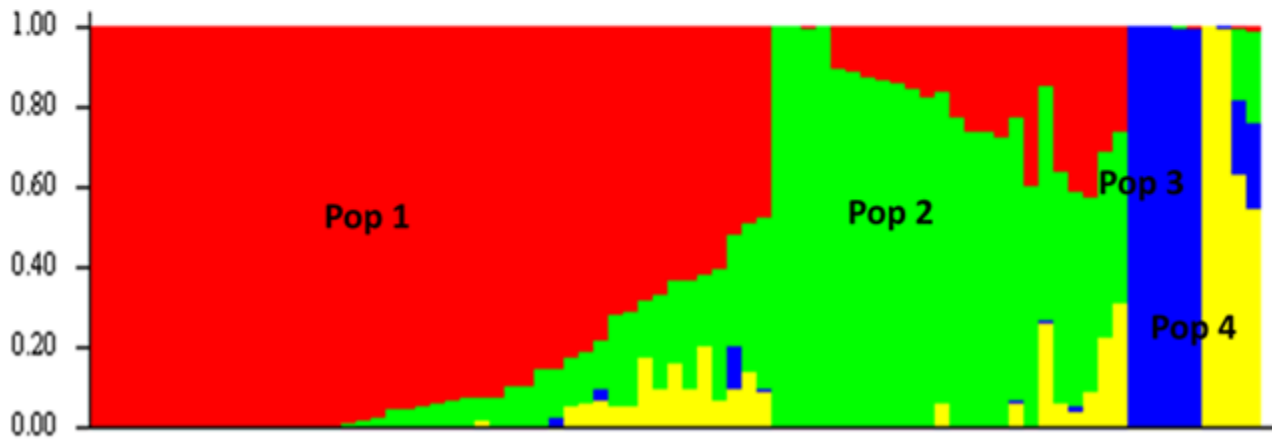


Figure 3

PCA of 79 *Oryza* sp computed with 5,526 polymorphic SNPs



A



B

Figure 4

a Graph estimated membership fraction for K=4

b Estimation of population structure of 79 rice germplasm accessions based on 5,526 polymorphic SNPs

Supplementary Files

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