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Research Article

Bottleneck and molecular variance analyses in Senegalese local cattle breeds using microsatellite markers

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Abstract

The native Senegalese cattle were extensively used for crossbreeding purposes and breed development, which are assumed to improve livelihood of the most rural populations. This study was conducted in 4 native cattle breeds (Gobra zebu, Maure zebu, Djakoré and N'Dama) to assess the current genetic variation at molecular levels by using AMOVA tests and Bottleneck analysis. A total of 120 unrelated samples were collected from breeds reared in three agro-ecological areas of Senegal. In this study, 11 specific highly polymorphic microsatellite makers recommended by Food and Agriculture Organization (FAO) were used for animals genotyping. The basic measures of within breed variation and genetic differentiation were computed using bioinformatics' software. All loci were polymorphic with a mean Polymorphic Information Content (PIC) of 0.76. The mean allelic richness per loci was 6.08. In average, high levels of heterozygosity was observed with a mean H_O and H_E of 0.71 and 0.79, respectively. The mean estimates of F_{IS} over all loci were 0.073 indicating a significant heterozygosity deficiency relatively due to inbreeding among the cattle breeds or the occurrence of population substructure. Analysis of molecular variance (AMOVA) revealed that 4.76% of the total genetic variation was due to differences between populations ($P<0.001$), while the remaining 88.24% corresponded to differences within individuals ($P<0.001$). The qualitative test of mode shift analysis supported the conservative SMM model which indicated absence of genetic bottleneck in the recent past in Senegalese cattle populations. It was concluded from the current study of microsatellite markers that Senegalese local cattle populations was characterized by high level of genetic diversity and moderate genetic differentiation.

Keywords: AMOVA; Bottleneck; cattle; microsatellite markers; Senegal

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Introduction

During the last decades, development of and increased focus on more efficient selection programs has accelerated genetic improvement in a number of breeds. Artificial insemination has facilitated the dissemination of genetic material (Groeneveld et al., 2010). As a result, highly productive breeds tend to

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replace local ones across the world. In Senegal, uncontrolled crossings have led to spreading of crossbreeds so that the genetic structure of local cattle is very confused (Ndiaye et al., 2012). This development has led to growing concerns about the erosion of genetic resources (FAO, 2007b). Furthermore, after the severe droughts in the 1970's and 1980's (FAO, 2012), transhumance is widely used in the traditional way of livestock management in West Africa. So, transhumance is another obvious way to genetic mixtures between cattle populations from different countries, because of the porosity of borders. Hence, effective management of cattle breeds requires comprehensive knowledge of breeds' characteristics, including data on population size and structure, geographical distribution, the production environment, and within- and between breed genetic diversity (Groeneveld et al., 2010).

In Senegal, four native cattle breeds have been distinguished by their history, their origin, and the use of these populations in different environments and production systems. So, typology by classification analysis showed that they constituted two phenotype groups. The first is characterized by a thoracic hump and a unique coat color (Gobra Zebu, Maure Zebu and Djakoré). Their average daily milk production varied between 2 and 4 liters even more than 4 liters. The second phenotype is identified by the absence of hump and a compound coat color (N'Dama taurine). His average milk production is less than 2 liters per day (Ndiaye et al., 2014).

However, maintaining sufficient diversity of livestock cattle is necessary to ensure their adaptation and development in the context of global climate change (Boettcher et al., 2015). Therewith, to allow effective monitoring and management in different production systems for enhancing traits associated with superior productivity and resilience in conditions expected to be prevalent of climate change and resistance to certain diseases (Boettcher et al., 2015), demographic characterization is fundamental for the assessment of the risk status of livestock breeds- a key step in the strategic planning of farm animal genetic resources (Groeneveld et al., 2010).

Gobra zebu, Maure zebu and N'Dama have been subject of population genetics analyses among studies conducted at a continental scale to retrace indicine and taurine migration across Africa (MacHugh et al., 1997; Hanotte et al., 2002; Freeman et al., 2004). However, the genetic architecture and bottleneck analysis of these four local cattle breeds including the Djakoré have not been carried out in their native environment. Hence, microsatellite analysis was conducted to assess the genetic variation at molecular levels and to test signatures of a recent demographic bottleneck in Senegalese local cattle.

Materials and Methods

This study was approved by the Ethics Committee of Cheikh Anta Diop University of Dakar. Signed consent of all participants was obtained after the study was fully explained.

Sampling was carried out in three agro-pastoral regions of Senegal namely Saint- Louis, Kaolack and Kolda, located into three agro-ecological areas that represent the distribution area of Gobra zebu, Maure zebu, Djakoré, and N'Dama breeds. Genomic DNA was isolated from blood samples of 30 unrelated animals of each breed with typical phenotypic features. Although no parentage records were available, to ensure equality, animals were selected from distinct localities after interviewing the farmers in detail (Ndiaye et al. 2014).

The genotyping included 11 cattle-specific microsatellites markers (BM2113, BM1818, ETH10, ETH225, ETH152, HEL1, HEL9, INRA037, INRA063, MM12, and TGLA53) which were selected from the panel recommended by the Food and Agriculture Organization and the International Society for Animal Genetics (FAO and ISAG) (FAO, 2011) (Table 1) to generate allelic data. The polymerase chain reaction (PCR) amplification of microsatellite loci were carried out in a thermal cycler (BIOMETRA® TGradient, version 4.20 gr, Model No.1912460, Whatman) using cycling conditions as: initial denaturation at 94°C for 3 min, followed by 35 cycles of 30 sec at 94°C, 30 sec at annealing temperature of 50, 55 or 60°C (according to the microsatellite) and 45 sec extension at 72°C, then final extension at 72°C for 8 min ended the reactions. The amplified products were subsequently resolved on 6.5% denaturing acrylamide-urea gels using a Li-Cor® automated sequencer (DNA Analyzer Model 4300) following the manufacturer's procedures. All gels were analyzed using SAGA^{GT} Generation 2.0 software.

The basic measures of genetic variation were computed using Genetix version 4.05.2 (Belkhir et al., 2004) and Fstat version 2.9.3.2 (Goudet, 2002). The Polymorphic Information Content (PIC) was estimated using Cervus 3.0.6, Field Genetics Ltd (Kalinowski et al., 2007). The exact test for Hardy-Weinberg equilibrium was performed using Genepop 4 version 4.2.2 (Rousset, 2008), whereas the test of linkage disequilibrium was done using Fstat version 2.9.3.2 (Goudet, 2002). To assess the distribution of genetic variation at molecular levels, Analysis of Molecular Variance (AMOVA) was conducted by using Arlequin version 3.5.1.3 (Excoffier and Lischer, 2010). To test whether a population has recently undergone a strong reduction of its effective size (bottleneck), the BOTTLENECK program version 1.2.02 (Cornuet and Luikart, 1996) was implemented. The bottleneck program was used as an alternative measure of genetic bottleneck to test for gene diversity excess relative to

that expected under mutation – drift equilibrium. Genetic reduction signatures of populations were determined using the Wilcoxon's heterozygosity excess test (Piry et al., 1999). The test verified the null hypothesis that all loci are in mutation – drift equilibrium. For the test, the three mutation models of microsatellite evolution were assumed: infinite allele model (IAM), stepwise mutation model (SMM) and two-phase model (TPM). Furthermore, a qualitative test of mode-shift indicator developed by Luikart et al. (1998) was performed to evaluate the frequency distribution of alleles at microsatellite loci.

Results

All loci showed high level of polymorphism in all populations with a total of 115 different alleles. The test of linkage disequilibrium between different combinations of loci under the study showed none significant deviations. The observed number of alleles per locus (Na) ranged from 6 alleles at locus INRA063 to 16 at locus TGLA53 (Table 2). The mean allele number was 10.45. The mean allelic richness per locus (Rt) was 6.08, so it ranged from 3.74 in INRA063 to 8.20 in TGLA53. All loci were highly informative with an overall mean of PIC value of 0.76. Thus, high levels of heterozygosity (> 0.60) was observed in all loci, except for INRA063, which generated H_O and H_E values of 0.44 and 0.60, respectively (Table 2). The overall mean of observed and expected heterozygosity was 0.71 and 0.79 respectively. Therefore, the total inbreeding coefficient was determined as being 7.3%, indicating a significant heterozygote deficiency in all populations ($P<0.05$). Considering all loci, all populations were deviated significantly from Hardy-Weinberg equilibrium ($\chi^2 = 151.6963$, $P<0.001$) (Table 2).

Table 1: Microsatellite markers, sequences, location and annealing temperature

Locus[(1)]	Chromosome number	Primer name	Primer sequences (5'→3') Forward / Reverse/Forward FM13 [(2)]	Annealing temp. (C°)
INRA063	18	INRA063F	ATTTGCACAAGCTAAATCTAACC	55
(D18S5)		INRA063R	AAACCACAGAAATGCTTGGAAG	
		INRA063FM13	CACGACGTTGTAAAACGACATTTGCACAAGCTAAATCTAACC	
INRA037	10	INRA037F	GATCCTGCTTATATTTAACCAC	50
(D10S12)		INRA037R	AAAATTCCATGGAGAGAGAAAC	
		INRA037FM13	CACGACGTTGTAAAACGACGATCCTGCTTATATTTAACCAC	
MM12	9	MM12F	CAAGACAGGTGTTTCAATCT	55
(D9S20)		MM12R	ATCGACTCTGGGGATGATGT	
		MM12FM13	CACGACGTTGTAAAACGACCAAGACAGGTGTTTCAATCT	
HEL9	8	HEL9F	CCCATTCAGTCTTCAGAGGT	60
(D8S4)		HEL9R	CACATCCATGTTCTCACCAC	
		HEL9FM13	CACGACGTTGTAAAACGACCCCATTCAGTCTTCAGAGGT	
HEL1	15	HEL1F	CAACAGCTATTTAACAAGGA	55
(D15S10)		HEL1R	AGGCTACAGTCCATGGGATT	
		HEL1FM13	CACGACGTTGTAAAACGACCAACAGCTATTTAACAAGGA	
ETH10	5	ETH10F	GTTCAGGACTGGCCCTGCTAACA	60
(D5S3)		ETH101R	CCTCCAGCCCACTTTCTCTTCTC	
		ETH10FM13	CACGACGTTGTAAAACGAC GTTCAGGACTGGCCCTGCTAACA	
ETH152	5	ETH152F	TACTCGTAGGGCAGGCTGCCTG	55
(D5S1)		ETH152R	GAGACCTCAGGGTTGGTGATCAG	
		ETH152FM13	CACGACGTTGTAAAACGACTACTCGTAGGGCAGGCTGCCTG	
BM1818	23	BM1818F	AGCTGGGAATATAACCAAAGG	55
(D23S21)		BM1818R	AGTGCTTTCAAGGTCCATGC	
		BM1818FM13	CACGACGTTGTAAAACGAC AGCTGGGAATATAACCAAAGG	
BM2113	2	BM2113F	GCTGCCTTCTACCAAATACCC	55
(D2S26)		BM2113R	CTTCCTGAGAGAAGCAACACC	
		BM2113FM13	CACGACGTTGTAAAACGACAGCTGCCTTCTACCAAATACCC	
ETH225	9	ETH225F	GATCACCTTGCCACTATTTCCT	55
(D9S1)		ETH225R	ACATGACAGCCAGCTGCTACT	
		ETH225FM13	CACGACGTTGTAAAACGACGATCACCTTGCCACTATTTCCT	
TGLA53	16	TGLA53F	GCTTTCAGAAATAGTTTGCATTCA	55
(D16S3)		TGLA53R	ATCTTCACATGATATTACAGCAGA	
		TGLA53FM	CACGACGTTGTAAAACGACGCTTTCAGAAATAGTTTGCATTCA	
TGLA122	21	TGLA122F	CCCTCCTCCAGGTAAATCAGC	55
(D21S6)		TGLA122R	AATCACATGGCAAATAAGTACATAC	
		TGLA122M13	CACGACGTTGTAAAACGACCCCTCCTCCAGGTAAATCAGC	

[(1)] The codes for each locus on the genetic map of bovine genome are put in parentheses. Source: FAO (2011).
[(2)] Forward primer whose sequence is provided with a tail M13 (sequence of 19 base pairs) to its 5 'end.

Table 2: Basic diversity indices of Senegalese local cattle breeds per microsatellite locus

Locus	Observed number of alleles (Na)	Allelic richness (Rt)	Average heterozygosity (Expected) H_E	(Observed) H_O	F_{IS} (WC)	PIC	χ^2HWE
BM1818	10	6.482	0.840	0.876	-0.049	0.815	3.2851^{NS}
BM2113	9	6.578	0.847	0.671	0.194	0.823	24.9024**
ETH10	8	5.887	0.808	0.670	0.141	0.778	10.9206^{NS}
ETH152	9	5.247	0.775	0.708	-0.020	0.737	29.2500***
ETH225	7	5.005	0.739	0.640	0.103*	0.699	9.5284^{NS}
HEL1	11	6.369	0.844	0.814	0.023	0.820	8.9110^{NS}
HEL9	14	7.318	0.870	0.804	0.063*	0.851	11.6563^{NS}
INRA063	6	3.745	0.608	0.446	0.212	0.551	19.9543*
INRA037	12	5.750	0.802	0.716	0.048*	0.769	15.2741*
MM12	13	6.381	0.781	0.778	-0.014	0.750	4.9452^{NS}
TGLA53	16	8.204	0.866	0.724	0.136	0.847	13.0689^{NS}
Mean	10.455	6.088	0.798	0.713	0.073*	0.767	151.6963***

PIC (Polymorphism information content); χ^2HWE (Khi-square values of Hardy-Weinberg equilibrium exact test); F_{IS} (inbreeding estimate); NS, not significant; *P<0.05; **P<0.01;***P<0.001

Table 3: Analysis of Molecular Variance (AMOVA) in Senegalese local cattle breeds

Populations were evaluated as a single group

Source of variation	Sum of squares	Variance components	Variation (%)	Fixation indices
Among populations	41.053	0.21178	4.76	F_{ST} = 0.047***
Among individuals within populations	381.251	0.31130	7	F_{IS} = 0.073***
Within individuals	347	3.92371	88.24	F_{IT} = 0.117***
	769.304	4.44680		

Populations were evaluated as two groups according to subspecies

Source of variation	Sum of squares	Variance components	Variation (%)	Fixation indices
Among subspecies [(1)]	29.045	0.44747	9.49	F_{CT} = 0.094***
Among populations within subspecies	12.007	0.02901	0.62	F_{SC} = 0.006*
Among individuals within populations	381.251	0.31130	6.61	F_{IS} = 0.073***
Within individuals	347	3.92371	83.27	F_{IT} = 0.167***
Total	769.304	4.71149		

[(1)]*Bos indicus* subspecies: Gobra zebu, Maure zebu, Djakoré; *Bos taurus* subspecies: N'Dama taurine; * P<0.05; *** P<0.001.

Table 4: Wilcoxon's heterozygosity excess test in Senegalese local cattle breeds

Bovine populations	Mutation model		
	IAM	TPM	SMM
Djakoré	0.00024*	0.04150*	0.89697
Gobra zebu	0.00049*	0.08740	0.86084
Maure zebu	0.00464*	0.16016	0.68115
N'Dama	0.00806*	0.44922	0.98950
Overall	S***	NS	NS

IAM (Infinite allele model); TPM (Two-phased model); SMM (Stepwise mutation model); *p-values correspond to unilateral Wilcoxon tests showing a significant excess of heterozygosity; S***: P<0.0001; NS, not significant: P>0.05.

The partition of genetic variation within and among populations was evaluated at two hierarchical levels of structure, the one considers all populations as a single group, and the other divided them into two groups according to the belonging subspecies (Table 3). In the AMOVA analysis, when populations as considered as a single group, virtually a little variation was detected among populations with 4.76% of the variation attributed to differences between populations. The corresponding value of this variation was evaluated by the F_{ST} (0.047), which indicated that the moderate differentiation found between breeds was highly significant (P<0.001). The remaining 88.24% of the variation was accounted for by differences between individuals. Whenever populations were grouped by subspecies, the highest percentage of variation (83.27%) corresponds to within individual's component. So, among populations within subspecies' component showed very low magnitude of variation (0.62%) but significant (P<0.05). Thereby, AMOVA indicated that 9.49% of the total genetic variation was strongly (P<0.001) due to differences between subspecies (Table 3).

The results of analysis of genetic bottleneck showed that a highly significant heterozygosity excess was obtained under IAM in all cattle populations (P<0.0001) (Table 4). In TPM model, the heterozygosity excess was detected only in Djakoré population (P<0.05). So, null hypothesis of mutation-drift equilibrium was rejected in all tests under IAM model and in one test under TPM model. But, in SMM model, null hypothesis of mutation-drift equilibrium was accepted in all tests (P>0.05) (Table 4). The mode-shift indicator test was also used to detect potential bottlenecks, as the non-bottleneck populations that are

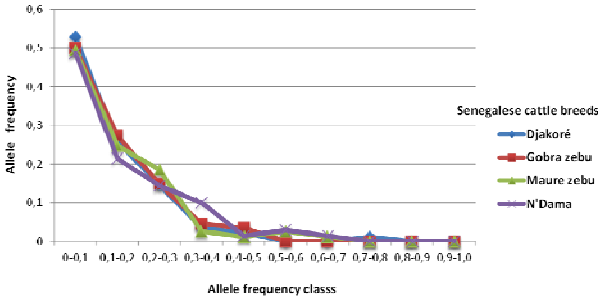

Fig. 1: Allele frequency spectra of Senegalese local cattle showing normal L-shaped distribution and absence of recent genetic bottleneck.

near mutation-drift equilibrium are expected to have a large proportion of alleles with low frequency. Thus, the figure 1 showed that the distribution of allele frequencies followed the normal L-shaped form. This ascertained that alleles with low frequencies (0.01-0.1) are the most numerous in all bovine populations. This distribution showed clearly that the considered cattle breeds have not experienced a recent genetic bottleneck.

Discussion

This study represented the first largest estimate of within breed genetic variation in local Senegalese cattle included the Djakoré which has not been previously characterized. Most of the loci used in this work had been analyzed in previous studies with different bovine populations such as European cattle breeds, Near East cattle breeds, African taurine and zebu and Asian zebu (MacHugh et al., 1997; Freeman et al., 2004; Cymbron et al. 2005; Dayo et al., 2009). The high levels of allelic diversity and heterozygosity showed that these loci give reliable information's on genetic diversity and population structure. The amount of genetic diversity observed in the four cattle breeds was comparable to those reported for other cattle breeds in different regions of Africa (MacHugh et al., 1997; Moazami-Goudarzi et al., 2001; Freeman et al., 2004; Bessa et al., 2009; Ngono Ema et al., 2014). So, the high values of genetic diversity obtained in this study well confirmed that Senegalese native cattle breeds represent an important reservoir of genetic variation.

A significant deficit of heterozygosity was found amongst populations. A considerable variance of deficit (F_{IS}) between subpopulations might due mainly by population substructure as regards to strong difference on null allele frequency across loci under high level of genetic differentiation. This deficiency of heterozygotes among populations is an indicator of inbreeding among cattle breeds or the occurrence of population substructure. Furthermore, the loci who have presented the signs of null alleles are different to those showed a deficit of heterozygotes. So, a high level of inbreeding should be the major reason of this deviation with regards to the production system. Furthermore, inbreeding occurred between closely related subpopulations by no-random mating (Ngono Ema et al., 2014).

In population's genetic studies, AMOVA allowed to determine the partitioning of genetic variation within and among populations. Through these analyses, the amount of genetic variability was tested among groups, among populations, among individuals within populations and within individuals. When populations as evaluated as a single or two groups, the highest amount of genetic variation was observed within individuals. Comparatively, Ndiaye et al. (2014) reported that the phenotypic diversity encountered in the same breeds, was also due to within individuals variability. The same trends were reported in many cattle breeds reared in different herds or production systems (Pienaar et al., 2014; Ozsensoy and Kurar, 2014). The Senegalese cattle breeds are weakly structured, due to little genetic differentiation between populations. This can possibly be due to the consequences of transhumance system of cattle rearing in Senegal that encourages genetic mixtures. Indeed, according to Dorji et al. (2003) migratory system fostered strongly genetic exchanges between populations. In addition the moderate level of genetic differentiation found between subspecies was evidently in order that they belonging to two distinct lineages as Taurine (*Bos taurus*) and Zebuine (*Bos indicus*) subspecies. In general between cattle populations, values of F_{ST} beyond 0.09 indicated that the concerned breeds were separated into subspecies (Dorji et al., 2003). So, the relatively low gene flow observed between these two subspecies was assumed by high reproductive isolation which mainly included mechanisms of speciation.

Regarding the Wilcoxon test, significant heterozygosity excess was detected in all populations under IAM model; nevertheless, in TPM and SMM models all populations were in mutation-drift equilibrium. This can be explained by the fact that for any given data set, IAM predicts lower equilibrium gene diversity than SMM, and hence, it is more likely to indicate significant heterozygosity excess (Thiruvenkadan et al., 2014). Senegalese cattle were found to deviate from equilibrium gene diversity under IAM; and under the statistically more conservative SMM, no deviation was noticed indicating thus, no genetic basis for demographic bottleneck. However, deviation from mutation-drift equilibrium observed in several populations was mainly associated with heterozygosity deficiency (Mahmoudi et al., 2012). The heterozygote deficiency observed in these populations as a result of inbreeding is a cause for concern. By this,

we deduce that these bovine populations have not undergone recent demographic bottleneck. It is shown that, whether a bottleneck has really occurred, it will be detected very strongly with the IAM hypothesis, moderately with TPM and weakly with SMM (De Meeûs, 2012). Whereas in case of absence of bottleneck in population structured into small subpopulations, a bottleneck signature with IAM can be falsely, but exceptionally (if ever) with TPM and never with SMM. In a nutshell, our populations have likely shown a false signature of bottleneck. These results were consistent with the normal L-shaped distribution of allele frequencies in all populations. Therefore, the results obtained here, support the fact that the null hypothesis of mutation-drift equilibrium was fulfilled in all breeds. This allowed ascertained unequivocal that Senegalese local cattle breeds had not undergo a genetic bottleneck in the recent past, i.e., any recent reduction in their effective population size.

Conclusion

The main findings of this study were a high within breed genetic diversity which implied a moderate genetic differentiation among Senegalese local cattle breeds. By demographic analysis of bottleneck, thus, it can be concluded although conservatively based on SMM and qualitative test for mode shift that Senegalese local cattle populations have not deviated from mutation-drift equilibrium, indicating the absence of genetic bottleneck in the recent past.

Controlling transhumance system of Senegalese indigenous cattle breeds by adopted effective management and breeding will make possible the preservation and improvement of special economic traits of breeds in interest in the context of the global climate changes.

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