

Genetic Characterization of *Balanites aegyptiaca* (L.) Del. Populations in the Sahelian Zone of Senegal

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Abstract

This study evaluated the molecular characterization of different ecotypes of *B. aegyptiaca* populations in the four sites: Koily alpha, Labgar, Ranérou and Ballou according to the environment with the aim of developing protection strategies. We sampled leaves of *B. aegyptiaca* in each individual from each site to extract and amplify a fragment of mitochondrial DNA including cytochrome b and then carefully preserved. DNA extraction, polymerase chain amplification and sequencing of *MT-CYB* were performed in 64 individuals. Genetic diversity and structure of *B. aegyptiaca* were determined using the MEGA, DNasp and Arlequin software. The results showed a high haplotype diversity and low nucleotide diversity, indicating a population expansion linked to an important gene flow. Genetic distances between populations were positively correlated with geographic distance. The importance of having highlighted this genetic differentiation of the *B. aegyptiaca* species between these sites is to be able to understand the degree of genetic heterogeneity of each and correlate it with adaptability because genetic diversity influences the adaptation of the species.

Keywords

Balanites aegyptiaca, Ferlo, *MT-CYB*, Morphotypes, Genetic Diversity

1. Introduction

Balanites aegyptiaca (L.) Delile is one of the priority native fruit trees for rural communities in the West African Sahel. It is a highly valued forest species due to its socio-economic and ecological interests in drylands [1]. Senegal is one of the Sahelian countries that corresponds to the area of choice for *B. aegyptiaca*. The majority of the population of this species is found in the Northern Sahelian, part of the country where it characterizes ecosystems next to *Acacia raddiana* and *B. senegalensis* [2]. The local population in this region places significant importance to the species. For example, in a survey conducted by Sagna [3], the evolution of the species in the area and the idea of diversity within the population of the species were widely emphasized by local populations. Approximately 2% of the population had actively traced the species evolution in the area. They report that *B. aegyptiaca* was predominantly found in the Cayor and along the Senegal River valley extending into Mauritania prior to the drought of the 1970s. It was during the onset of these drought years that the species began to gradually spread into the Ferlo center, a process facilitated by zoochory during cattle transhumances (Sagna *et al.*, 2015). About the perception of species diversity, a high proportion of respondents (94%) recognized the existence of distinct morphotypes of *B. aegyptiaca*. In this perception, the fruit was identified as the primary descriptor that is used especially with respect to the bitter or sweet taste of the pulp and the size of the nut that interests the population for the extraction of *Balanites* oil. Previous genetic studies revealed an overall genetic diversity of 81.5% across the species' range, and with intra-population diversity varies by region [4]. According to this study, *Balanites* populations in Niger, Mali, Algeria and Côte d'Ivoire exhibit high homogeneity, whereas populations in Senegal, Chad and Burkina Faso display greater genetic diversity. This study highlights that the genetic diversity observed in Senegal is particularly notable, as the samples analyzed are collected from trees within a radius of less than 100 m at the level in the Senegal river valley, specifically in the Diéri.

In this context, our study was undertaken with the overarching objective of conducting an in-depth evaluation of *Balanites aegyptiaca* populations to enhance our understanding of their biology and evolutionary dynamics in the Senegalese Sahel.

2. Material and Method

2.1. Presentation of the Study Area

The study area (**Figure 1**) has a typical Sahel climate, with a rainy and dry season [5]. The precipitation season lasts two to three months (July to September) and is characterized by annual rainfall ranging from 200 to 400 mm/year [5]. The dynamics of ecosystems in this region are influenced by rainfall [6]. Average temperatures range from 35°C to 43°C, sometimes up to 45°C in some places [6]. The Sandy Ferlo terrain combines low, monotonous plateaus with sandstone accumulations forming dunes separated by shallow areas occupied by temporary ponds

during the rainy season [7]. This part of the Sahel is occupied by tropical ferrous soils with sandy to sandy-clay texture. At the end of the rainy season, vegetation takes the form of a continuous herbaceous carpet dotted with trees and shrubs often spiny that never form a continuous stratum [8], dominated by *Balanites aegyptiaca* (L.) Del, *Boscia senegalensis* (Pers.) Lam. Ex Poir, *Acacia senegal* (L.), *Acacia tortilis* (Forsk.) Hayne ssp. *raddiana* (Savi) Brenan and *Calotropis procera* (Aiton) [5] [9]-[11].

The study was conducted within the natural range of *B. aegyptiaca* in northern Senegal, focusing on four specific sites: Koily alpha, Labgar, Ran  rou and Ballou (Figure 1). These sites were selected based on their floral distinct and ecological characteristics but also following the increasing rainfall gradient North-West/South-East.

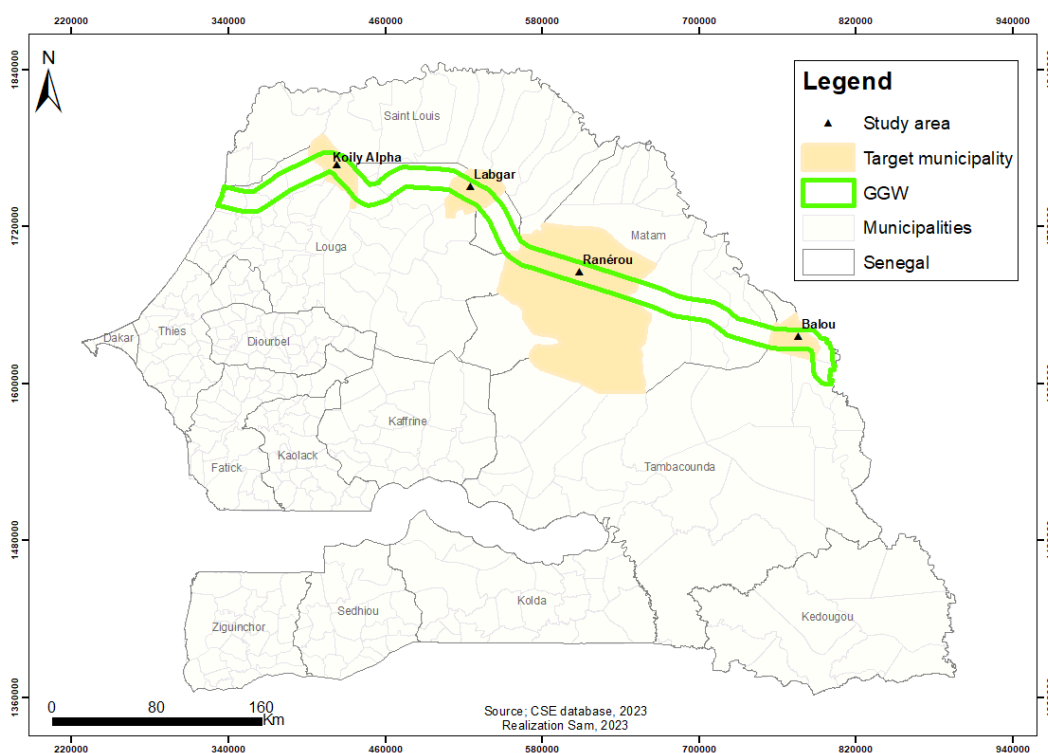


Figure 1. Geographic location of study sites [5] (Sam, 2023).

2.2. Samples

Table 1. Sampling summary table.

Sites	Sample codes	Number of samples
Koily alpha	B KA	13
Labgar	B LAB	17
Ran��rou	B RAN	17
Ballou	B BAL	17

Note: B = *Balanites*; KA = Koily alpha; LAB = Labgar; RAN = Ran  rou; BAL = Ballou.

The study was conducted on leaf samples collected from individuals representing different groups identified through the morphological analysis. At each site, 20 to 30 individuals were sampled and labeled with codes derived from the first syllable of their respective localities (**Table 1**). For each individual, 100 g of leaves were freshly harvested and carefully stored in labeled envelopes for subsequent analysis as suggested by Gawal & Jarret (1991).

2.3. DNA Extraction, Polymerase Chain Reaction and Sequencing

DNA from leaves was extracted with the Zymo Research Kit following the manufacturer's instructions. The mitochondrial gene *MT-CYB*, which codes for cytochrome b, was amplified for this study. This gene is found in the mitochondrial membrane of plants (Esposti *et al.*, 1993). Indeed, the choice of cytochrome b (*mtcyb*) is explained by its peculiarity to be kept very long. PCR was performed using a reaction volume of 25 μ l containing: 2 μ l of diluted DNA extract to the tenth; 1.5 μ l of $MgCl_2$; 17.8 μ l of ultra-pure water; 2.5 μ l of buffer 10X; 0.5 μ l of dNTP; 0.2 μ l of Taq polymerase and 0.25 μ l of each amorce which are:

F 5'TATGTACTACCATGAGGACAAATATC3' and
R 5'ATTACACCTCCTAATTTATTAGGAAT3'.

It took place in an Eppendorf thermocycler, under the following conditions: initial denaturation at 94°C (3 min); repetition of 35 cycles of denaturation at 94°C (1 min), hybridization at 47°C (1 min) and elongation at 72°C (1 min); final elation at 72°C (10 min at 10°C).

After blue light revelation, the sequencing reactions were performed in a MJ Research PTC-225 Peltier thermocycler with the ABIPRISM BigDye™ Terminator Cycle kits. Each sample was sequenced using the sense primer, with 10 μ l of PCR products.

2.4. Genetic Analysis

Sequences were manually corrected using chromatograms and aligned using the clustal w multiple alignment algorithm in BioEdit software version 7.1.9 [12]. The resulting sequences were grouped into localities based on the distribution of the sites. Genetic variability parameters such as sample size, number of sites (total length of the sequence without gaps), number of singleton variable sites (sites with at least two types of nucleotides, one of which has a higher frequency than the other), number of informative sites (sites with at least two types of nucleotides and each is present in at least two compared sequences) and haplotypic frequency were determined using the DnaSP version 5.10 [13]. Genetic diversity and geographic distance were calculated from MEGA version 7.0.14 software [14].

The genetic structure was determined using Nei distances and *F_{st}*, as well as molecular variance analysis (AMOVA) under Arlequin version 3.5.1.3 [15]. Mismatch analysis distribution was constructed using DnaSP and Arlequin. Two phylogenetic affinities were estimated between populations of *B. aegyptiaca* using the

MEGA software version 7.0.14 [16] and MrBayes software version 3.2.5 [17]. The Neighbor-Joining method and the maximum likelihood were used to estimate phylogenetic affinities. The Bayesian method was used to test the probability of a posteriori events based on the Tamura Nei + Gamma model. The best evolutionary model was found using jmodeltest, with node robustness evaluated across 1000 bootstraps. Reconstructions were rooted using a sequence of *Balanites aegyptiaca*.

3. Results and Discussion

3.1. Results

3.1.1. Polymorphism and Genetic Diversity

A total of 64 sequences were obtained with a total number of 394 pb. Of these sequences, 13.45% were variable sites, of which 28.30% were simple sites and 71.70% informative sites. Haplotypes are individuals who have sequences that are identical in every respect. The most common haplotype was h4, found in 38 individuals mainly found at the Labgar site with 15 individuals, the Koily alpha site (13) and the Ranérou site (10).

3.1.2. Analysis of Genetic Differentiation and Structuring

1. Intra and inter-population distance

Overall, the intra-population genetic distances of each site are relatively small; they range between 0 and 0.034. Thus, the results obtained showed that the genetic distance between individuals of the same site is greater in Ranérou. In contrast, the distance between Koily alpha individuals is zero, indicating that the *B. aegyptiaca* population at this site is genetically homogeneous.

The greatest genetic distance is observed between Labgar and Ballou individuals (0.095) and the smallest distance between Koily alpha and Labgar individuals (0.00). These results show that the Labgar and Koily alpha populations are genetically close. These results are shown in **Table 2**.

Table 2. Intra and inter-population distance of *B. aegyptiaca*.

Sites	Intra-population distance \pm standard deviation	Inter-population distance \pm standard deviation		
		Ballou	Koily alpha	Labgar
Ballou	0.003 \pm 0.0009			
Koily alpha	0.00 \pm 0.00	0.093 \pm 0.015		
Labgar	0.003 \pm 0.0009	0.095 \pm 0.015	0.002 \pm 0.00	
Ranérou	0.034 \pm 0.005	0.073 \pm 0.012	0.022 \pm 0.004	0.024 \pm 0.004

2. Genetic Differentiation Factor (Fst)

Analysis of **Table 3** shows that the Ballou population is significantly different from the Labgar, Koily alpha and Ranérou populations. But there is also a significant genetic difference between the Labgar and Ranérou populations, and between the Koily alpha and Ranérou populations.

Table 3. Fst values between sites.

Sites	Ballou	Labgar	Koily alpha
Ballou			
Labgar	0.96621 (0.0000)		
Koily alpha	0.98041 (0.0000)	0 (0.99099)	
Ran�rou	0.73506 (0.0000)	0.19711 (0.0000)	0.18038 (0.01802)

Notes: bold values are significant.

3. AMOVA test (genetic structuring test)

The AMOVA test corroborates the strong genetic differentiation of *B. aegyptiaca* according to site. Therefore, *B. aegyptiaca* is genetically structured according to site (**Table 4**).

Table 4. Molecular variance analysis (AMOVA).

Source of variation	d.f	sum of squares	Variance components	Percentage variance
Between populations	3	376.909	7.75413 Va	79.05
Within a population	60	123.294	2.05490 Vb	20.95
Total	63	500.203	9.80903	100

3.1.3. Demographic Change

1. Genetic tests

Tajima's D, D and F tests reveal that mutations have an effect on the evolution of *B. aegyptiaca* in the Ballou, Labgar and Ran rou populations. In contrast, for the Koily alpha population, mutations are selectively neutral (**Table 5**).

Table 5. Genetic neutrality tests.

Index	Ballou	Koily alpha	Labgar	Ranerou
dNdS	-0.914 (1)	1.541 (0.063)	0.132 (0.448)	1.315 (0.095)
D Tajima	-2.20533 (0.001*)	0	-2.20533 (0.003*)	0.31789 (0.69200)
D et F	1.4367 (0.802)	0	1.43678 (0.79100)	3.71239 (0.92700)

*Significant P-value (p < 0.05).

2. Analysis of "Mismatch distribution" or Pairwise difference

The distribution curves of Mismatch of *B. aegyptiaca* populations for the Ballou, Labgar and Ran rou sites are multimodal (**Figures 2-4**). This generally indicates that *B. aegyptiaca* individuals are in demographic balance

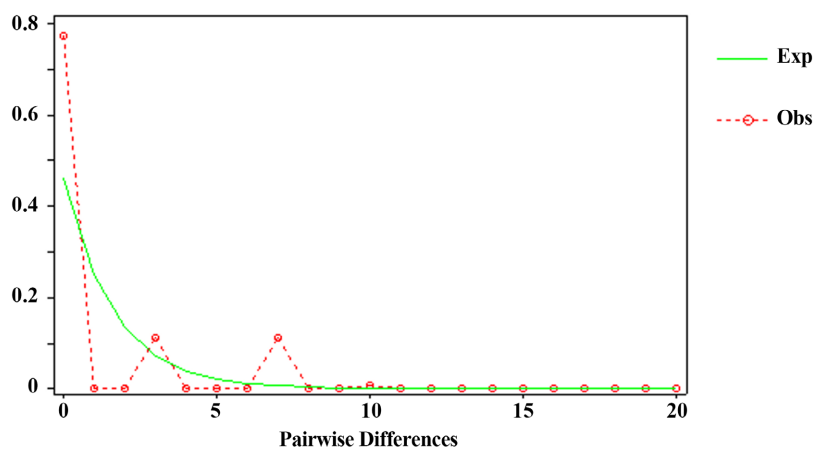


Figure 2. Distribution of the number of haplotypes taken in pairs (Distribution of Mismatches) at the Ballou site.

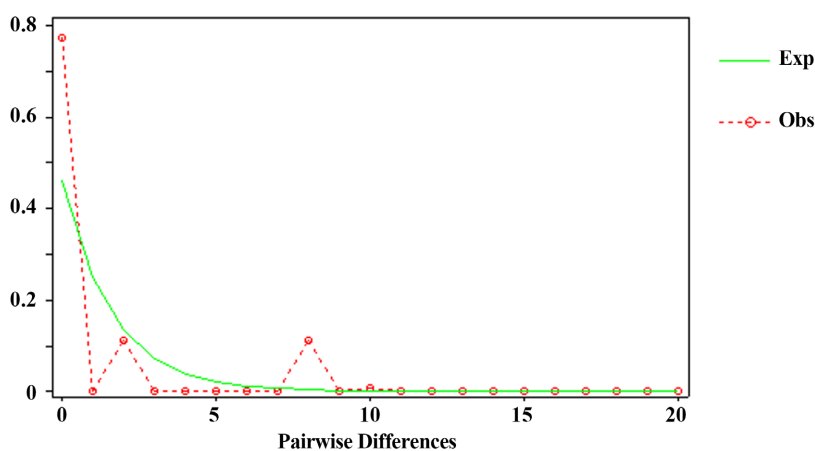


Figure 3. Distribution of the number of haplotypes taken in pairs (Distribution of Mismatches) at the Labgar site.

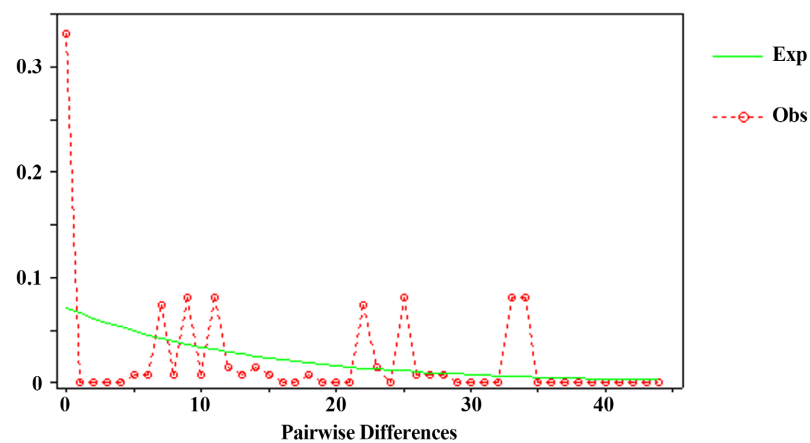
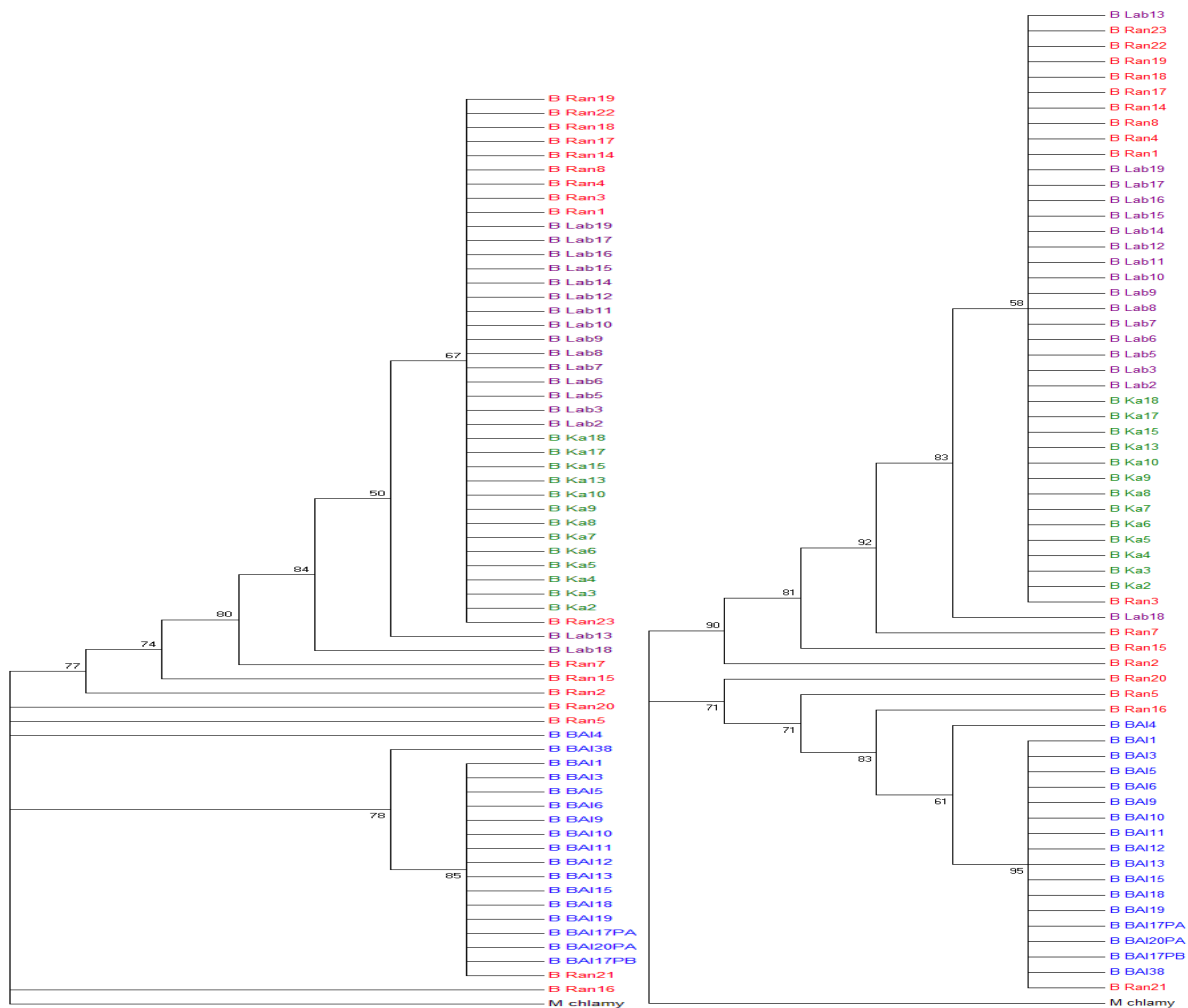


Figure 4. Distribution of the number of haplotypes taken in pairs (Distribution of Mismatches) at the Ranerou site.

3.1.4. Phylogenetic Trees

Phylogenetic trees constructed according to the methods of maximum likelihood

and neighbor-joining have both highlighted clades. A clade grouping the individuals of Koily alpha, Labgar and Ranerou geographically distant, supported by the three populations with high values ranging from 80% to 100% of Bootstrap and another clade consisting solely of Ballou individuals and supported by a 78% value of Bootstrap (Figure 5).



Note: color red = Ranerou, color mauve = Labgar, color green = Koily alpha, and color blue = Ballou.

Figure 5. Phylogenetic trees between nucleotide sequences of the *MT-CYB* gene of *B. aegyptiaca* (maximum likelihood and neighbor-joining).

3.2. Discussion

The aim of this study was to perform a genetic characterization of *Balanites aegyptiaca* at four study sites with similar climatic conditions. Genetic analyses using the *MT-CYB* showed that of the 394 *B. aegyptiaca* sequence sites, 13.06% were invariant. However, it is observed that in the sites of Koily alpha, Labgar and Ballou populations are more monomorphic and homogeneous compared to those of Ranerou. At least 12 halotypes were identified in the four sites, most of which are transitions (69.19%) and protein structure mutations suggesting poor population

differentiation. These results are consistent with those of Sagna [2]. The haplotypic diversity observed in the Ranerou site (0.669 ± 0.129) is stronger compared to those found in the Koily alpha (0), Labgar (0.228 ± 0.129) and Ballou sites (0.228 ± 0.129). This high haplotype diversity could be due to the commercialization of these non-wood products in the market of this site, which may lead to the importation of haplotypes from other locations. Indeed, according to Sinama [17], the high haplotype diversity and low nucleotide diversity noted in the four sites, reflect rapid population growth from an ancestral population with a low population size and for which there has not been enough time to recover a high diversity between haplotypes. The values of F_{st} between sites range from 0 to 0.98041 and are significant. However, the F_{st} is zero between the sites of Koily alpha and Labgar. This shows that there is no genetic differentiation between these two sites, so they form a homogeneous population. These results are similar to those of Tong [18]. In addition, trade between these communities would be reduced as they share similar climate and edaphic provinces, which could be another factor leading to low differentiation. Our study also reveals that in the site of Koily alpha, the value of the D of Tajima is zero which probably indicates a random evolution of the populations of *B. aegyptiaca* in this site. According to Excoffier [19], a negative Tajima's D could be associated with population growth. At the Labgar and Ballou sites, Tajima's D values (-2.20533) are negative and significant. This shows that the *B. aegyptiaca* individuals found in these localities are expanding. The Ranerou population, on the other hand, would have been subject to negative selection, as its Tajima's D value (0.31789) is positive and insignificant. The results of this study also showed that there is a correlation between genetic distance and geographic distance.

This is due to anthropogenic dispersal which increases gene flow between *B. aegyptiaca* populations and the absence of geographical barriers between sites. These results are in line with those of Sagna [2] and Mint Abdelaziz *et al.* [20] in a genetic study on the same species in Mauritania but contrary to those of Semeao *et al.* [21].

All genetic structuring parameters showed strong genetic differentiation of the *B. aegyptiaca* species between sites. This genetic structuring of *B. aegyptiaca* according to localities was even corroborated by the AMOVA test. Thus, the analysis of molecular variance shows a significantly high percentage of variance (79.05%) between populations. However, the percentage of variance within a population is 20.95%. Because the sites have different ground-climate characteristics, it is suggested that they may be responsible for genetic differentiation. This may be due to the fact that cytochrome *b* is a rapidly evolving gene. However, genetic neutrality tests suggest that populations of *B. aegyptiaca* are expanding. This result is confirmed by the measurement of the distribution of genetic distances between individuals in a population taken two to two with mismatch graphs that show a multimodal distribution reflecting rapid growth of populations at sites. In addition, the robustness of the distribution mismatch exploitation is supported by the

values of the SSD and Raggedness indices which are positive and not significant. Considering the different sites, we find 12 halotypes on the 64 sequences where the site of Ranerou which includes the most (8) of halotypes. Phylogenetic trees showed a kinship relationship between the populations of Koily alpha, Labgar (characterized by sandy soils and low rainfall) and Ranerou and a greater proximity between the populations of Ballou and Ranerou (limonic-clay soils with significant precipitation) as described by Kébé *et al.* (2020) [22] compared to other sites. These results seem to confirm the idea of evolution of the *balanite* population from the Ferlo valley towards the center mentioned in the work of Sagna [3]. Michel Benoit, who had mapped and characterized the landscapes of Ferlo in the 1950s located facies I and II dominated by *B. aegyptiaca* in the extreme north of Senegal [23]. These results are consistent with those of Sagna [3], who report that the populations of Koily Alpha, Labgar or even Ranerou may originate from the Cayor area of preference for the species. The absence of large geographical barriers between the three sites studied could facilitate gene flow. In addition, seed dispersal through grazing animals could help maintain gene transfer between populations located at different locations [24].

The genetic structure of *B. aegyptiaca* populations as presented in this study suggests a scenario of evolution of two populations (Ferlo Valley and Cayor) towards the centre of Ferlo with a slight change in populations in the Ferlo valley, hence their almost total absence in Koyli and Ranerou. However, the date trees of the Cayor must be studied to confirm this hypothesis.

4. Conclusion

This study based on sequencing and genetic analysis of the Cytochrome b of *B. aegyptiaca* revealed a genetic structuring according to the four study sites. The results of demographic evolution showed that populations of *B. aegyptiaca* found in sites are expanding. From then on there was genetic differentiation of *B. aegyptiaca* populations according to these localities and the greatest diversity of this species is found in Ranerou. The study of phylogenetic relationships between populations of *B. aegyptiaca* showed the impact of trade and geographic distance between sites on the genetic affinities of populations of this species. The evolution of date-tree populations in the Sahel Senegal hides a mystery to be elucidated because there is no relationship between the populations of Ballou and Koyli. Further studies would provide a better understanding of the relationships between *B. aegyptiaca* populations in different localities to develop sustainable strategies for the protection of the species taking into account the environment for local communities.

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Conflicts of Interest

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

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