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Is the introgression of Lobi/Baoulé cattle by zebuine genes in Burkina Faso Lobi cattle threatened?

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Burkina Faso livestock is made up of two main cattle population, namely Zebuine and Taurine. Transhumance and settlement of Zebu cattle breeders in tsetse challenged areas lead to cross-breeding Zebu and Taurine. Introgression of the Zebu cattle may have changed the structure of the trypanotolerant Lobi/Baoulé breed. The objective of the present study was to appreciate the introgression of Zebu genes into Baoulé population by assessing the structure and the genetic diversity of cattle populations across the tsetse belt in Burkina Faso. Therefore, 450 blood samples were taken for genotyping in 29 villages of 3 main regions where Baoulé, BaouléxZebu and Zebu populations are found. Twenty five loci of 22 autosomes have been genotyped. The mean of observed alleles per locus was 12.44 ± 4.31 while the mean of expected alleles was 4.67 ± 1.48 . The heterozygosity ranged from 0.34 to 0.76 and 0.36 to 0.87, respectively for observed and expected heterozygosity across loci. The average heterozygosity across population was 0.73 ± 0.10 . The mean estimates of F -statistics were $F_{IS} = 0.117 \pm 0.019$, $F_{IT} = 0.158 \pm 0.019$ and $F_{ST} = 0.047 \pm 0.005$. The phylogenetic tree showed the Baoulé South-West segregating apart from the other populations, BaouléxZebu being an intermediate genetic group between Baoulé South-West and Zebu North populations. The Baoulé West could not be differentiated from crosses. The Baoulé breed seems to be impacted by the introgression of Zebu genes to its biotope and pure Baoulé seems to be confined to the South-West with very few pure individuals in the West.

Key words: Burkina Faso, Zebu, BaouléxZebu, Baoulé, introgression, microsatellite.

INTRODUCTION

African cattle populations are said to be originated from 2 wild aurochs populations (Loftus et al., 1994, 1999; Bradley et al., 1994). *Bos taurus* (taurine), the humpless descendants of aurochs were domesticated in either the Near East or on the African continent (Epstein, 1971; Clutton-Brock, 1989; Bradley et al., 1996; Hanotte et al., 2002). Several investigations indicated that African Zebu cattle are an admixture of *Bos indicus* and *B. taurus* (MacHugh et al., 1997; Hanotte et al., 2002). Analysis of mitochondrial DNA sequences and microsatellites loci indicate that *B. indicus* may have diverged from *B. taurus* (Bradley et al., 1996; MacHugh et al., 1997; Hanotte et al., 2002). In West Africa, cattle populations are representative of both shorthorn (*B. taurus brachyceros*) and longhorn (*B. taurus longifrons*) humpless taurines, humped zebus (*B. indicus*) and Zebu/Taurine cattle (Gautier et al., 2009).

In Burkina Faso, indigenous cattle are very important for the subsistence and economic development of the country. These indigenous cattle provide essential food products, draft power, manure, and income for rural people. Indigenous breeds are well adapted to local environment thus they have developed disease tolerance and adaptation to harsh climatic conditions. This adaptation favoured the survival under stresses and exploitation of poor quality feeds stuff (Sodhi et al., 2005; Gautier et al., 2009).

With different drought episodes in 1973 and 1983 that occurred in Burkina Faso (Paturel et al., 1998) and the shift of the Northern limit lines of tsetse flies (Courtin et al., 2010) there has been an introgression of Zebu cattle genes through the movement of pastoralist people in the tsetse challenged areas (Grace et al., 2007) seeking for grass and water for livestock. In addition, some of the transhumant livestock keepers settled for long in the tsetse challenged areas rearing and crossing the Zebu breed to the local taurine to control the recurrent trypanosomosis disease. Local mixed livestock-crops farmers crossbreed also the Zebu to the local taurine since the 1920s to 1930s (Grace, 2005) to get hybrid animals that are used as draught animals. The intermediate sized animal is preferred because the local taurine is smaller and less powerful. These trends may have changed the structure of the populations in the tsetse challenged zones. It was therefore important to ascertain the introgression of Zebu genes into Baoulé breed in order to help guide decisions on improvement and conservation priorities. This is especially necessary owing to the husbandry systems practiced by local livestock farmers, which may affect diversity levels

through high gene flow between breeds.

MATERIALS AND METHODS

Animals

1045 blood samples were taken from animals belonging to Baoulé also named Lobi cattle, Zebu and crossbred of BaouléxZebu cattle populations (471 males and 574 females) out of which 450 samples have been randomly selected as per location for genotyping. The animals have been sampled in 29 villages of three different regions and different altitudes. The North (5 villages) being a tsetse free region, the South-West and the West are tsetse challenged regions (Figure 1). Tsetse free is in upper part of the map and separated from the tsetse challenged regions by the northern limit lines of *Glossina tachinoides*, *Glossina morsitans submorsitans* and *Glossina palpalis gambiensis*

Six populations have been considered in the analysis (Table 1); Zebu of the challenged areas have been merged (Other Zebu) due to low number (4) of Zebu samples in the West. BaouléxZebu population in the West was the biggest sample out of the six populations. That results from crossbreeding the 2 main breed (Zebu and Baoulé) to control trypanosomosis disease in the tsetse challenged areas of Burkina Faso in general. Crossbreed population had the highest size in the genotyped sampled (158). On the other hand, the trypanotolerant Baoulé was more important in terms of size in the South-West than the other regions.

DNA extraction

Whole blood of each individual was dropped onto a Whatman FTA card according to Whatman protocol BD09. The samples were kept in multi-barrier pouch till punching day.

Three millilitres diameter Harris punch has been used to remove sample discs from the spotted cards. Genomic DNA was isolated according to a modified protocol of Whatman (Soudré, 2011).

DNA amplification

Microsatellites (31) primers were chosen for the amplification of the genomic DNA. 15 were donated by the International Livestock Research Institute, Nairobi, Kenya. PCR conditions were optimized and all the 31 microsatellites tested for polymorphism. A final panel of 25 polymorphic microsatellites has been used for genotyping of the cattle populations (BM1818, BM1824, BM2113, CSSM066, ETH3, ETH10, ETH185, ETH225, HAUT24, HAUT27, HEL1, HEL5, HEL9, HEL13, ILSTSS005, ILSTS006, INRA023, INRA032, TGLA53, TGLA122, TGLA126, TGLA227, AGLA293, ILSST033 and MGTG4B). Microsatellites were selected combining information from both the National Centre for Biotechnology Information (NCBI, <http://www.ncbi.nlm.nih.gov/>) database and BOVMAP (<http://locus.jouy.inra.fr/cgi-bin/bovmap/intro2.pl>) covering 22 autosomal chromosomes regions. PCRs were then performed using Applied Biosystems GeneAmp[®] PCR System 9700 thermal cyclers.

Genotyping process

The PCR products were diluted 1/10 in distilled water, and

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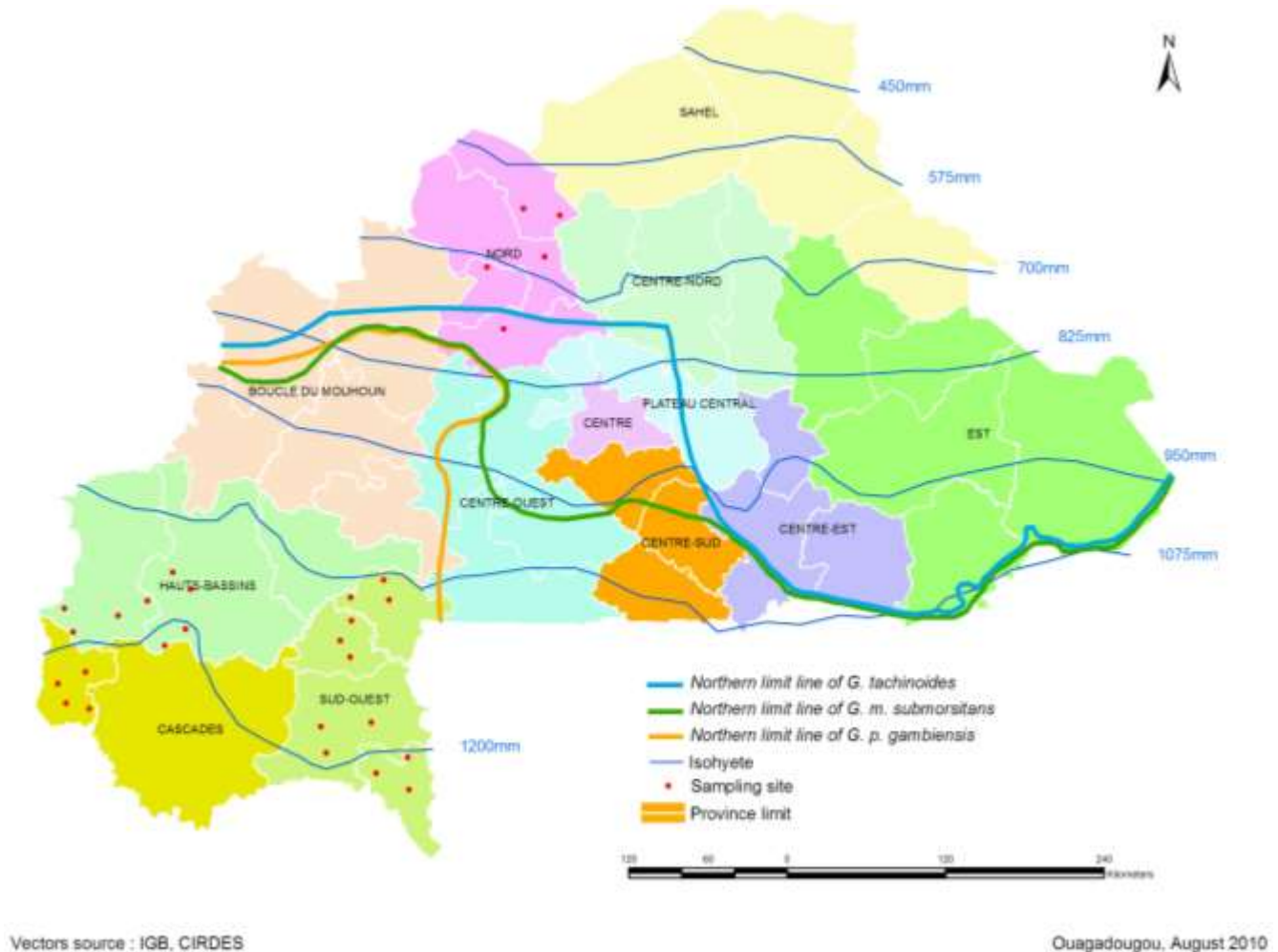


Figure 1. Northern limit lines of different tsetse flies species in Burkina Faso.

genotyping was performed on MegaBACE™ 500, fluorescence-based DNA system utilizing capillary electrophoresis. Alleles were called and scored under MegaBACE™ Genetic Profiler Software Suite v2.2 system.

Statistical analysis

Estimates of total number of alleles, mean number of alleles, effective number of alleles, observed heterozygosity (H_o), and unbiased gene diversity (expected unbiased heterozygosity, H_e) for each population were obtained with POPGENE program version 1.31 (Yeh et al., 1999). H_e the most common measure of variability (Petit et al., 1998; Caballero and Toro, 2002) was estimated using the algorithm of Levene (1949), which is the same as Nei's (1987) unbiased heterozygosity. Convert package version 1.31 (Glaubitz, 2004) has been used to determine the allele frequencies and detect breed-specific alleles.

Deviations from Hardy-Weinberg Equilibrium (HWE) probability exact test with unbiased exact P -value of Guo and Thompson (1992) was performed using GENEPOP package version 4.0.10 of Rousset (2008) according to the Markov Chain parameters,

dememorization (1000), batches (100), and iteration per batch (1000).

Using the variance-based of Weir and Cockerhan (1984), F -statistics (F_S , F_T , F_{ST}) for each locus and overall values were calculated using FSTAT version 2.9.3.2 (Goudet, 2002). Significance tests on the estimates F -statistics for each microsatellite locus were obtained by constructing 95 and 99% confidence intervals based on the standard deviations estimated by jackknifing across populations using FSTAT.

POPULATION 1.2.30 software (Langella, 1999) was used to construct a phylogenetic tree of populations with bootstrap on locus using Reynolds et al. (1983) least squares. That was run using UPGMA and 1000 trials. The tree was visualized with TreeView 1.6.6 software (Page, 1996).

The Bayesian clustering method, as implemented by the STRUCTURE 2.3.3 program (Pritchard et al., 2000; Falush et al., 2003, 2007; Hubisz et al., 2009) was run five times with burnin period of $5 \cdot 10^4$ iterations followed by 10^5 number of MCMC repeats after burnin assuming $k=2$. The admixture model was used with the sampling locations as a prior. Correlated allele frequencies model was used as well. The clustering has also been performed with Bayesian Analysis of Population Structure (BAPS) package version

Table 1. Allele numbers, heterozygosity, deviation from HWE, intra-population diversity the 6 populations.

Breed/Population	N	TNA	MNA	MNe	Ho	He	HWE	F _{IS}
Zebuine	117	229	9.56 (3.03)	4.22 (1.19)	0.66 (0.11)	0.774 (0.11)	-	0.102
Zebu North	66	218	8.72 (2.96)	4.20 (1.15)	0.65 (0.13)	0.74 (0.13)	4	0.116
Other Zebu	51	205	8.20 (2.40)	4.02 (1.29)	0.67 (0.11)	0.73 (0.11)	2	0.084
Taurine	145	284	10.04 (3.45)	3.80 (1.46)	0.60 (0.13)	0.70 (0.13)	-	0.121
Baoulé South-West	124	239	9.56 (3.44)	3.56 (1.31)	0.60 (0.14)	0.68 (0.14)	6	0.122
Baoulé West	21	176	7.04 (2.09)	4.03 (1.40)	0.65 (0.15)	0.74 (0.11)	1	0.120
Crosses	158	364	11.20 (3.96)	4.69 (1.39)	0.67 (0.11)	0.77 (0.09)	-	0.122
BaouléxZebu South-West	35	205	8.20 (2.87)	4.28 (1.26)	0.63 (0.17)	0.75 (0.12)	5	0.157
BaouléxZebu West	153	270	10.80 (3.82)	4.70 (1.45)	0.68 (0.10)	0.77 (0.08)	8	0.114

N, Sample size; TNA, total number of alleles; MNA, mean number of alleles observed; MNe, mean number of effective alleles; *Ho*, observed heterozygosity; *He*, expected heterozygosity; (2.96), standard deviation; HWE, locus-population deviation ($P < 0.0001$); *F_{IS}*, intra-population heterozygosity deficiency.

5.3 (Corander et al., 2008) that showed the same pattern as STRUCTURE.

RESULTS

Alleles (311) were detected from the 25 loci surveyed, giving a mean number of alleles 12.44 ± 4.31 observed and mean of effective alleles number was 4.67 ± 1.48 (Table 1). The number of alleles ranged from 3 at CSSM066 to 22 at TGLA122 (Table 2). The lowest number of effective allele number was observed at CSSM066 (1.57) and the highest number at TGLA53 (7.65). The total number of alleles per population ranged from 176 to 270 alleles, respectively for Baoulé in the West and Zebu Baoulé in the West. The lowest number of alleles in Baoulé West population may be due to the small size of the Baoulé population (21) from this region in the sample. The total number of allele in taurine was somehow higher than in Zebuine may be because most of the primers are taurine based designed. Many have been designed from Hereford for example.

Some 7% of the total alleles have been detected as breed-specific alleles using Convert package, 12 private alleles of Zebu at 11 loci and 10 private alleles of Baoulé at 9 loci.

For loci in the study, 14 of them have deviated from HWE ($P < 0.0001$ using the probability exact test of Fisher) as shown in Table 2; markers displaying a highly significant deviation from HWE are in italics. Furthermore, deviations from HWE were statistically significant ($P < 0.0001$) for 26 locus-population combinations. Out of the 25 loci analyzed in each population, 1 to 8 deviated significantly from HWE. All populations also deviated from HWE ($P < 0.0001$) probably because of heterozygote's

deficiency.

Expected heterozygosity has been generally higher than observed heterozygosity not only at marker level but also at population level. At population level, the most diversified population was the Zebu Baoulé in the West with the highest observed and expected heterozygosity ($Ho = 0.68 \pm 0.10$, $He = 0.77 \pm 0.08$) and the less diversified the Baoulé from the South-West ($Ho = 0.60 \pm 0.14$, $He = 0.68 \pm 0.14$). In the overall population, the crosses as expected are more diversified ($He = 0.77 \pm 0.09$) than the pure breeds (Zebu and Baoulé) followed by Zebu ($He = 0.74 \pm 0.11$). Observed heterozygosity ranged from 0.34 (CSSM066) to 0.76 (INRA032 and TGLA227). The most variable marker in this study was TGLA53 ($He = 0.87$) compared to CSSM066 ($He = 0.36$). The marker which contributed much to the variability was INRA032 and HEL 9 (Ave. Het. = 0.82). The mean number of migrants per generation for all loci estimated based on the formula $Nm = 0.25(1-F_{ST})/F_{ST}$ as implemented in POPGENE was 6.06.

BaouléxZebu population from the South-West showed the highest value of *F_{IS}* (0.157). Comparisons of *F_{IS}* of the 3 groups were not statistically significant as well as the comparisons of the *F_{ST}* values.

The locus ETH10 (0.121) contributed the most to the population differentiation. But the overall *F_{ST}* being < 0.15 , the population differentiation seems to be moderate. The mean global *F_{ST}* ranged from 0.012 (MG TG4B) to 0.121 (ETH10) among different microsatellite loci with an estimated mean value of 0.047 ($P < 0.01$), indicating 4.7% of the total variation being attributed to between breed differences.

A neighbor-joining dendrogram constructed based on unbiased genetic distances showed 2 main clusters, one cluster composed of Baoulé South-West and the second

Table 2. Alleles number per locus, observed, expected, *P*-values, *F*-Statistics (Weir and Cockerhan, 1984), standard errors for each locus across populations.

Loci	NA	NE	Ho	He	P-value§	F _{IS}	F _{IT}	F _{ST}
BM1824	9	3.45	0.65	0.71	0.0476	0.059 (0.045)	0.098 (0.036)	0.042 (0.033)
BM2113	17	6.19	0.67	0.84	0.0000	0.173 (0.046)	0.227 (0.083)	0.063 (0.051)
INRA023	11	4.52	0.70	0.78	0.0000	0.056 (0.035)	0.114 (0.072)	0.060 (0.046)
MGTG4B	15	5.12	0.73	0.81	0.0000	0.084 (0.017)	0.095 (0.017)	0.012 (0.007)
AGLA293	15	5.84	0.74	0.83	0.0090	0.074 (0.014)	0.124 (0.022)	0.055 (0.037)
ETH10	10	4.75	0.65	0.79	0.0000	0.099 (0.037)	0.211 (0.112)	0.121 (0.096)
ILSTS006	9	3.47	0.52	0.71	0.0000	0.266 (0.050)	0.292 (0.038)	0.036 (0.028)
HEL9	11	6.18	0.75	0.84	0.0000	0.085 (0.036)	0.114 (0.050)	0.032 (0.028)
ETH225	13	3.96	0.65	0.75	0.0020	0.064 (0.029)	0.148 (0.048)	0.092 (0.072)
ILSTS005	9	3.01	0.60	0.67	0.0004	0.076 (0.025)	0.109 (0.047)	0.035 (0.032)
INRA032	17	5.96	0.76	0.83	0.0086	0.068 (0.010)	0.094 (0.023)	0.029 (0.019)
HEL13	7	3.01	0.58	0.67	0.0167	0.061 (0.025)	0.141 (0.072)	0.085 (0.061)
ILSTS033	12	3.19	0.54	0.69	0.0000	0.153 (0.076)	0.241 (0.125)	0.100 (0.076)
CSSM066	3	1.57	0.34	0.36	0.0181	0.051 (0.134)	0.159 (0.169)	0.106 (0.045)
HEL1	8	5.04	0.44	0.80	0.0000	0.417 (0.039)	0.466 (0.063)	0.082 (0.058)
TGLA53	19	7.65	0.60	0.87	0.0000	0.278 (0.025)	0.321 (0.041)	0.059 (0.043)
ETH185	13	3.85	0.63	0.74	0.0000	0.148 (0.034)	0.163 (0.028)	0.018 (0.011)
TGLA227	16	6.07	0.76	0.84	0.0000	0.055 (0.007)	0.107 (0.042)	0.055 (0.041)
ETH3	11	3.36	0.69	0.70	0.7610	-0.005 (0.011)	0.028 (0.027)	0.033 (0.025)
TGLA126	9	4.40	0.75	0.77	0.0722	0.023 (0.019)	0.044 (0.024)	0.021 (0.016)
HEL5	12	5.41	0.67	0.82	0.0000	0.153 (0.034)	0.168 (0.038)	0.018 (0.011)
TGLA122	22	3.30	0.65	0.70	0.0000	0.061 (0.042)	0.083 (0.057)	0.022 (0.017)
HAUT24	19	6.90	0.71	0.86	0.0000	0.133 (0.047)	0.177 (0.033)	0.052 (0.017)
BM1818	12	6.33	0.74	0.84	0.0068	0.087 (0.028)	0.133 (0.023)	0.050 (0.033)
HAUT27	12	4.32	0.65	0.77	0.0003	0.127 (0.037)	0.163 (0.031)	0.042 (0.017)
Total	311	-	-	-	-	-	-	-
Mean	12.44	4.67	0.65	0.76	-	-	-	-
St. Dev	4.30	1.48	0.10	0.10	-	-	-	-
Overall	-	-	-	-	-	0.117 (0.019)**	0.158 (0.019)	0.047 (0.005)*

NA, Observed number of alleles; NE, effective number of alleles; *H_o*, observed heterozygosity; *H_e*, expected heterozygosity; §Fisher's probability exact test across all populations with deviations from HW (P<0.0001); *, 95% confidence interval. **, 99% confidence interval.

being composed of the remaining populations (Figure 2). In the second cluster, the populations clustered further into 3 genetic groups; the first group had Baoulé×Zebu South-West and Other Zebu. That group had the smallest genetic distance ($D_A = 0.0434$ in Table 3). The last group had only Zebu North. The unbiased genetic distance between Baoulé South-West and Zebu North was the longest one ($D_A = 0.3390$). A phylogenetic tree (Figure 2) supports it with a bootstrap value of 75%. The bootstraps showed the Baoulé South-West segregating from the other populations with 100% of replicates.

Using STRUCTURE, the most likely K is that where $\ln \Pr(G|K)$ is maximized. The maximum value of $\ln \Pr(G|K)$ was obtained at $K = 2$ (Figure 3), that provided an explanation of the genetic structure and levels of admixture for the populations. This assumption has been supported by farmers' assumption as well about clusters

on the field. The clusters shown in Figure 2 have been confirmed using BAPS program.

DISCUSSION

The genetic diversity of Burkina Faso cattle populations sampled from different regions across the country was assessed. The mean number of observed alleles was almost similar to the 11.4 alleles per locus reported by Loftus et al. (1999) but considerably higher than the 8.4 reported by MacHugh et al., (1997), 9.7 reported by Thévenon et al. (2007) in the Southern-West of Burkina Faso, 4.59 and 4.37 reported in Pakistan breeds by Rehman and Khan (2009), 7.11, 7.41 and 6.74 reported in Arabic Zebu, Bororo Zebu and Kuri cattle, respectively (Grema et al., 2017). This difference may reflect an

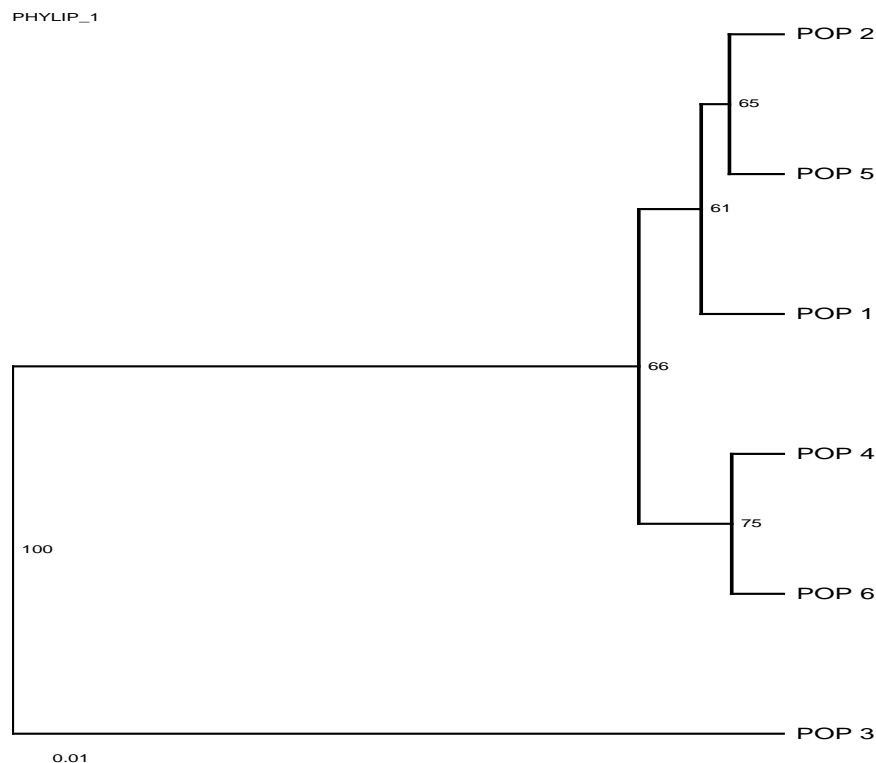


Figure 2. Neighbor joining tree summarizing genetic distances among 6 cattle populations (POP 1: Zebu North; POP 2: Other Zebu; POP 3: Baoulé South-West; POP 4: Baoulé West; POP 5: BaouléxZebu South-West; POP 6: BaouléxZebu West). Bootstrap values indicating the degree of support for each branch point are shown beside the node as the percentage of replicates in which the cluster to the right of the node was recovered.

Table 3. Nei's (1978) unbiased genetic identity (above diagonal) and genetic distance (below diagonal).

Parameter	Zebu North	Other Zebu	Baoulé South-West	Baoulé West	BaouléxZebu South-West	BaouléxZebu West
Zebu North	-	0.9500	0.7125	0.8868	0.9425	0.9362
Other Zebu	0.0513	-	0.7469	0.8974	0.9575	0.9384
Baoulé South-West	0.3390	0.2918	-	0.8562	0.8456	0.8272
Baoulé West	0.1202	0.1083	0.1552	-	0.9209	0.9569
BaouléxZebu South-West	0.0592	0.0434	0.1677	0.0824	-	0.9548
BaouléxZebu West	0.0659	0.0636	0.1897	0.0441	0.0462	-

unexpected bias in the selection of the loci but also the absence of selection pressure in cattle in Burkina Faso. In such a situation, direct comparisons may not be possible because of the markers sets and techniques used. Compared to Thévenon et al. (2007), the results were almost similar when considered only the mean number of alleles per locus from tsetse challenged area from where samples were taken as well.

In Burkina Faso, Zebu population is known to consist of

Fulani Zebu, M'Bororo Zebu, Azawak Zebu originated from Niger, and a few years ago Gudali Zebu which was formally from Nigeria. Individuals from these Zebu types are thought to be included. Also, the analyses showed that a certain number of animal migrated per generation in the present populations. That is very common in diversity studies and it may be due to cattle movement along with human. In Burkina Faso, it may be due to the transhumance. The deviation in Baoulé population may

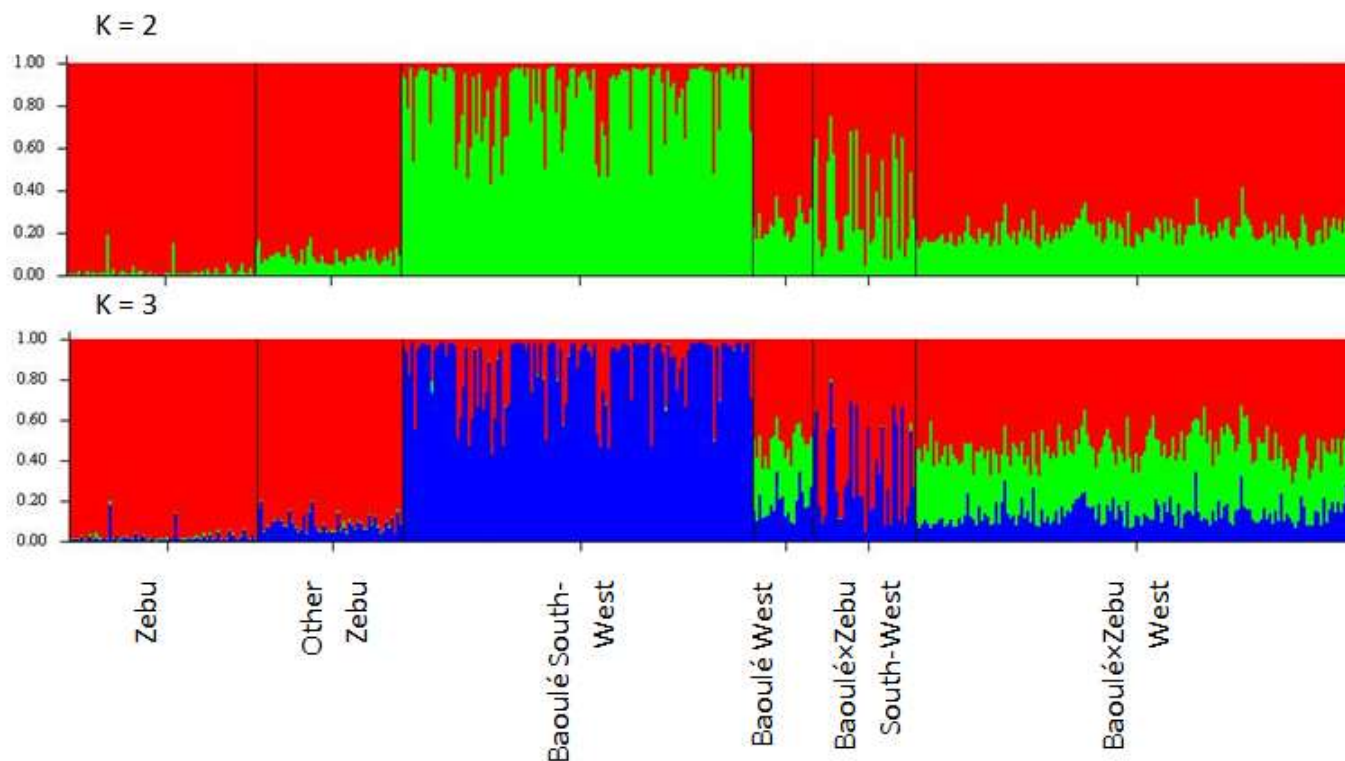


Figure 3. Genetic structure of the six cattle populations. Each individual animal is represented by a single vertical line divided into K colours, where K is the number of clusters assumed and the length of the coloured segment represents the individual's ancestry proportion of membership to a particular cluster estimate. Black lines separate individual populations whose names are indicated below the diagram.

result from misclassifying N'Dama type or their cross bred in Baoulé type. N'Dama cattle were present in the South-West in the International Centre for Research and Development in Animal Husbandry in Subhumid Zones (CIRDES) research farm for scientific experiences and some individuals have been introduced in farmers' herds. One more reason of departure from HWE could be the admixture linkage disequilibrium, the correlations that arise between linked markers in admixed populations, as described by Falush et al. (2003).

Observed and expected heterozygosity across populations were similar or comparable to those reported by Moazami-Goudarzi et al., (1997), Ibeagha-Awemu et al. (2004) in West and Central African cattle populations, Sodhi et al. (2005) in Indian cattle populations, Zerabruk et al., (2007) and Dadi et al. (2008) in Ethiopian indigenous cattle populations. But lightly different from Martin-Burriel et al. (2007) may be because the populations in the study were endangered. Average heterozygosity was within the range of 0.3 to 0.8 as suggested by Takezaki and Nei (1996) to be useful for measuring genetic variation. The overall F_{ST} revealed a moderate level of genetic differentiation among the populations in the study. The overall value of F_{ST}

observed is similar to that observed in Ankole cattle in Uganda (Kugonza et al., 2010), lower than that reported in 2 Indian cattle populations (Sodhi et al., 2005) greater than that observed in Ethiopian populations (Dadi et al. 2008), in Ankole cattle in the African Great lakes region (Ndumu et al., 2008). The moderate genetic differentiation could be a result of gene flow from other populations. In the Northern part the animals are reared without any trypanosomiasis pressure therefore there is less or no crossing with the taurine breed. But in the tsetse challenged regions where trypanosomiasis is the most important disease in cattle (Soudré et al., 2009) crossbreeding is frequent. In addition, the pastoral production systems, long distance migrations within and across countries, utilization of communal pastures, exchange of breeding animals, uncontrolled mating facilitate constant gene flow.

Conclusion

Moderate genetic differentiation among indigenous cattle populations in Burkina Faso across the loci makes possible to use these breeds to improve the genetic for

production and conservation and diversity in general. Regarding trypanosomosis, it may help to improve the tolerance of Zebu breed to trypanosomosis in the tsetse infested regions. Added to these advantages, little is known about the genetic diversity, structure and degree of admixture among Burkina Faso cattle populations. This supports the statement of Hanotte and Jianli (2005), knowledge of both the global diversity of the breeds and admixture events will be needed in order to be able to make sound priority decisions. Actions should be drawn to conserve the Baoulé breed which is threatened by the introgression of Zebu breed to its biotope. The Baoulé West as reported by the study cannot be differentiated from the crosses. The introgression of Zebu in the Southern areas of Burkina Faso will be perhaps more important with the climate change.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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