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ORIGINAL PAPER

Spatio-temporal dynamics of genetic diversity in *Sorghum bicolor* in Niger

Monique Deu · F. Sagnard · J. Chantereau · C. Calatayud · Y. Vigouroux · J. L. Pham · C. Mariac · I. Kapran · A. Mamadou · B. Gérard · J. Ndjeunga · G. Bezançon

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Abstract The dynamics of crop genetic diversity need to be assessed to draw up monitoring and conservation priorities. However, few surveys have been conducted in centres of diversity. Sub-Saharan Africa is the centre of origin of sorghum. Most Sahel countries have been faced with major human, environmental and social changes in recent decades, which are suspected to cause genetic erosion. Sorghum is the second staple cereal in Niger, a centre of diversity for this crop. Niger was submitted to recurrent drought period and to major social changes during these last decades. We report here on a spatio-temporal analysis of sorghum genetic diversity, conducted in 71 villages covering the rainfall gradient and range of agro-ecological conditions in Niger's agricultural areas. We used 28 microsatellite markers and applied spatial and genetic clustering methods to investigate change in genetic diversity over a 26-year period (1976–2003). Global genetic differentiation between the two collections was very low ($F_{st} = 0.0025$). Most of the spatial clusters presented no major differentiation, as measured by F_{st}, and showed stability or an increase in allelic richness, except for two of them located in eastern Niger. The genetic clusters identified by Bayesian analysis did not show a major change between the two collections in the distribution of accessions between them or in their spatial location. These results suggest that farmers' management has globally preserved sorghum genetic diversity in Niger.

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M. Deu (✉) · F. Sagnard · C. Calatayud
CIRAD, UMR DAP, Avenue Agropolis, TA-A 96/03, 34398 Montpellier, France
e-mail: monique.deu@cirad.fr

F. Sagnard
International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), P.O. Box 39063, Nairobi, Kenya

J. Chantereau
CIRAD, UPR AIVA, 34398 Montpellier, France

Y. Vigouroux · J. L. Pham
Institut de Recherche pour le Développement (IRD), UMR DIAPC, Avenue Agropolis, BP 64501, 34394 Montpellier Cedex 5, France

C. Mariac · G. Bezançon
Institut de Recherche pour le Développement (IRD), UMR DIAPC, BP 11416, Niamey, Niger

I. Kapran · A. Mamadou
Institut National de la Recherche Agronomique du Niger (INRAN), BP 429, Niamey, Niger

B. Gérard · J. Ndjeunga
International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), BP 12404, Niamey, Niger

Introduction

Crop genetic diversity and its dynamics are the results of a complex process involving both natural and anthropogenic drivers. Diversity can be threatened at different levels in agrosystems: species, varieties and within varieties. The replacement of ancestral landraces by improved varieties in centres of genetic diversity has been identified as the greatest source of genetic erosion, i.e. loss of genetic diversity, on an intraspecific level (as reported by Brush 1989). However, farmers in many parts of the world are conserving traditional varieties even as they modernize and

adopt improved varieties. The rate and extent of landrace replacement by modern varieties is context-specific (Brush 1989; Brush and Meng 1998). Small-scale farmers address multiple concerns that no single variety can satisfy and this diversity of interests and concerns translates into the use of diverse varieties (Bellon 2009).

Factors that influence farmers in maintaining intraspecific diversity were classified by Bellon (1996) who distinguished economic, ecological, political, social and cultural factors. Socio-economic, environmental and cultural data have been used as potential diversity or genetic erosion indicators in centres of traditional crop diversity (Cromwel and van Oosterhoust 2000; Peroni and Hanazaki 2002; Van Etten 2006; Willemen et al. 2007; Rana et al. 2007). These proxy indicators, coupled with farmers' perception and knowledge of currently cultivated and abandoned landraces, have made it possible to assess both the gain and loss of traditional varieties.

Indicators for investigating genetic structure of landraces range in technique from molecular genetic to anthropological (cited in Brown 2000). This author assembled them in five classes: allelic richness and genotypic diversity, special adaptation to the local environment, scale of localized diversity, temporal changes in genetic composition to meet environmental variation and crop evolutionary process. Some of these indicators have made it possible to assess the temporal trend of genetic diversity and, above all, to understand the impact of plant breeding for major crops cultivated in Europe (bread and durum wheat, maize, barley and oat) thanks to the accessions registered in Genebanks at different periods (Donini et al. 2000; Roussel et al. 2004; Le Clerc et al. 2005, 2006; Martos et al. 2005; Roussel et al. 2005; Reif et al. 2005; Nersting et al. 2006; Figliuolo et al. 2007; Malysheva-Otto et al. 2007). Most of these studies concluded either on a reduction in genetic diversity due to the modernization of agriculture, or to stability even though regional change might occur.

The difficulty of temporal analysis based on on-farm diversity principally resides in the need to collect similar data at different periods. Studies to estimate in situ genetic erosion in centres of diversity with time-series data are still scarce. Teshome et al. (2007) collected sorghum varieties in the same 260 fields randomly selected across Ethiopian communities at intervals over 8 years. Morin et al. (2002) took a similar approach on rice at intervals of over 2 years in 15 villages of the north-eastern Philippines. The time scale considered in both studies was small, as was the spatial scale. To obtain larger-scale spatial and temporal analyses, well-documented and conserved genebank collections are an asset. They can serve as a starting point for temporal studies of varietal and genetic diversity in traditional agrosystems. This approach was taken by Teklu and Hammer (2006), Mekbib (2008) and Barry et al. (2008) who re-sampled wheat and sorghum landraces in eastern Ethiopia and rice landraces in Maritime Guinea, respectively.

A similar approach, using a germplasm collection and re-sampling at the same sites, was taken in this project. We focused our analysis on Niger, where intensive collection was carried out in evenly distributed villages in 1976. In that country, sorghum is the second most cultivated crop and the largest share of sorghum production still comes from landraces grown in traditional agrosystems under rainfed conditions. Major human and environmental changes have occurred in Niger in recent years. Annual sorghum production and the human population have steadily increased over the past three decades. Several recurrent droughts occurred in the Sahel during the 1970s and 1980s. A substantial continuous rainfall deficit of roughly 20–50% was reported by different authors over the 1970–1990 period compared to the previous twenty-year period (Hulme 2001; Nicholson 2005). All these factors are assumed to cause genetic erosion. We assessed changes in the diversity and geographical distribution of cultivated sorghum and pearl millet varieties in Niger between 1976 and 2003 based on their names and on their botanical groups (Bezançon et al. 2009). No erosion of sorghum varietal diversity was noted on a national scale. Few changes were observed in the geographical distribution of certain varieties, mainly varieties from the bicolor race, known to be the major source of sweet sorghums.

We report here on a complementary analysis of the temporal dynamics of sorghum genetic diversity assessed with molecular markers. We used a panel of methods including spatial analysis and GIS tools to investigate change in genetic diversity on different scales. Genetic clustering methods were also used to track the dynamics of genetic diversity within genetic groups. We used different diversity statistics to investigate the dynamics of genetic diversity. Genetic differentiation between the two collections was also investigated with the extensively used F_{st} parameter, based on the H_e index and a measure of differentiation based on corrected allelic richness, as proposed by El Mousadik and Petit (1996).

Materials and methods

Collection of sorghum varieties

The two reference collections for the temporal analysis were 1976 and 2003. The 1976 sample was collected in 183 villages (FAO-Orstom 1977) and conserved at IRD (Montpellier, France). The second sample was collected in 79 villages previously sampled in 1976. The villages were selected to cover the rainfall gradient and range of

agro-ecological conditions. Our second collection and sampling strategy were fully described elsewhere (Deu et al. 2008; Bezançon et al. 2009). Briefly, during the two collections, varietal inventories and associated information on crop uses, seed origins, agricultural systems and social organizations were reported through farmer interviews. In each village visited, varietal inventories were followed by sampling of all named varieties. Each named variety in a village was collected and represented by one sample (or accession), provided by one farmer. In 2003, modern varieties were also collected as opposed to the 1976 collection, which focused solely on traditional varieties or landraces. We finally analysed the genetic diversity for sorghum accessions in 71 common villages where sorghum varieties were found for the two collections.

Racial characterisation

Cultivated sorghums (*Sorghum bicolor* L. Moench), which are predominantly selfing, belong to the ssp. bicolor. They are classified in five main botanical races (bicolor, caudatum, durra, guinea, and kafir) and ten intermediate races (Harlan and de Wet 1972).

Racial characterisation, based on panicle and spikelet morphology, was carried out in accordance with this classification. In addition, we used Snowden's taxonomy (1936) to identify margaritiferum varieties within the guinea race and membranaceum within the durra race.

SSR analysis

For each accession collected, DNA was extracted from a single plant. Twenty-eight SSRs distributed throughout the 10 chromosomes of sorghum (Kim et al. 2005) were assayed on the 244 accessions collected in 1976. The 2003 collection had been previously characterized with the same set of markers (Deu et al. 2008). Genotyping was conducted at the Languedoc-Roussillon Génopole platform located on the CIRAD campus in Montpellier (France) following methods previously described (Barnaud et al. 2007; Deu et al. 2008).

Genetic diversity and erosion indices and distribution

Nei's unbiased gene diversity or expected heterozygosity (H_e, Nei 1987), observed heterozygosity (H_o), the total number of alleles (A^t) and their frequencies, and allelic richness were estimated for each locus and each collection using FSTAT software (Goudet 2002). Allelic richness (R_s), based on the rarefaction method (Petit et al. 1998), is an evaluation of the expected number of alleles for an equalized sample size. The number of private alleles (A^p) was detected by GDA software version 1.1 (Lewis and Zaykin 2001). We also calculated the mean number of alleles (A) and the mean allelic richness (R_{sm}) across loci. The significance of R_s, H_e and H_o between samples was tested using a Wilcoxon paired-rank test.

We used F statistics to compare collection differentiation. An estimator of F_{st} (θ, Weir and Cockerham 1984) was computed with Genetix software and tested for its significance with 10,000 permutations (Belkhir et al. 2002).

To explore genetic diversity and its evolution and distribution on smaller scales, we used a panel of methods to cluster accessions within each collection, and to compare clusters between collections. First, we defined "a priori" clusters, based on geographical and/or climatic data as described in Deu et al. (2008). Three longitudinal classes (4° interval), which roughly corresponded to western, central and eastern regions in Niger were created. In addition, three main annual rainfall classes were also defined: "less than 400 mm", "between 400 and 500 mm", and "more than 500 mm". Secondly, we defined spatial clusters based on longitudes and latitudes of the inventoried villages. As the villages where accessions had been collected were not completely evenly spaced, a distance method could have resulted in some spatial clusters having many villages and others with few, and within some of them, a smaller number of accessions. This can be dealt with by setting the neighbourhood size to some number of nearest neighbours. However, although this method controls the number of villages (and accessions) in each neighbourhood, it does not assume a constant area for each spatial unit. We fixed the number of villages at 9 in each cluster in order to avoid too large a spatial scale and to have a minimum number of 15 accessions per cluster in each collection. This limit was a constraint arising from the collection carried out in 1976, for which fewer accessions were collected in most villages. We obtained 71 clusters of villages that were not independent spatial units, i.e. one village was attributed to different spatial units and consequently one accession was attributed to various clusters. Thirdly, we defined genetic clusters of varieties by using Bayesian model-based clustering implemented in Structure version 2.1 software (Pritchard et al. 2000; Pritchard and Wen 2002). We applied this method to assess comparisons of paired genetic clusters between the two collections. We used the admixture model, without prior population information, which assumed that the genome of individuals was a mixture of genes originating from K unknown ancestral populations. This model estimated the proportion of membership (genome ancestry) of each individual in each of the K ancestral populations. We ran analyses on the joined set grouping the two collections. The main modelling assumption was Hardy–Weinberg equilibrium within populations. This assumption could be relaxed by using haploid data (Ostrowski et al. 2006). For each sorghum accession, the residual heterozygosity found at

some loci was transformed into missing data. It was thus possible to obtain haploid data, which were more accurate in our study due to the self-breeding system of cultivated sorghum and the merging of two sets of varieties collected on different dates. We restricted our analyses to the correlated frequency model. This model was considered more efficient for detecting a subtle population structure or complex genetic structure and more accurate when a single domestication was established. We set other parameters to their default values. We ran analyses 10 times for each K value from one to 15 with a burn-in period of 500,000 followed by 1×10^6 iterations. To assess the number K of populations supported by the dataset, we used the log likelihood and the change in the second order of the log likelihood ΔK (Evanno et al. 2005). For complex data sets, inferring K is difficult because the algorithm may converge to numerous distinct clustering schemes for a given value of K, so that estimated probabilities differ across runs (Rosenberg et al. 2002). A division of data sets into different groups corresponding to the best assignment of individuals to groups made by Structure is efficient in some complex hierarchical schemes to detect the hidden within-groups structure (Evanno et al. 2005). Consequently, as multiple solution clustering appeared for $K \geq 2$, we subdivided our initial sample for further analyses into the two clusters identified at the uppermost level. The second round of analyses was only applied to accessions showing more than 80% ancestry in one cluster. We ran a new structure analysis, within each cluster, for K values from 1 to 10, with identical parameters to those applied to the whole set. Finally, we also tested the Bayesian model-based clustering implemented in the InStruct software (Gao et al. 2007). This model eliminates the assumption of Hardy–Weinberg equilibrium within clusters and could be more appropriate to inbreeding species, such as sorghum. We ran analyses with a total number of 200,000 iterations, including a burn-in period of 100,000 iterations. We made both inference of population structure and the selfing rates for subpopulations and performed five independent simulations for each K value (from 1 to 10).

Genetic diversity parameters (H_e, R_s) and genetic differentiation (F_{st}) were calculated for each cluster defined by the three methods (geographical and climatic clusters, spatial clusters and genetic clusters). We calculated allelic richness with the same smallest sample size for the different clusters: geographical clusters (63 accessions), climatic clusters (41 accessions), genetic groups obtained on the finer level of structuring (11 accessions).

For spatial clusters, allelic richness was calculated cluster by cluster, with a number of accessions varying between clusters. In addition, for each spatial cluster, we computed a differentiation for allelic richness according to the method proposed by El Mousadik and Petit (1996):

$$\rho_{ST}(n) = 1 - \frac{R_{S(n)} - 1}{R_{T(n)} - 1}$$

where $R_{S(n)}$ is the average across the two collections of the allelic richness across loci and $R_{T(n)}$ is average allelic richness across loci, the two collections being pooled.

We also calculated the diversity difference between the two collections $\Delta R_{sm} = R_{sm(2003)} - R_{sm(1976)}$ and $\Delta H_{em} = H_{e(2003)} - H_{e(1976)}$. These differences between the two collections were projected for each spatial cluster onto the Niger map with Quantum GIS software version 1.1.0 (http://qgis.osgeo.org).

Variation in the distribution of accessions within the genetic clusters was assessed with a χ^2 test performed on contingency tables. Changes in genetic cluster locations were also assessed between the two collections. To do so, a Student test was used to compare latitudes and longitudes of varieties belonging to each cluster between the two collections.

Results

Country-scale analysis

The collections comprised 244 accessions in 1976 and 454 accessions in 2003 for 71 villages. The maximum numbers of accessions collected per village in 1976 and 2003 were 8 and 15, respectively, with averages of 3.4 and 6.4.

The 28 SSR loci were able to discriminate 236 and 440 different genotypes, respectively, within the 1976 and 2003 collections (96% of identification in each collection). Most of the accessions sharing identical multi-locus genotypes were differently named by farmers and were collected in different villages. The 28 SSR loci, which were polymorphic in the two collections, displayed 248 and 289 alleles, respectively, in the 1976 and 2003 collections (Table 1). The number of alleles having a frequency under 5% was 146 (58.9%) and 184 (63.7%) for the 1976 and the 2003 collections, respectively. A total of 220 alleles was shared by the two collections. Finally, 28 private alleles (i.e. alleles specific to a collection) were identified in the 1976 collection and 69 in the 2003 collection. Genetic differentiation between the two collections was very low ($F_{st} = 0.0025$) although significant ($P < 0.05$). Allelic richness and gene diversity showed a significant increase ($P < 0.01$) in the 2003 collection ($R_{sm} = 9.78$; $H_e = 0.617$) compared to the 1976 collection ($R_{sm} = 8.83$; $H_e = 0.596$). In contrast, observed heterozygosity was significantly ($P < 0.001$) lower in the 2003 collection ($H_o = 0.042$) compared to the 1976 collection ($H_o = 0.067$). Finally, we identified 23 modern varieties based on information obtained from farmers, and complementary field characterisations of all

Table 1 Genetic diversity parameters within the two collections according to a priori and genetic groups

	Year	N	A^{t}	A^{p}	A	R_{sm}	H_e	H_o	F_{st}
Global		698	317	–	11.32	–	0.610	0.051	–
	1976	244	248	28	8.86	8.83**	0.596**	0.067***	0.0025*
	2003	454	289	69	10.32	9.78	0.617	0.042	
Regions									
West	1976	81	200	25	7.14	7.02*	0.657	0.090**	0.0068*
	2003	181	239	64	8.54	7.57	0.648	0.061	
Centre	1976	94	183	18	6.54	6.31***	0.584***	0.066***	0.0038
	2003	190	233	68	8.32	7.46	0.606	0.030	
East	1976	69	145	20	5.18	5.16*	0.409*	0.044	0.0070
	2003	83	168	43	6	5.87	0.432	0.031	
Rainfall classes									
<400 mm	1976	124	198	20	7.07	6.16***	0.549**	0.062**	0.0025
	2003	231	250	72	8.93	6.87	0.585	0.041	
400–500 mm	1976	68	190	21	6.79	6.47*	0.613	0.067***	NS
	2003	142	235	66	8.39	7.16	0.628	0.036	
>500 mm	1976	52	171	29	6.11	6.02	0.621	0.080	0.0028
	2003	81	195	53	6.96	6.51	0.625	0.060	
Genetic groups									
UNC	1976	16	115	25	4.11	nc	0.516	0.139***	0.0235*
	2003	34	141	51	5.04	nc	0.528	0.055	
Cluster 1	1976	129	225	24	8.04	7.78***	0.659	0.077***	0.0015
	2003	253	268	67	9.57	8.67	0.669	0.046	
Cluster 2	1976	99	127	21	4.54	4.47	0.299	0.043	0.0122**
	2003	167	156	50	5.57	4.98	0.316	0.034	

N number of varieties included in each group, A^{t} total number of alleles, A^{p} number of private alleles (present in a single group), *A* mean number of alleles, R_{sm} mean allelic richness (R_s) across loci for each group based on a minimum number of gene copies, H_e unbiased gene diversity (or expected heterozygosity), H_o observed heterozygosity, F_{st} average genetic differentiation between 1976 and 2003 collections for each group, *NS* not significant, *nc* parameter not calculated (due either to a reduced number of varieties within groups, or to the non-assignment of varieties), UNC designed varieties that could not be assigned to a genetic cluster at $K = 2$ by structure analysis

* Significant at the 5% threshold; ** Significant at the 1% threshold; *** Significant at the 1‰ threshold

collected accessions. All the results presented here were similar if we excluded "modern varieties" in the 2003 collection.

Smaller-scale analysis

Geographical and climatic clusters

Three geographical regions were considered: East, Centre and West. Significant genetic differentiation between the two collections was only detected in western region ($F_{st} = 0.0068$, $P < 0.05$). Three climatic zones were considered but no significant genetic differentiation was found (Table 1). Allelic richness was significantly higher in the 2003 collection for the three defined regions (West, Centre and East), and for the three climatic zones, except for the most humid zone (>500 mm). Gene diversity also showed a significant increase in the 2003 collection in two regions (Centre and East) and in the drier area. Observed heterozygosity was significantly lower in the 2003 collection in two regions (West and Centre) and two climatic zones.

Spatial clusters

The clustering method based on aggregation of the 9 closest villages gave 71 clusters, each of them centred on one village. The number of accessions per cluster and per collection varied from 15 to 94. The average number of accessions by cluster was 30.7 and 56.3 for the 1976 and the 2003 collections, respectively.

Genetic differentiation (F_{st}) between the two collections varied from 0 to 0.034 for the 71 clusters. Nine clusters showed a significant differentiation ($P < 0.05$) with F_{st} above 0.018. This number was higher than one would have expected by chance with a 5% threshold and 71 tests ($\chi^2 = 8.8$, $P < 0.004$). These nine clusters were found in two main areas (Fig. 1a): south-western Niger and

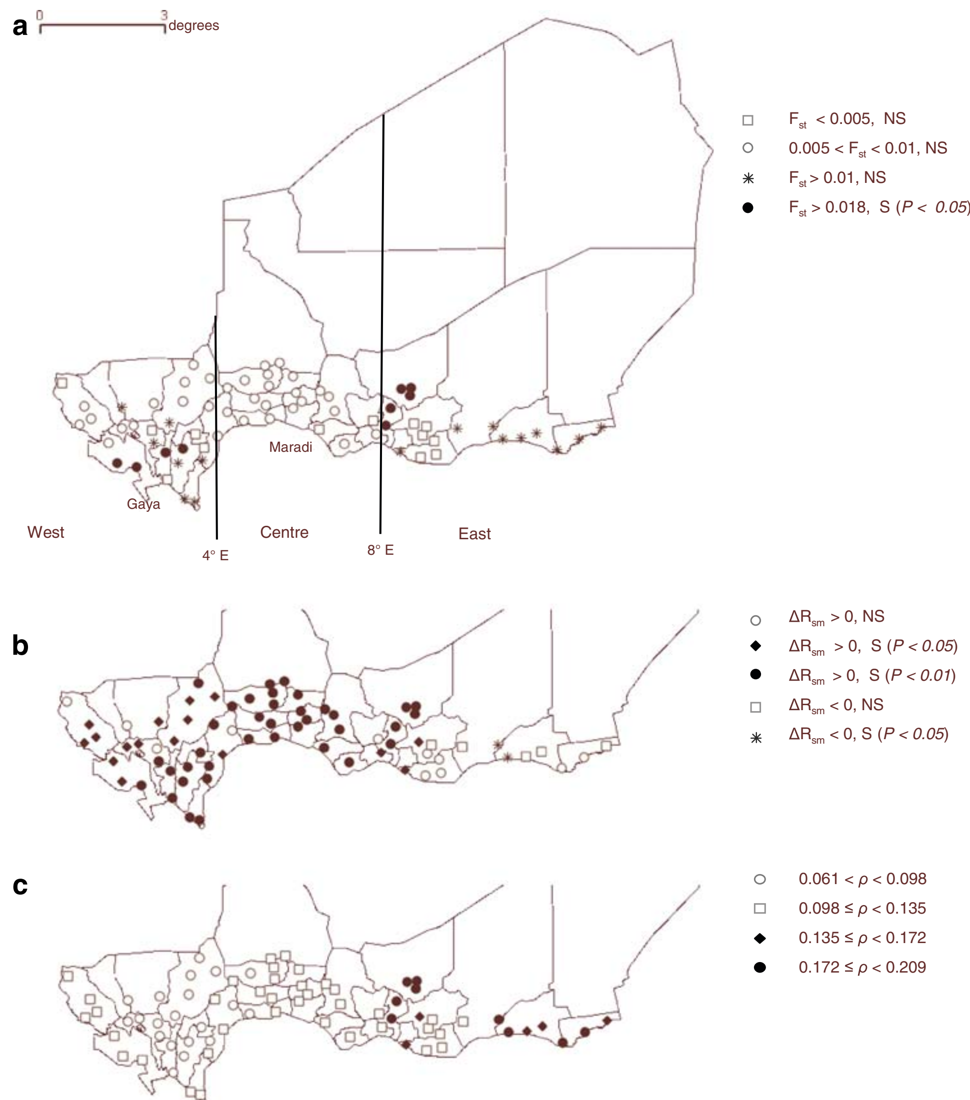

Fig. 1 Genetic diversity parameters between the 1976 and 2003 collections for each of the 71 spatial clusters. Spatial clusters were built using the 8 closest sampling points of a given village. For each spatial cluster, genetic diversity parameters were plotted according to the geographical coordinates of the village used to define the 8 nearest neighbours. **a** Differentiation, assessed using F_{st} and statistically tested, for each of the 71 spatial clusters. Significant differentiation is seen in the north-eastern and south-western parts of Niger. **b** Evolution of allelic richness ($\Delta R_{sm} = R_{sm(2003)} - R_{sm(1976)}$) for each of the 71 spatial clusters. The significance of the difference for each cluster was assessed by a Wilcoxon paired test. Allelic richness increases in the central and western parts of Niger and in five clusters located in north-eastern Niger. **c** Differentiation based on allelic richness ($\rho_{ST(n)}$) for each of the 71 spatial clusters. The differentiation was measured according to the method proposed by El Mousadik and Petit (1996). ρ values were distributed into four classes showing equal intervals. Allelic differentiation is higher in clusters located in eastern Niger. *S* significant, *NS* non-significant

north-eastern Niger. We also found a significant increase in allelic richness in these nine clusters (Fig. 1b), eight of them being significant at $P < 0.01$. The increase in allelic richness appeared greater in north-eastern Niger ($\Delta R_{sm} > 1.5$) compared to south-western Niger (ΔR_{sm} from 0.6 to 0.9). Finally, we also observed a decrease in allelic richness ($\Delta R_{sm} = -0.47$, $P < 0.05$) for two closed clusters located further east and south (average longitude and latitude: 10.82 and 13.56) from the north-eastern area identified above. Globally, most of the clusters showed an increase in allelic richness. The increase was significant ($P < 0.05$) in 53 clusters (54.9%) and still significant in 37 of them at $P < 0.01$. Gene diversity (data not shown) also increased in a large number of them (64.8%) and the increase was significant for 26 clusters at $P < 0.05$ and for 18 of them at $P < 0.01$. In north-eastern Niger, gene diversity also significantly increased ($P < 0.001$) in the same five clusters described above. Surprisingly, a significant decrease of gene diversity was also revealed in four clusters (data not shown) located in the most extreme part of western Niger ($P < 0.01$). These clusters presented a non-significant F_{st} and an increase in allelic richness ($P < 0.05$).

Finally, patterns of differentiation based on allelic richness indicated that differentiation was greater (from 0.06 to 0.208) than that calculated with F_{st} (Fig. 1c). This differentiation was particularly high in most of the clusters located in eastern Niger (above 8° longitude).

Genetic clustering

A Bayesian population structure analysis implemented in the Structure software was first performed on the whole panel, i.e. constituted by merging the two collections. The log likelihood increased steadily from $K = 1$ to $K = 15$ (shown in Supplementary Electronic File 1). To assess the number of populations K retained, we considered the parameter ΔK based on the changes in log likelihood (Evanno et al. 2005). The ΔK identified a K value of 2 as a possible value (shown in Supplementary Electronic File 1). For larger values of K, we did not observe constant membership coefficients for a large number of individuals, suggesting some instability in the inference of higher population structure. Using $K = 2$, we found 382 accessions showing more than 80% ancestry to one cluster (named cluster 1) and 266 to the second one (named cluster 2). Fifty accessions showed membership coefficients under 80% for either cluster. These two clusters broadly corresponded to a geographical first-order differentiation between varieties from western and eastern Niger. This geographical differentiation was confirmed by the highly significant Student test performed on longitudes ($P = 3.81 \times 10^{-33}$, average longitudes of 4.43 and 7.05 for cluster 1 and 2, respectively).

To identify the sub-structure present in each "upper genetic group", we separately ran new structure analyses on each of the two identified clusters. For the first cluster, we observed a steady increase in the log likelihood (shown in Supplementary Electronic File 1) from $K = 1$ to $K = 10$. We thus selected the smallest value of K that captured the major structure in the data as proposed by Pritchard and Wen (2002), which assured the congruence between the different runs and made it possible to assign a large share of varieties. Within cluster 1, we adopted $K = 5$, as for that value a larger number of accessions could be attributed to the sub-groups [88.2% of accessions were assigned at the threshold of 80% of the genome in the group and most of the assigned accessions (90.2%) had membership coefficients over 90%]. The different sub-groups within cluster 1, called a, b, c, d and e, respectively corresponded broadly to a racial structure already detected in the 2003 collection (Deu et al. 2008). Sub-group a was mainly composed of durra, intermediate durra, some bicolor (called Takanda: sugary sorghums) and unclassified accessions. Originating from the western region, sub-group b was composed of caudatum accessions: a large share of them were called Jan Jare, both present in the two collections, or were improved varieties only present in the recent collection. Sub-group c was mainly composed of caudatum and intermediate caudatum accessions. Sub-group d only contained guinea margaritiferum accessions (characterized by their smaller grain compared to other guinea) and sub-group e was mainly composed of guinea non-margaritiferum. Sub-group d was also the most homogenous for the vernacular names: three names (Socomba, Malle and Kierma) defined 94% of the accessions in this sub-group. The other sub-groups clustered accessions bearing a larger diversity of names. An extreme case was found in sub-group e, in which most accessions were differentially named within each collection (16 names for 18 accessions and 27 names for 31 accessions, respectively within the 1976 and 2003 collections).

Within cluster 2, the log likelihoods increased steadily from $K = 1$ to $K = 4$ and then tended to show a plateau (shown in Supplementary Electronic File 1). If we excluded a run from $K = 3$ with a log likelihood of −3,467 showing a clear convergence to a local maximum (the other 9 log likelihoods varied between −3,365 and −3,367 for $K = 3$), both biological significance and ΔK (shown in Supplementary Electronic File 1) enabled us to choose $K = 3$. For this value, 83.5% of accessions could be assigned and, of them, 89.6% had membership coefficients over 90%. The different sub-groups called f, g and h corresponded broadly to a geographical structure. Sub-group h was significantly located at the extreme East of Niger (average longitude: 8.06), while the average longitudes for f and g were 6.12 and 6.52, respectively ($P < 0.001$). The differentiation between sub-groups f and g was also due to the botanical types. Two principal varieties called Matche da Koumnya and Makaho da Wayo constituted sub-group f (64.5% of the accessions). These varieties had specific morphotypes described in Deu et al. (2008).

The second Bayesian model implemented in the Instruct software also permitted to identify two clusters on the whole panel. We found 364 accessions showing more than 80% ancestry in cluster 1 (all of them were also attributed to cluster 1 with Structure software) and 259 in the cluster 2 (all except 2 were also attributed to this cluster with the Structure software). Seventy-five accessions showed membership coefficients under 80% (compared to the 50 identified by the Structure software). Within this new cluster 1, we also identified the same five sub-groups that were previously defined with the Structure software. Most accessions were attributed to the same sub-group with the two models. Among the 312 accessions attributed with the InStruct software to each one of the five sub-groups, 307 were identically attributed with the Structure software. So, we finally presented the results obtained with the Structure software which has permitted to attribute a larger number of accessions in the whole panel and then, within the cluster 1.

Table 2 Genetic diversity parameters within the two collections according to the finer level of genetic structuration

	Year	N	A^t	A^p	A	R_{sm}	H_e	H_o	F_{st}
Within cluster 1									
Sub-group a	1976	28	113	16	4.04	3.38**	0.461*	0.076*	0.0059
	2003	66	156	59	5.57	3.89	0.507	0.044	
Sub-group b	1976	20	100	19	3.57	3.11	0.371*	0.078***	0.0382*
	2003	52	130	49	4.64	3.39	0.437	0.028	
Sub-group c	1976	35	116	20	4.14	3.38	0.489	0.063**	0.0089
	2003	54	138	42	4.93	3.57	0.485	0.031	
Sub-group d	1976	16	60	8	2.22	2.15*	0.334	0.040	NS
	2003	17	72	20	2.57	2.52	0.376	0.045	
Sub-group e	1976	18	108	20	3.86	3.45	0.448	0.103	NS
	2003	31	120	32	4.29	3.49	0.495	0.079	
Unc Cl1	1976	12	118	13	4.21	nc	0.611	0.136***	NS
	2003	33	178	73	6.36	nc	0.664	0.076	
Within cluster 2									
Sub-group f	1976	3	nc	nc	nc	nc	nc	nc	nc
	2003	28	nc	nc	nc	nc	nc	nc	nc
Sub-group g	1976	49	89	19	3.18	2.36	0.285	0.043	0.0068
	2003	63	90	20	3.21	2.22	0.259	0.033	
Sub-group h	1976	30	66	11	2.36	2.07	0.193	0.019	0.011
	2003	49	85	30	3.04	2.18	0.203	0.017	
Unc Cl2	1976	17	98	35	3.5	nc	0.363	0.091	0.0224*
	2003	27	96	33	3.43	nc	0.343	0.092	

Within cluster 1, a, b, c, d, e are the genetic sub-groups identified by structure analysis and within cluster 2, f, g, and h are the genetic sub-groups identified by structure analysis. Unc Cl1 and Unc Cl2, respectively designate the varieties assigned at $K = 2$ in cluster 1 and 2 that could not be attributed to a sub-group by structure analysis

N number of varieties included in each group, A^t total number of alleles, A^p number of private alleles (present in a single group), A mean number of alleles, R_{sm} mean allelic richness (R_s) across loci for each group based on a minimum number of gene copies, H_e unbiased gene diversity (or expected heterozygosity), H_o observed heterozygosity, F_{st} average genetic differentiation between 1976 and 2003 collections for each group, *NS* not significant, *nc* parameter not calculated (due either to a reduced number of varieties within groups, or to the non-assignment of varieties)

* Significant at the 5% threshold; ** Significant at the 1% threshold; *** Significant at the 1‰ threshold

For the first cluster, we observed the same pattern of variety distribution among the five sub-groups (a, b, c, d, e) between the 1976 and 2003 collections ($\chi^2 = 6.15$, $P = 0.19$). A moderate significant differentiation between the collections appeared for sub-group b ($F_{st} = 0.0382$, $P < 0.05$). F_{st} between collections for groups a, c, d, and e were not significant (Table 2). Allelic richness and gene diversity significantly increased in the 2003 collection for sub-group a (durra and some accessions from the variety named Takanda), H_e increased for sub-group b (caudatum) and R_s for sub-group d (guinea margaritiferum). For the second cluster, the distribution of accessions in the three sub-groups (f, g, h) showed a highly significant change between the two collections ($\chi^2 = 12.16$, $P = 0.002$). This significant change was mainly due to a large increase in frequency of sub-group f accessions, and, to a lesser extent, to a reduction in sub-group g in the 2003 collection. However, these sub-groups did not present a significant genetic differentiation between the two collections, as highlighted by the different estimators (F_{st}, H_e, and R_s).

Finally, to assess the changes in the location of genetic clusters between the two collections, we compared the latitude and the longitude of accessions present in each cluster in 1976 and 2003 (Supplementary File 2). Only two sub-groups (b within cluster 1 and h within cluster 2) showed a significant shift towards the West (analysis of longitude) between 1976 and 2003 ($P < 0.01$). Student tests performed on latitudes indicated no significant shift towards the South between 1976 and 2003.

Discussion

The evolution of sorghum genetic diversity in Niger was assessed over the past three decades in 71 villages, covering the rainfall gradient and range of agro-ecological

conditions of Niger's agricultural areas. The starting point was the germplasm collection constituted in 1976 and this collection was compared to a new collection assembled in 2003.

SSR markers pinpointed significant greater allelic richness and gene diversity in the 2003 collection but the differentiation between the two collections was low ($F_{st} = 0.0025$). On a more localized scale, significant but low differentiation was only found in western Niger ($F_{st} = 0.0068$) and allelic richness increased both within regions and within climatic zones, except in the most humid zone. Our results indicate that the evolution of genetic diversity identified over these last three decades, was moderate, positive and unevenly distributed. A decrease of observed heterozygosity in the 2003 collection is also observed. We speculated that farmers have paid more attention to their seed production and have better controlled the purity of the varieties that they grown. Our hypothesis is supported by the stronger decrease of observed heterozygosity in central Niger, which was more affected by rural development and presented the most advances in term of agricultural practices. We cannot attribute the maintenance of the genetic diversity solely to the presence of modern varieties in the 2003 collection. The rate of farmers' adoption of improved varieties found in Niger is low (4.8%) and close to the other estimations in western Africa (Bezançon et al. 2009). We have tested their impact by discarding them from the global analysis and the analyses conducted for geographical and climatic clusters (data not shown). Results on gene diversity, observed heterozygosity, allelic richness and differentiation were similar. The increase of allelic richness remained only significant in the central region and in the drier zone when improved varieties were discarded.

Globally, our results are in agreement with the maintenance of sorghum varieties in eastern Ethiopia for 40 years assessed by a temporal survey based on both the number and names of varieties (Mekbib 2008). Similar results were obtained in Maritime Guinea by Barry et al. (2008) in their diachronic assessment of rice genetic diversity measured with both the names and numbers of collected varieties, and SSR markers. Opposite results were found by Teklu and Hammer (2006) who identified strong genetic erosion (i.e. loss of landraces) in tetraploid wheat landraces in eastern Ethiopia.

The uneven distribution of loss/gain in sorghum landraces between communities or regions was also reported in Ethiopia (Teshome et al. 2007), and in Mali (Kouressy et al. 2008). In Mali, a great loss of varieties was reported in the more humid Sudanian zone, which was not balanced by the introduction of new varieties. Kouressy et al. (2008), however, pinpointed the appearance of some varieties in the Sahel zone. These authors suspected that these new varieties are improved ones, diffused by the Malian research center (IER, Institut d'Economie Rurale). This loss of sorghum varieties in southern Mali was attributed to competition with maize for a limited area (Traoré et al. 2000), a crop that makes better use of inputs arising from the development of cotton cultivation. In Ethiopia, teff and chickpea tended to displace sorghum varieties, because of their higher commercial value and their quick maturation (Teshome et al. 2007). In Niger, annual sorghum production has steadily increased over the past three decades in response to the doubling of the population. The larger share of sorghum production still comes from farmers' landraces as the adoption of modern varieties is limited. The increase in arable land was around 40% between 1980 and 2000 and the land used for permanent crops doubled over the same period (FAO 2008). No cash crop competes in Niger with traditional cereal crops as in Mali. In this context, we suspected that the use of marginal lands in Niger, linked to the strong increase in the human population, might induce farmers to increase their selection criteria for growing specific varieties for new agro-ecological niches. Farmers have reported a clear increase in the varietal sorghum portfolio managed on a village scale in the last three decades (Costis 2005; Bezançon et al. 2009). This result was reflected in both the number of collected accessions and the number of names given by farmers in most of the villages visited in 2003. Seed exchange enhanced by repeated crisis periods might explain the increase in the number of accessions (Bezançon et al. 2009) and contribute to the observed increase in genetic diversity.

Our results seem to disagree with the common assumption that climatic changes are factors of decline in varietal and genetic diversity; however, caution is called for. We analysed only two temporal collections, in the light of total annual rainfall, a unique variable which would not be sufficient to consider climate changes over time on this large spatial scale. Lacy et al. (2006) reported that farmers' varietal choice in southern Mali was greatly influenced by the date of onset and the consistency of rainfall. Secondly, while all climatologists agreed with the onset of drought around 1968 and the continuation of relatively low rainfall in the Sahel from then until the mid-1990s, some of them recorded a "recovery" of rains in recent years (Olsson et al. 2005; Nicholson 2005; Ben Mohamed et al. 2002). Lastly, our 1976 collection was also assembled a few years after the serious Sahel drought. Farmers may have adopted a local strategy to respond to climate shifts after that drought. A range of coping (changes in farming practices) and adaptation (utilising the spatial and temporal diversity of the environment) strategies may be used by farmers to respond to climate shift. Thomas et al. (2007) found that generic strategies across regions and specific local strategies have been adopted by farmers in South Africa.

We suspected that if the net change in varietal diversity and allelic richness was positive on a country scale, and in most "a priori" groups, there could be a loss or a displacement of some types of accessions, linked to local anthropogenic and/or environmental factors. In Niger, geographical and ethnic patterns of botanical sorghum distribution exist (Deu et al. 2008). The guinea sorghums are mainly cultivated by the Zarma/Songhai group in Niger, where rainfall is more abundant. Kanuri people, who live in the eastern part of the country, cultivate almost exclusively durra sorghums, which are better adapted to dry areas.

We used structure analysis to assign accessions to genetic groups and to overcome the weakness of temporal analysis based only on names or on botanical classification. Variety names do not accurately reflect genetic distinctiveness because farmers' taxonomies can be typically localized and culturally determined. Striking evidence of cultural taxonomy was noticed in our collection for Socomba and Malle called varieties which all belong to the same sub-race (guinea margaritiferum), but were differentially named by the ethnic groups growing sorghum in Niger: Socomba and Malle were, respectively the translation of "rice" in Zarma and Hausa languages**.** In addition to this "cultural" taxonomy, a recent survey conducted by Mekbib (2007) in Ethiopia highlighted that folk descriptors used to discriminate one sorghum variety from another are mostly morphology-related traits (panicle type, seed colour, maturity, plant height, etc.), use-related traits (e.g. stalk sweetness), and biotic and abiotic stress-related traits. In Niger, we also found that most folk names are based on morphological traits. A large share of the names corresponded to "inclusive" categories (or upper categories) like Hamo Kwarey for "white grain sorghum" and Hamo Kirey for "red grain sorghum" in the Zarma language or Fara Dawa and Ja Dawa used in the Hausa language for naming the same categories. Mota ("car" used to designate short-maturing sorghum) was another popular name corresponding to an inclusive category. Among frequent names, some were specific to morphotypes (Jan Jare, Kaoura, etc.). Finally, the reliability of names as indicators is likely to decrease as the geographical scale of sampling increases and the pairs of varieties differing in names are not equally divergent genetically (Jarvis et al. 2008). Inclusive categories encompassed varieties belonging to different sorghum races in Niger (Bezançon et al. 2009) and in Ethiopia (Mekbib 2007).

Structure analysis showed that even accessions sharing specific names and showing specific morphological traits could be attributed to different genetic sub-groups. Among Jan Jare accessions (caudatum named by Hausa farmers and characterized by their red grains and fusoid panicles), predominant in sub-cluster b, 17% were attributed to other sub-clusters. This may have been due to gene exchange between varieties or to farmers' local seed selection. As expected, the assignation to different groups appeared more frequent for accessions sharing names corresponding to inclusive categories: accessions named Hamo Kirey were frequent in sub-group a, however, 35% of accessions sharing that name were distributed in four other genetic groups.

We detected no major loss of some types of accessions, as shown by the conserved distribution of accessions in the main two clusters C1 and C2. We only identified a decrease in accessions belonging to one sub-group of durra and intermediate durra from eastern Niger (sub-group g in cluster C2) and a strong increase in accessions from sub-group f (clustering late durra with a crossed peduncle and accessions belonging to the taxon *membranaceum* (Deu et al. 2008). The eight sub-clusters identified by the Bayesian analysis were not affected by a reduction in genetic diversity, as measured with R_s and H_e. Our findings showed that the spatial distribution of the genetic groups was relatively stable over time. Globally, it was not possible to confirm the hypothesis of a North to South displacement or loss of accessions in any one of the eight genetic sub-groups with SSR markers, even in those that were more adapted to high annual rainfall (guinea or guinea margaritiferum types).

As environmental and socio-economic changes could have impacted on the evolution of diversity on smaller scales, the spatial method (clustering of neighbouring villages) was applied.

A significant but moderate differentiation (F_{st} above 0.018) was found for nine spatial clusters between the two collections. These clusters were localized in two areas (south-western and north-eastern Niger) and displayed a significant increase in allelic richness and/or gene diversity. The increase in allelic richness in these two areas is in line with the marked increase in sorghum accessions and the appearance of accessions belonging to genetic groups which were not represented in the 1976 collection (data not shown). New accessions mainly from cluster 2 were observed in south-western Niger, while the new accessions that appeared in north-eastern Niger were attributed to sub-groups a, b and d (within cluster 1) and f (within cluster 2). Most of these new accessions were remote from the barycentre of their genetic groups. This could be indicative of active formal or informal seed exchanges in those two areas. Bezançon et al. (2009) argued that the Gaya and Maradi departments presented the most advanced agricultural development, based on the improvement of traditional crop systems, and that in the latter, sorghum benefited from numerous active development projects. This could have led to enhanced and increased genetic diversity maintained by farmers in this region. Cromwel and van Oosterhoust

(2000) also refuted the commonly held assumption that greater contact with extension agents results in farmers being less interested in maintaining a large number of crops and varieties on-farm.

Conversely, the extreme East of Niger appeared as an area that could be threatened by genetic erosion. The marked decrease in allelic richness (and in gene diversity) found in this area was in line with a loss of some accessions attributed to more "western" genetic groups. According to farmers interviewed during the 2003 collection, some varieties were recently introduced into this area. These recently introduced varieties were attributed to "eastern genetic groups" and were probably recovered from neighbourhood villages. Bezançon et al. (2009) argued that this eastern region has developed irrigated agriculture, and new crops such as peppers are now exploited to the detriment of millet and sorghum. Farmers have probably preferred to devote their time to their new crops and to their traditional and frequent sorghum varieties to the detriment of "exotic" varieties that could be more difficult to recover and to maintain in this drier area (Cromwel and van Oosterhoust 2000).

Surprisingly, the four spatial clusters located at the extreme West of Niger and at higher latitudes, were characterized by a significant decrease in gene diversity but by a significant increase in allelic richness. This could be attributed not to the loss of accessions classified in some genetic groups but by a decrease in frequencies of accessions belonging to the guinea groups (clusters d and e). Perhaps this could be linked to local climate change, as these sorghum types are mostly cultivated in more humid zones.

We have stressed the loss of some accessions belonging to "exotic" genetic groups (i.e. not common in the area) on a smaller scale in the extreme East of Niger, and a slight change in western Niger. We could only suspect that the loss of these accessions was their scarceness in this area. This pinpointed the need for further collections to take into account not only richness (as in our collection) but also evenness (frequency). The extent of these two parameters in single-crop studies has been recently proposed by Jarvis et al. (2008). Brown and Brubaker (cited in Jarvis et al. 2008) also suggested that the area planted to a specific variety, an approximation of sample size, could serve as an indicator of genetic diversity for temporal and spatial comparisons.

Our genetic study was based on SSR markers, which are commonly used as neutral and are characterized by high mutation rates (Vigouroux et al. 2002). For the short time scale we considered, their high variability might not have caused problems and the conclusions are certainly robust to their high mutation rates. Genome-wide analysis reveals that microsatellite diversity is not generally associated with adaptation and seems to behave and mostly fit a neutral evolution, as previously shown in sorghum (Casa et al. 2005) and maize (Vigouroux et al. 2005). So for our study they certainly mainly reflected the "neutral history" of the sample. However, it would be interesting to also investigate adaptation of varieties across the two temporal samples. This highlighted the need to also compare the evolution of varieties with morphological traits as well as SNP markers linked to adaptive traits. In the future, such an analysis could provide a clearer understanding of the dynamics of neutral and selected diversity.

Conclusion

Our study revealed that no major loss in genetic diversity has appeared in Niger over the last 26 years.

However, it also confirmed the uneven evolution of allelic richness and gene diversity driven by socio-economic factors that are not constant across regions, and for some of them, greatly dependent on the cultural identity of farmers. This emphasized the need in further studies to include not only additional localized climatic data (rainfall per day, number of rainy days per month, number of dry spells, etc.), but also socio-economic and anthropological data, and even additional years of collection to better understand the evolution of genetic diversity in cultivated species. Specific surveys on seed exchanges could also greatly contribute to a better understanding of evolution in the genetic diversity and adaptation of landraces. In pearl millet, AFLP markers have been successfully used in a seed flow study. They demonstrated that farmers' strategies for seed exchanges varied between villages in south-western Niger (Allinne et al. 2008). Finally, this study showed that some contrasting results could be obtained when the dynamics of genetic diversity in cultivated species were analysed with different indicators, such as gene diversity and allelic richness. This was emphasized in the four clusters located in the extreme West of Niger. Diverging trends between heterozygosity and allelic richness were first highlighted with isozyme markers in the European Beech by Comps et al. (2001). The larger coefficients of differentiation obtained with allelic richness compared to those based on gene frequencies raises the question of the suitability of classical measures of F_{st} for genetic dynamic studies, as allelic richness is considered more important, especially in the field of conservation genetics (El Mousadik and Petit 1996; Petit et al. 1998).

From a methodological perspective, our study shows that using different spatial scales and combining spatial scale with genetic groups yields deeper information about temporal variation in allele frequencies and richness and provides a clearer understanding of the underlying processes at work. However, the identification of appropriate

spatial and temporal scales is still a challenge. Additional research is needed to understand the exact implications of varying scales and sampling configurations and to develop analytical approaches that effectively account for the spatio-temporal dynamics associated with environmental, socio-economic, cultural and genetic data. In addition, genetic variation can be spatially structured for many reasons (e.g., social interactions, historical influences, etc.). Thus, effective use of GIS to create precise maps of both small and large-scale features is crucial for correct inferences on the evolutionary forces that have shaped the observed distribution of genetic diversity and for the implementation of in situ conservation programmes.

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References

Allinne C, Mariac C, Vigouroux Y, Bezançon G, Couturon E, Moussa D, Tidjani M, Pham JL, Robert T (2008) Role of seed flow on the pattern and dynamics of pearl millet (*Pennisetum glaucum* [L.] R. Br.) genetic diversity assessed by AFLP markers: a study in south-western Niger. Genetica 133:167–178

Barnaud A, Deu M, Garine E, McKey D, Joly H (2007) Local genetic diversity of sorghum in a village in northern Cameroon: structure and dynamics of landraces. Theor Appl Genet 114:237–248

Barry MB, Pham JL, Béavogui S, Ghesquière A, Ahmadi N (2008) Diachronic (1979–2003) analysis of rice genetic diversity in Guinea did not reveal genetic erosion. Genet Resour Crop Evol 55:723–733

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2002) Genetix 4.04, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France. (Available from http://www.univ-montp2.fr/~genetix/genetix/genetix.htm)

Bellon MR (1996) The dynamics of crop infraspecific diversity: a conceptual framework at the farmer level. Econ Bot 50:26–39

Bellon MR (2009) Do we need crop landraces for the future? Realizing the global option value of in situ conservation. In: Kontoleon A, Pascual U, Smale M (eds) Agrobiodiversity, conservation and economic development. Routledge, New York, pp 51–61

Ben Mohamed A, Van Duivenbooden N, Abdoussallam S (2002) Impact of climate change on agricultural production in the Sahel—methodological approach and case study for millet in Niger. Clim Change 54:327–348

Bezançon G, Pham JL, Deu M, Vigouroux Y, Sagnard F, Mariac C, Kapran I, Mamadou A, Gérard B, Ndjeunga J, Chantereau J (2009) Changes in the diversity, geographic distribution of cultivated millet (*Pennisetum glaucum* [L.] R. Br.), sorghum (*Sorghum bicolor* (L.) Moench) varieties in Niger between 1976 and 2003. Genet Resour Crop Evol 56:223–236

Brown AHD (2000) The genetic structure of crop landraces and the challenge to conserve them in situ on farms. In: Brush SB (ed) Genes in the field: on-farm conservation of crop diversity. IPGRI/IDRC/Lewis Publishers, Boca Raton, pp 29–48

Brush SB (1989) Rethinking crop genetic resource conservation. Conserv Biol 3:19–29

Brush SB, Meng E (1998) Farmers' valuation and conservation of crop genetic resources. Genet Resour Crop Evol 45:139–150

Casa AM, Mitchell SE, Hamblin MT, Sun H, Bowers JE, Paterson AH, Aquadro CF, Kresovich S (2005) Diversity and selection in sorghum: simultaneous analyses using simple sequence repeats. Theor Appl Genet 111:23–30

Comps B, Gömöry D, Letouzey J, Thiebaut B, Petit RJ (2001) Diverging trends between heterozygosity and allelic richness during postglacial colonization in the European beech. Genetics 157:389–397

Costis C (2005) Diversité des mils et sorghos cultivés au Niger: facteurs agro-économiques, socio-économiques et les modes de gestion des variétés. Mémoire de DESS "Gestion des systémes agro-sylvo-pastoraux en zones tropicales", Université Paris XII, p 51

Cromwel E, van Oosterhoust S (2000) On-farm conservation of crop diversity: policy and institutional lessons from Zimbabwe. In: Brush SB (ed) Genes in the field: on-farm conservation of crop diversity. IPGRI/IRDC/Lewis Publishers, Boca Raton, pp 217–238

Deu M, Sagnard F, Chantereau J, Calatayud C, Hérault D, Mariac C, Pham JL, Vigouroux Y, Kapran I, Traoré PS, Mamadou A, Gérard B, Ndjeunga J, Bezançon G (2008) Niger-wide assessment of in situ sorghum genetic diversity with microsatellite markers. Theor Appl Genet 116:903–916

Donini R, Law JR, Koebner RMD, Reeves JC, Cooke RJ (2000) Temporal trends in the diversity of UK wheat. Theor Appl Genet 100:912–917

El Mousadik A, Petit RJ (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor Appl Genet 92:832–839

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14:2611–2620

FAO-Orstom (1977) Prospections des mils pénicillaires et sorghos en Afrique de l'Ouest – Niger- Campagne 1976. Report

FAO (2008) FAOSTAT database. Available from http://www.fao.org/

Figliuolo G, Mazzeo M, Greco I (2007) Temporal variation of diversity in Italian durum wheat germplasm. Genet Resour Crop Evol 54:615–626

Gao H, Williamson S, Bustamante CD (2007) An MCMC approach for the joint inference of population structure and inbreeding rate from multi-locus genotype data. Genetics 176:1635–1651

Goudet J (2002) FSTAT, a program to estimate and test gene diversity and fixation indices (version 2.9.3.2). Available from http://www.unil.ch/izea/softwares/fstat.html

Harlan JR, de Wet JMJ (1972) Simplified classification of cultivated sorghum. Crop Sci 12:172–176

Hulme M (2001) Climatic perspectives on Sahelian desiccation: 1973–1998. Global Environ Change 11:19–29

Jarvis DI, Brown AHD, Hung Cuong P, Collado-Panduro L, Latournerie-Moreno L, Gyawali S, Tanto T, Sawadogo M, Mar I, Sadiki M, Thi-Ngoc Hue G, Arias-Reyes L, Balma D, Bajracharya J, Castillo F, Rijal D, Belqadi L, Rana R, Saidi S, Ouedraogo J, Zangre R, Rhrib K, Rhrib K, Chavez JL, Schoen D, Sthapit B, De Santis P, Fadda C, Hogdkin T (2008) A global perspective of the richness and evenness of traditional crop-

variety diversity maintained by farming communities. Proc Natl Acad Sci USA 105:5326–5331

Kim J-S, Klein PE, Klein RR, Price HJ, Mullet JE, Stelly DM (2005) Chromosome identification and nomenclature of *Sorghum bicolor*. Genetics 169:955–965

Kouressy M, Traoré S, Vaksmann M, Grum M, Maikano I, Soumaré M, Traoré PS, Bazile D, Dingkuhn M, Sidibé A (2008) Adaptation des sorghos du Mali à la variabilité climatique. Cah Agric 17(2):95–100

Lacy SM, Cleveland DA, Soleri D (2006) Farmer choice of sorghum varieties in southern Mali. Hum Ecol 34(3):331–353

Le Clerc V, Bazante F, Baril C, Guiard J, Zhang D (2005) Assessing temporal changes in genetic diversity of maize varieties using microsatellite markers. Theor Appl Genet 100:294–302

Le Clerc V, Cadot V, Canadas M, Lallemand J, Guèrin D, Boulineau F (2006) Indicators to assess temporal genetic diversity in the French catalogue: no losses for maize and peas. Theor Appl Genet 113:1197–1209

Lewis PO, Zaykin D (2001) Genetic data analysis: computer program for the analysis of allelic data. Available from http://hydrodictyon.eeb.uconn.edu/people/plewis/software.php

Malysheva-Otto L, Ganal MW, Law JR, Reeves JC, Röder MS (2007) Temporal trends of genetic diversity in European barley cultivars (*Hordeum vulgare* L.). Mol Breed 20:309–322

Martos V, Royo C, Rharrabti Y, Garcia del Moral LF (2005) Using AFLPs to determine phylogenetic relationships and genetic erosion in durum wheat cultivars released in Italy and Spain throughout the 20th century. Fields Crop Res 91:107–111

Mekbib F (2007) Infra-specific folk taxonomy in sorghum (*Sorghum bicolor* (L.) Moench) in Ethiopia: folk nomenclature, classification and criteria. J Ethnobiol Ethnomed 3:38

Mekbib F (2008) Genetic erosion of sorghum (*Sorghum bicolor* (L.) Moench) in the centre of diversity, Ethiopia. Genet Resour Crop Evol 55:351–364

Morin SR, Calibo M, Garcia-Belen M, Pham JL, Palis F (2002) Natural hazards and genetic diversity in rice. Agric Hum Values 19:133–149

Nei M (1987) Molecular evolutionary genetics. Columbia University press, New York

Nersting LG, Andersen SB, Von Bothmer R, Gullord M, Jørgensen RB (2006) Morphological and molecular diversity of Nordic oat through one hundred years of breeding. Euphytica 150:327–337

Nicholson S (2005) On the question of the ‘‘recovery’’ of the rains in the West African Sahel. J Arid Environ 63:615–641

Olsson L, Eklundh L, Ardö J (2005) A recent greening of the Sahel—trends, patterns and potential causes. J Arid Environ 63:556–566

Ostrowski MF, David J, Santoni S, McKhann H, Reboud X, Le Corre V, Camilleri C, Brunel D, Bouchez D, Faure B, Bataillon T (2006) Evidence for a large-scale population structure among accessions of *Arabidopsis thaliana*: possible causes and consequences for the distribution of linkage disequilibrium. Mol Ecol 15:1507–1517

Peroni N, Hanazaki N (2002) Current and lost diversity of cultivated varieties, especially cassava, under swidden cultivation systems in the Brazilian Atlantic Forest. Agric Ecosyst Environ 92:171–183

Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. Conserv Biol 12:844–855

Pritchard JK, Wen W (2002) Documentation for Structure software: version 2 (http://pritch.bsd.uchicago.edu)

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Rana RB, Garforth C, Stapith B, Jarvis D (2007) Influence of socio-economic and cultural factors in rice varietal diversity management on-farm in Nepal. Agric Hum Values 24:461–472

Reif JC, Hamrit S, Heckenberger M, Schipprack W, Maurer HP, Bohn M, Melchinger AE (2005) Trends in genetic diversity among European maize cultivars and their parental components during the past 50 years. Theor Appl Genet 111:838–845

Rosenberg NA, Pritchard JK, Weber JL, Cann HM, Kidd KK, Zhivotovsky LA, Feldmann MW (2002) Genetic structure of human populations. Science 298:2381–2385

Roussel V, Koenig J, Beckert M, Balfourier F (2004) Molecular diversity in French bread wheat accessions related to temporal trends and breeding programmes. Theor Appl Genet 108:920–930

Roussel V, Leisova L, Exbrayat F, Stehno Z, Balfourier F (2005) SSR allelic diversity changes in 480 European bread wheat varieties released from 1840 to 2000. Theor Appl Genet 111:162–170

Snowden JD (1936) The cultivated races of sorghum. Adlard, London, pp 1–274

Teklu Y, Hammer K (2006) Farmers’ perception and genetic erosion of tetraploid wheat landraces in Ethiopia. Genet Resour Crop Evol 53:1099–1113

Teshome A, Patterson D, Asfew Z, Torrance JK, Arnason JT (2007) Changes of *Sorghum bicolor* landrace diversity and farmers’ selection criteria over space and time, Ethiopia. Genet Resour Crop Evol 54:1219–1233

Thomas DSG, Twyman C, Osbahr H, Hewitson B (2007) Adaptation to climate changes and variability: farmer responses to intra-seasonal precipitation trends in South Africa. Clim Change 83:301–322

Traoré SB, Reyniers FN, Vaksmann M, Koné B, Sidibé A, Yoroté A, Yattara K, Kouressy M (2000) Adaptation à la sècheresse des écotypes locaux de sorghos au Mali. Sècheresse 11:227–237

Van Etten J (2006) Changes in farmers’ knowledge of maize diversity in highland Guatemala, 1927/37–2004. J Ethnobiol Ethnomed 2:12

Vigouroux Y, Jaqueth JS, Matsuoka Y, Smith OS, Beavis WD, Smith JS, Doebley J (2002) Rate and pattern of mutation at microsatellite loci in maize. Mol Biol Evol 19(8):1251–1260

Vigouroux Y, Mitchell S, Matsuoka Y, Hamblin M, Kresovich S, Smith JSC, Jaqueth J, Smith OS, Doebley J (2005) An analysis of genetic diversity across the maize genome using microsatellites. Genetics 169:1617–1630

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Willemen L, Scheldeman X, Soto Cabellos V, Rafael Salazar S, Guarino L (2007) Spatial patterns of diversity and genetic erosion of traditional cassava (*Manihot esculenta* Crantz) in the Peruvian Amazon: an evaluation of socio-economic and environmental indicators. Genet Resour Crop Evol 54:1599–1612