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MICROSATELLITE ANALYSIS CHARACTERIZES BURKINA FASO AS A GENETIC CONTACT ZONE BETWEEN SAHELIAN AND DJALLONKÉ SHEEP

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A total of 123 sheep belonging to the Djallonké, Mossi, and Burkina-Sahel breeds, along with 41 Spanish Xalda sheep were genotyped for 27 microsatellites. The pair Djallonké-Mossi had the highest between breeds molecular coancestry. Admixture analysis informed on the parental role of the Burkina-Sahel and Djallonké breeds. The Mossi breed was a hybrid population nearer to the Djallonké breed. Only half of the Mossi individuals were correctly assigned to their breed. The Burkina-Sahel and Djallonké breeds can be considered ancestrally different genetic entities. Differentiation between the Djallonké and Mossi breeds may be due to introgression of Sahelian sheep.

Keywords: Burkina-Sahel sheep; Djallonké sheep; Genetic resources; Genetic variability; Mossi sheep; West Africa

Burkina Faso is a sub-Saharan West African country that can be divided into three main environmental areas according to climate conditions and types of vegetation (1–3): (a) the arid Sahel area, covering the Northern part of Burkina Faso (from latitude 13°5′ N to 15°3′ N, approximately); (b) the Sudan area, covering the Southern part of Burkina Faso (latitude from 9°3′ N to 11°3′ N) with annual rainfall higher than 900 mm; and (c) the Sudan-Sahel area, covering the central part of the country and very variable rainfall, with an average of 750 mm per year.

Each of these environmental areas is the habitat of a different sheep breed: (a) the Burkina-Sahel breed, which inhabits Northern Burkina Faso and

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Western-Central Mali and is kept by the Peul (Fulani) agropastoral communities; (b) the Djallonké dwarf breed, located in the Sudan area, which is a hairy thin-tailed sheep belonging to the West African Dwarf sheep group; and (c) the Mossi breed, located in the Sudan-Sahel area of Burkina Faso that, at the morphological level, is considered a transitional breed probably nearer to the Djallonké breed (3). The sheep populations of these three environmental areas approximately number, respectively, 2,135,297 (Sahel), 1,555,600 (Sudan), and 3,011,743 (Sudan-Sahel) head (4). Sheep play a major role in the maintenance of rural populations living under conditions of extreme poverty and are of major cultural importance due to their traditional use in rites and celebrations (5).

Documentation on existing genetic resources, including the description of the population phenotypic characteristics, performance, cultural importance and genetic uniqueness is one of the main areas of livestock conservation activities (6, 7). A description of genetic diversity can also provide information on possibilities of further sustainable intensification of animal production aimed at addressing increasing human needs for food. In spite of their regional importance, genetic studies involving West African sheep are scant (8), and no genetic studies have been carried out to characterize the Burkina Faso sheep population. The first step in the genetic characterization of local livestock breeds is usually carried out using microsatellite sets (9–12). The aim of the present research was to contribute to the characterization of the Burkinabé sheep populations and ascertain the between-populations genetic relationships and gene flow using microsatellite marker polymorphism. To address this task, the rare Xalda of Spain (13–15) will be used as outgroup.

MATERIALS AND METHODS

Sampling and Genotyping

Blood samples were obtained from a total of 123 reproductive-age individuals belonging to the three Burkinabé sheep populations. Of these, 39 Burkina-Sahel individuals (20 males and 19 females) were sampled in three different villages (Dori, Yakouta, and Katchari), 43 Djallonké individuals (20 males and 23 females) were sampled in two different villages (Gaoua and Kampti) and 41 Mossi individuals (21 males and 20 females) were sampled in five different villages (Ouaga, Sapone, Kamboinse, Pabre, and Koubri). Between two and five different flocks were sampled in each village. In addition, 41 samples belonging to the endangered Spanish Xalda sheep breed previously characterized in a study by Álvarez et al. (15) (see cohort 4 of that study) were used as an outgroup.

Total DNA was isolated from blood samples following standard procedures (16). Twenty-seven microsatellites were analyzed for all samples (Table 1). Genotyping was performed on an Automatic Sequencer ABI 310 (Applied Biosystems, Barcelona).

Statistical Analyses

Molecular information was analyzed using the program MolKin (17; current version 3.0). For descriptive purposes, the number of observed alleles, the observed

Table 1 Number of alleles per marker (n), expected (He) heterozygosity and polymorphic informative content (PIC) values per marker in the analyzed dataset

Marker	n	He	PIC
BM2504	6	0.649	0.600
BM6526	10	0.646	0.604
BM757	7	0.779	0.745
BM8125	6	0.623	0.587
BMS1948	8	0.597	0.564
BMS2461	12	0.608	0.584
BMS2626	4	0.582	0.508
BMS2843	6	0.656	0.608
BMS356	2	0.434	0.340
CP34	9	0.769	0.732
CSSM08	7	0.634	0.581
CSSM15	6	0.569	0.498
CSSM31	20	0.837	0.823
CSSM43	16	0.862	0.848
CSSM66	16	0.843	0.825
FCB128	12	0.833	0.815
ILSTS05	10	0.774	0.742
ILSTS11	8	0.538	0.514
INRA26	7	0.219	0.209
LSCV29	13	0.742	0.710
McM527	11	0.830	0.808
McM53	15	0.793	0.776
McMA26	19	0.885	0.874
OarHH64	11	0.736	0.699
RBP3	9	0.737	0.700
SPS115	16	0.807	0.784
TGLA53	12	0.865	0.850

(Ho) and expected (He) heterozygosity, and the polymorphic informative content (*PIC*, 18) computed as

$$PIC = 1 - \sum_i p_i^2 - \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} 2p_i^2 p_j^2,$$

where p_i and p_j are respectively the frequency of the alleles i and j of a given locus, were computed at the locus level and for the whole dataset. The following parameters were computed at the population level: observed (Ho) and expected (He) heterozygosity, raw number of alleles per locus (A), and number of alleles per locus corrected for sampling size using Hurlbert's rarefaction method (19). The latter is computed as

$$A[g] = \sum_i \left[1 - \prod_{k=0}^{g-1} \frac{N - N_i - k}{N - k} \right],$$

where g is the specified sampled size, N the number of gene copies examined in a given locus ($N > g$), and N_i the number of occurrences of the i-th allele among the

N sampled gene copies to account for sample size. Here, g was fitted to 50, which is twice the minimum number of individuals within a cohort of known genotype for all the microsatellites.

Likewise using the program MolKin, the between-individuals and populations shared allele distance (D_{AS}, 20) was computed as $D_{AS} = 1 - \frac{2\overline{P}_{SAkm}}{\overline{P}_{SAk}+\overline{P}_{SAm}}$, where $\overline{P}_{SAk}$ and $\overline{P}_{SAm}$ are respectively the average proportion of shared allele between individuals belonging to population k or m, and $\overline{P}_{SAkm}$ the average proportion of shared allele between individuals belonging to populations k and m. Additionally, the within- and between-individuals molecular coancestry matrix was computed. The molecular coancestry (f_{ij}) between two individuals i and j is the probability that two randomly sampled alleles from the same locus in two individuals are identical by state (21). Molecular coancestry between two individuals i and j at a given locus can be computed using the following scoring rules (21, 22): $f_{(m)ij,l} = \frac{1}{4}[I_{11} + I_{12} + I_{21} + I_{22}]$, where I_{xy} is 1 when allele x on locus l in individual i and allele y on the same locus in individual j are identical, and zero otherwise. Notice that this value can only have four values: 0, $\frac{1}{4}$, $\frac{1}{2}$ and 1. The molecular coancestry between two individuals i and j (f_{ij}) can be obtained by simply averaging over L analyzed loci. Within- and between-populations molecular coancestry was computed by simply averaging the corresponding values for all the within- or between-population pairs of individuals.

A neighbor-joining tree was constructed on the between-individuals D_{AS} matrix using the program MEGA 4.0 (23).

The program STRUCTURE (24) was used to ascertain the degree of admixture of the three Burkinabé sheep breeds under study. Following Beaumont et al. (25) and Kumar et al. (26), we analyzed the Burkinabé individuals forcing K = 2 (using burn-in and data collection periods of 100,000 iterations) to obtain the mean of the posterior distribution of each individual's admixture coefficient, ($\hat{q}$), which represents an estimate of the amount of an individual's genome that is derived from the inferred parental populations. This approach assumes that there are two parental populations and others (here the Mossi breed) derived (25, 26). Parental populations were defined as those with $\hat{q}$ ranging from 0 to 0.1 or from 0.9 to 1.0, whilst hybrid populations would be those with $\hat{q}$ ranging from 0.1 to 0.9 (25, 26). Note that if one population is not actually derived from those expected to be parental, the individuals belonging to the analyzed populations can obtain intermediate or extreme $\hat{q}$ values at random.

With the aim of ascertaining the recent history of the analyzed breeds, probabilities of assignment of the genotyped individual to a particular breed were computed using the Bayesian method described by Rannala and Mountain (27) as implemented in the program GENECLASS 2.0 (28, 29). This Bayesian procedure computes the likelihood of a genotype in a given population assuming an equal prior probability density of the allelic frequencies of each locus in each population. This method shows better assignment performance than exact or distance-based methods both in simulated or real populations (28, 29).

RESULTS

Table 1 gives information on the variation of the genotyped markers. The number of alleles per locus varied from 2 (BMS356) to 20 (CSSM31), with 25 out

Table 2 Number of individuals analyzed (N), expected heterozygosity (He), within-population molecular coancestry (f_{ii}), heterozygote deficiency within population (F_{IS}), raw average number of alleles per locus (A) and average number of alleles per locus rarefacted (corrected for sampling size) to 24 copies ($A_{(24)}$) per analyzed breed and for the whole dataset

Breed	N	He	f_{ii}	F_{IS}	A	$A_{(56)}$
Burkina-Sahel	39	0.634	0.364	0.086	6.4	6.1
Djallonké	43	0.629	0.371	0.087	6.5	6.0
Mossi	41	0.671	0.333	0.116	7.7	7.2
Xalda	41	0.661	0.342	0.041	7.1	6.6
Totals	164	0.698	0.298	0.083	10.3	7.6

of 27 markers having six or more alleles. The expected heterozygosity varied from 0.219 (INRA26) to 0.885 (McMA26). Up to 25 and 23 markers, respectively, had He and PIC values above 0.5, indicating that, overall, the analyzed microsatellite set was useful for assessing among-breeds genetic relationships.

Parameters characterizing genetic variability of the analyzed sheep populations are given in Table 2. Except for Mossi, the African breeds had He values lower than those computed for the endangered Xalda population, the lowest He value being found in the Djallonké breed (0.629), which was also the breed showing the highest within-population genetic identity ($f_{ii} = 0.371$) and the lowest corrected (rarefacted) average number of alleles per locus (6.0). The Mossi breed had the highest heterozygote deficiency ($F_{IS} = 0.116$) and average number of alleles in the dataset (7.2).

The between-breeds molecular coancestry (f_{ij}) and shared allele distance (D_{AS}) matrices are given in Table 3. As expected, the lower f_{ij} values were found between each Burkinabé breed and the outgroup, varying from 0.245 ± 0.008 to 0.252 ± 0.007. The highest between-Burkinabé breeds f_{ij} value was found for the pair Djallonké-Mossi (0.325 ± 0.011), whilst the lowest was found between the Burkina-Sahel and the Djallonké breeds (0.298 ± 0.007). This information was consistent with that given by the between-breeds D_{AS} matrix. The highest between-Burkinabé breeds D_{AS} value was found between the Burkina-Sahel and the Djallonké breeds (0.206 ± 0.014), whilst the lowest was found for the Djallonké-Mossi pair (0.090 ± 0.012).

Table 3 Between-populations molecular coancestry (below diagonal) and shared-allele distance (above diagonal) in the analyzed dataset. Standard deviation of the estimates obtained using bootstrapping (1000 replicates) are in brackets

	Burkina-Sahel	Djallonké	Mossi	Xalda
Burkina-Sahel		0.206 (0.014)	0.139 (0.012)	0.297 (0.016)
Djallonké	0.298 (0.007)		0.090 (0.012)	0.314 (0.014)
Mossi	0.305 (0.010)	0.325 (0.011)		0.278 (0.013)
Xalda	0.252 (0.007)	0.249 (0.007)	0.245 (0.008)	

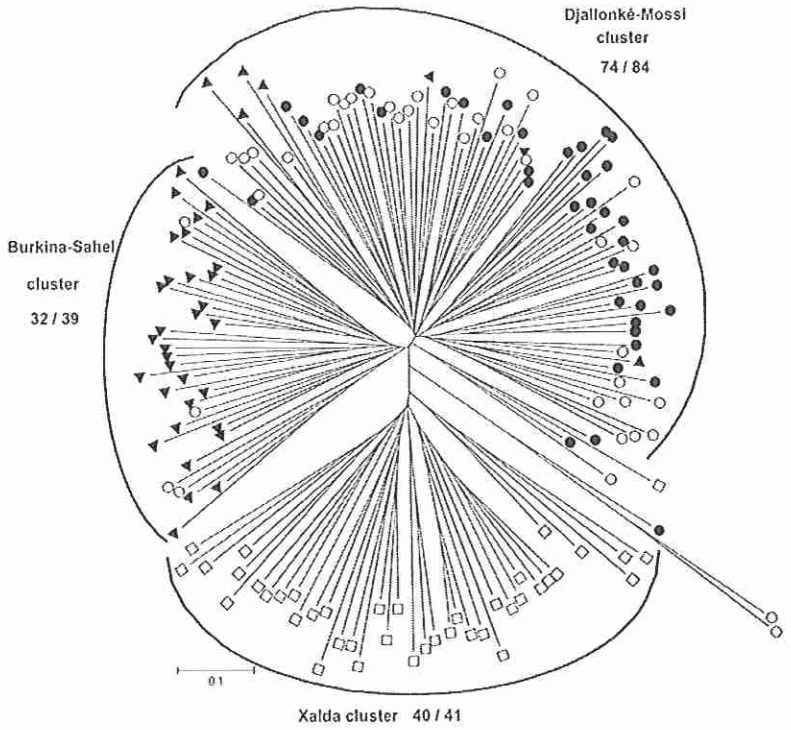

Figure 1 Neighbor-joining tree constructed from the between-individuals shared allele distance matrix. Djallonké individuals are in black circles, Mossi individuals are in open circles, Burkina-Sahel individuals are in black triangles, and Xalda individuals are in open squares. The number of individuals from a particular breed grouped into a cluster is indicated.

Figure 1 shows the neighbor-joining tree constructed from the between-individuals D_{AS} distance matrix. A considerable degree of differentiation was revealed: of the 164 genotyped individuals, 146 (89%) formed three discrete clusters, basically coinciding with the Xalda breed used as outgroup, the Burkina-Sahel breed and the Djallonké and Mossi individuals which cluster together. No Djallonké individuals clustered within Burkina-Sahel clade; however, seven Burkina-Sahel samples grouped into the Djallonké-Mossi clade and four Mossi individuals clustered into the Burkina-Sahel clade.

The results obtained using the program STRUCTURE are presented in Figure 2. The posterior distributions of admixture proportions of all the individuals were not uniform; however, the Burkina-Sahel and Djallonké individuals showed narrow distributions with mean ($\hat{q}$) values of 0.948 and 0.037, respectively. In contrast, the mean ($\hat{q}$) value for the Mossi individuals was 0.262 (nearer to the Djallonké individuals), a wide distribution and a considerable number of extreme values near the Burkina-Sahel individuals. In summary, most Djallonké (96.3%) and Burkina-Sahel (94.8%) individuals were assigned to each cluster inferred; however, 73.8% of the Mossi individuals were assigned to the Djallonké cluster and 26.2% to the Burkina-Sahel cluster. These assignment results are not dependent on the presence of the Mossi individuals. The analysis was rerun including only the Burkina-Sahel and the Djallonké individuals. Djallonké (94.4%) and Burkina-Sahel (96.5%) individuals clustered separately.

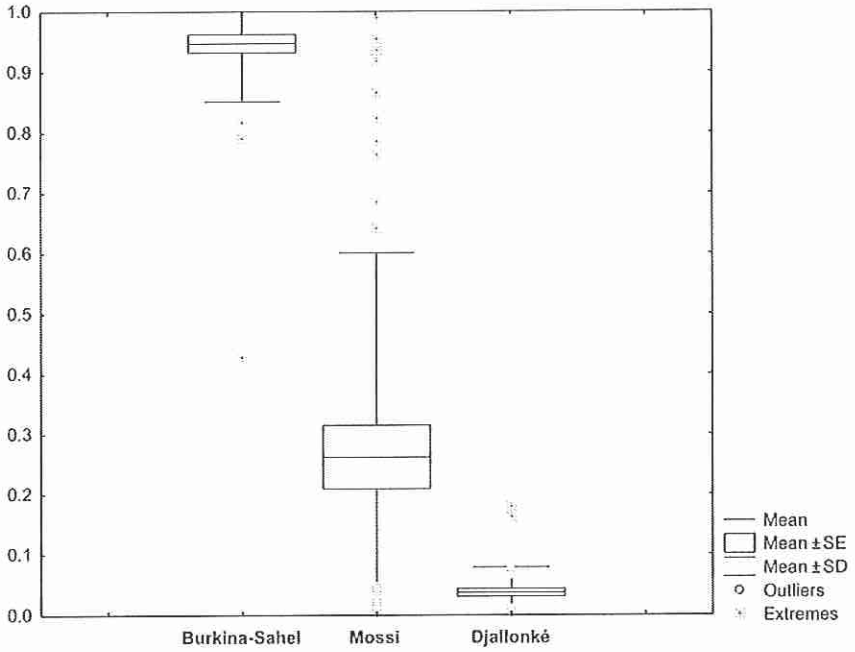

Figure 2 Boxplot of mean individual admixture coefficient, ($\hat{q}$), for each Burkinabé individual grouped by breed. The box represents the range that contains the values within the limits of the standard error of the mean, the line within the box indicating the mean value. The whiskers are the lines that extend from the box to the ± standard deviation, excluding outliers and extreme values. Outliers, which are represented by circles, are values that are 1.5–3 standard error lengths from the upper or lower edge of the box. Extreme values, which fall outside the standard deviation limits, are represented by asterisks.

Assignment of individuals to the corresponding breeds was assessed using the GENECLASS 2.0 program under the Bayesian algorithm developed by Rannala and Mountain (27). Overall, there were large assignment errors except for the Xalda breed (Table 4). Even though most Djallonké and Burkina-Sahel individuals were correctly assigned to their breed (86.1% and 89.7%, respectively), roughly 10% of them were assigned to the Mossi breed. Moreover, only half of the Mossi individuals were assigned to their breed, whilst a quarter of them were assigned to the Djallonké breed and roughly 20% were assigned to the Burkina-Sahel breed.

Table 4 Assignment of the genotyped individuals to the four predefined sheep breeds using the program GENECLASS 2.0. Assignments are given in absolute frequencies and in percentage (in brackets)

	Assigned population			
Breed of origin	Djallonké	Mossi	Burkina-Sahel	Xalda
Djallonké	37 (86.1)	6 (13.9)	—	—
Mossi	11 (26.8)	22 (53.7)	8 (19.5)	—
Burkina-Sahel	—	4 (10.26)	35 (89.74)	—
Xalda	—	—	—	41 (100)

DISCUSSION

Microsatellite studies in sub-Saharan sheep are scant (8, 31) and not directly comparable with the present analysis because of the different microsatellite sets used. Buduram (31) genotyped four native South African sheep breeds (Damara, Pedi, Zulu, and Swazi) for 24 microsatellites. Reported mean number of alleles and expected heterozygosity in that study varied from 4.64 to 7.04 and from 0.581 to 0.698, respectively. Wafula et al. (8) analyzed 11 Djallonké sheep populations from Guinea, Mali, Senegal and The Gambia using 15 microsatellites and reported adjusted mean number of alleles varying from 5.76 to 7.35 and expected heterozygosities varying from 0.656 to 0.706. In general, these values agree with those reported here (Table 2).

As repeatedly reported in African cattle (32, 33), it is not easy to assess genetic relationships among African livestock because definition of breeds is mainly based on the farm-holding ethnic groups or geographical areas within which the individuals are found. In this respect, the definition of breeds in Africa (and in our Burkinabé dataset) is based on consensus among rural communities around the country to roughly recognize livestock entities that can be considered as breeds (34, 35). Within such a scenario, the use of appropriate outgroups is needed to obtain sound assessments of between-African breeds genetic relationships (8). The main breeds analyzed here (Burkina-Sahel and Djallonké) showed values for parameters characterizing genetic variability lower than those obtained for the Spanish Xalda sheep. The 11 Djallonké sheep populations analyzed by Wafula et al. (8) also showed lower values for genetic variability parameters than each of the three reference sheep populations (from Mali, Nigeria, and Portugal) used in that study. In any case, the lower diversity values found here in the Burkinabé sheep breeds may simply result from the fact that the microsatellite set used was developed in European sheep. In two populations with actual equal diversity, the estimated diversity will appear higher in the population in which the microsatellite set was developed. This would lead to lower estimates for diversity in African breeds.

Overall, this study points to a close genetic relationship between the Djallonké and Mossi breeds. The STRUCTURE analysis identified both the Burkina-Sahel and the Djallonké breeds as ancestrally separated genetic entities despite the fact that they inhabit geographical areas with strong, centuries-old commercial flows (3), which could lead to a reduction of between-breeds genetic differentiation. The STRUCTURE analysis also allows admixed individuals to be included in the process of characterizing the ancestral allele frequencies of parental populations (26). The main genetic background of the Mossi breed is closer to Djallonké sheep (with various extreme genotypes clearly assignable to the Djallonké breed) than to the Burkina-Sahel breed; although, there are a significant number of extreme $\hat{q}$ values that are genetically similar to Burkina-Sahel individuals. These results are consistent with the higher molecular coancestry and lower D_{AS} values found between the Djallonké and Mossi populations when compared to those obtained for the Burkina-Sahel linked pairs. Molecular coancestry tends to characterize ancestral genetic identity scenarios, whereas D_{AS} characterizes recent differentiation events (10). Moreover, the neighbor-joining tree constructed from the between-individuals clearly groups the Mossi individuals together with the Djallonké population. Arranz

et al. (30), analyzing Spanish sheep breeds with no expected between-breeds recent gene flow according to the between-individuals D_{AS} matrix, reported that the proportion of individuals forming discrete clusters coinciding with a particular breed was 77%. If we consider the Djallonké and the Mossi breeds as differentiated genetic entities, our results would be considerably lower; however, if we consider the Mossi breed as a Northern Burkinabé representative of the Djallonké breed, which would in turn be ancestrally different from the Burkina-Sahel population, the clustering ability of the evolutionary tree constructed here would be considerably higher.

Assuming that Djallonké and Mossi sheep belong to the same original population, the assignment analysis carried out using the program GENECLASS 2.0 indicates recent introgression of Burkina-Sahel sheep southwards into the central area of Burkina Faso. In a recent analysis of morphological traits obtained from 6,440 Burkinabé sheep, Traoré et al. (3) considered the Mossi sheep breed to be a geographical subpopulation belonging to the Djallonké breed showing certain particularities, namely larger body size and larger variation in qualitative morphological traits. These differences would be due to the particular environmental conditions of the area in which this breed is managed (Sudan-Sahel) and continuous gene flow from Sahelian sheep, probably more intense as a result of the desertification process of Western Africa, mediated by the action of the Peuls (36), nomadic stockbreeders inhabiting the Sahelian area of Burkina Faso and other countries of West Africa, that are also active operators in the sheep market all over the country. The genetic results obtained in the present study are consistent with those from morphology. Note that no crossed-assignment between Burkina-Sahel and Djallonké individuals has been assessed. The introgression of the Sahelian sheep into the Sudan areas may be limited and mediated by the Sudan-Sahel population due to the fact that the Sahelian sheep is not trypanotolerant, thus restricting its possibilities of introgression in the southernmost Burkina Faso flocks.

CONCLUSIONS

Genetic characterization of Burkina Faso sheep using microsatellites indicated the existence of two main populations, each with a well differentiated genetic background, specifically dwarf Djallonké and Sahelian, with high gene flow between the two. This gene flow is mainly due to the introgression southwards of Sahelian sheep and has formed a sheep type, the Mossi, which is recognized as a separate breed by farm-holders despite the fact that, in genetic terms, it can be considered a mixed sheep breed. Central Burkina Faso has been shown to be a genetic contact zone between the main West African genetic groups of sheep. Increasing emphasis on studying resistance to trypanosomosis points to Burkina Faso as a country of choice to carry out this kind of research.

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