Pl. Syst. Evol. 193: 81–93 (1994)

Plant Systematics and Evolution

Isozymic classification of pearl millet (*Pennisetum glaucum, Poaceae*) landraces from Niger (West Africa)

SERGE TOSTAIN

Received January 11, 1994; in revised version March 21, 1994

Key words: *Poaceae, Pennisetum glaucum.* – Isozymes, genetic polymorphism. – Flora of Niger, West Africa.

Abstract: The principal landraces of the pearl millet, *Pennisetum glaucum* (L.) R. BR., from Niger have been analysed for their genetic structure at eight enzyme systems coded by 12 loci and 46 alleles. Three groups have been identified: (1) early-maturing pearl millets, cultivated between 8° and 13° E longitude, including the oases from Aïr mountains; (2) early-maturing millets situated more to the west (1° and 8° E longitude), and (3) late-maturing millets. Group 1 shows the highest isozyme diversity. The differences between the accessions represent 8.8% of the total diversity and the differences between the three groups 4.5%. The accessions from groups 1 and 3 are the least distant. When considering pearl millets from areas outside Niger, the chadian and sudanese millets are enzymatically close to the Niger group 1. The pearl millets from Niger group 2 are close to millets from east Mali, northern Burkina Faso and Senegal, and the Niger group 3 to the late-maturing millets group from West Africa. This study should help breeders to select the landraces for improvement and parents for crosses from cultivars of Niger and introduced germ plasm.

Pearl millet, *Pennisetum glaucum* (L.) R. BR., an annual diploid cereal with an allogamous reproductive system is the staple food in West Africa, particularly in Niger (CATHERINET & al. 1963, CLEMENT 1985). In Niger, several landraces were first described by MARCHAL (1950). Based on spike morphology, he defined three landrace types with spindle-shaped spikes, cylindrical spikes, and large spikes.

Traditional cultivars from West Africa were collected between 1975 and 1983 by the International Board for Plant Genetic Resources (IBPGR) and the Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM) notably in Niger in 1975 and 1976 (CLEMENT 1985). The 403 accessions collected in 1975 were classified into 11 groups based on information obtained from the farmers and observations on spike characteristics (BORGEL & SEQUIER 1977). In 1990, a collection mission was undertaken in Niger by a joint team of the International Crops Research Institute for the Semi-Arid tropics (ICRISAT)-ORSTOM. The collectors noted a change in the composition of the landraces and varieties grown by the farmers. This change was attributed to the distribution of seed of improved varieties by the official agricultural services of Niger following the severe droughts of 1973 and 1974.

BONO (1973), MARCHAIS (1975), BRUNKEN & al. (1977), and CLEMENT (1985) have described the morphological diversity of West African pearl millets, and have provided evidence for distinct landrace groups and their distribution within each country. The morphological differentiation of pearl millet within Niger is the greatest in West Africa and is characterized by the shortest and longest spikes (in the Batchouchiné and Zongo cultivars respectively). In the west, varieties are characterized by long and thin cylindrical spikes, and in the east by short spindle spikes with a shaped large circumference. Even today farmers of Niger select "true-to-type" spikes from their traditional cultivars for use as seed for the following year. It was of interest to investigate whether the Niger landraces, grouped on the basis of morphological traits, could be distinguished by their enzymatic constitution.

In this paper we examine the enzymatic diversity of pearl millet landraces from Niger, and relate this diversity to other West African landraces. The results obtained were compared with previous classification attempts based on morphological characters.

Material and methods

Plant material. Fifty accessions from the 108 accessions collected in Niger in November 1990 were used. In addition, 16 accessions of the collection from 1976 (TOSTAIN & MARCHAIS 1989) were included. Seeds were obtained after threshing of about 10 spikes, all collected from the granaries of farmers. These 66 accessions were collected from the principal pearl millet growing zones of Niger: a large area south of the 16th parallel where millet is cultivated during the rainy season and a small area in the Aïr mountains (onses) where millet is cultivated during the rainy season and a small area in the Aïr mountains (oases) where millet is cultivated under irrigation (Fig. 1). The principal landraces collected and studied were: Haïni Kiré, Maiwa, Zongo, Guerguéra, Ba-Angouré, Ankoutess, Boudouma, Zan-

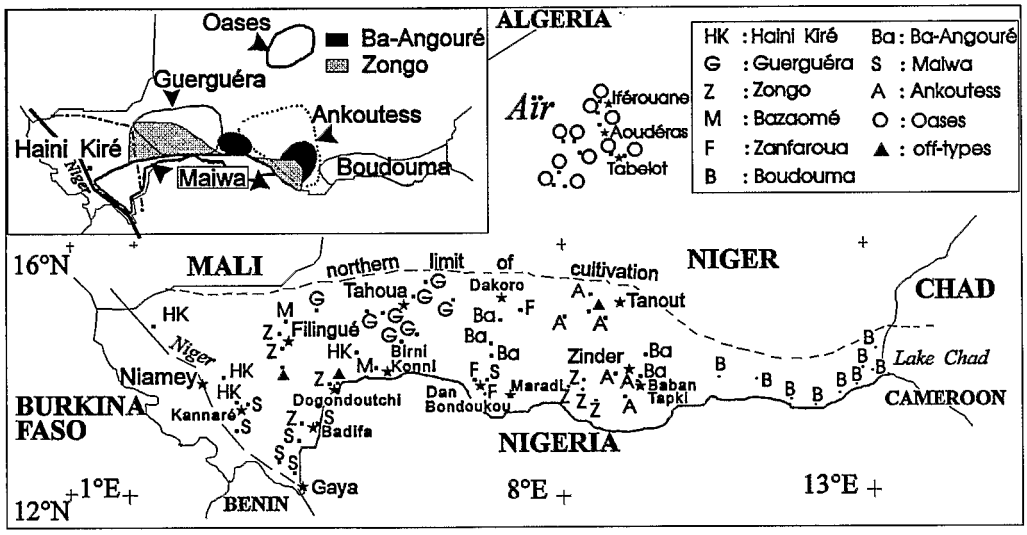

Fig. 1. Localisation of the 66 accessions from Niger analyzed by isozyme electrophoresis. The accessions are represented by symbols: *HK* Haini Kiré; *G* Guerguéra; *Z* Zongo; *M* Bazaomé; *F* Zanfaroua; *Ba* Ba-Angouré; *S* Maiwa; *A* Ankoutess; *B* Boudouma; *O* oases; ▲ off-types. Inset: delimited cultivation zones of main Niger cultivars in 1990

faroua (cultivated from Maradi to Dakoro), Bazaomé (cultivated from Birni Konni to Filingué), and the oases cultivars. The spike lengths show two groups of early maturing landraces: 6 cultivars from west with long spikes and 4 from east Niger with short spikes (Table 1). Individual farmer selections within landraces characterized by traits such as bristles and brown seed selected for religious reasons, were excluded from the analysis, being unrepresentative for the total diversity of the cultivars (MARCHAL 1950).

Information on the maturity duration of the landraces was obtained from the farmers. The early-maturing pearl millet cultivars have a maturity duration of about 95 days and the late-maturing millets of about 120 days (BILQUEZ & CLEMENT 1969). According to this criterion, the accessions represented 59 early-maturing and 7 late-maturing cultivars.

These Niger pearl millet cultivars were compared to 186 accessions of pearl millet from 15 countries in West Africa s.l., including 106 already studied (TOSTAIN & MARCHAIS 1989): Senegal (8), Mauritania (5), Mali (42), Algeria (10), Tunisia (4), Burkina Faso (40), Côte-d'Ivoire (5), Ghana (12), Togo (7), Benin (3), Nigeria (8), Cameroon (8), Central African Republic (5), Chad (23), and Sudan (6).

Electrophoretic analysis. Eight enzymatic systems were analyzed by electrophoresis: carboxylic esterases (EST), alcohol dehydrogenases (ADH), catalases (CAT), malate dehydrogenases (MDH), glutamate oxaloacetate transaminases (GOT), 6-phosphogluconate dehydrogenases (PGD), phosphoglucoisomerases (PGI), and phosphoglucomutases (PGM). Twenty-six grains were used for the study of esterases, and 20 (seeds or seedlings) for the study of other enzymes.

The techniques used for electrophoresis and for statistical analysis of data have been described in TOSTAIN & al. (1987). Twelve polymorphic loci corresponding to 46 alleles were observed. Principal component analysis was performed on the unstandardized allelic frequencies (covariance matrix), as was discriminant analysis and an automatic classification on Euclidean distances of weighted averages. Genetic diversity was calculated for each accession and each locus (H_x). The total genetic diversity (H_t) and the average diversity (H_s) were calculated for each group defined by principal component analysis. The coefficient

Table 1. Spike lengths of pearl millet cultivars from Niger collected in 1990 (three spikes for each accessions) with standard error

Region/ Maturity	Cultivars	Number of accessions	Spike length: Mean (cm) ± S.E.
West	Haini Kiré	5	78 ± 8
Early maturing	Guerguéra	8	62 ± 6
	Zongo	8	101 ± 11
	Zanfaroua	3	78 ± 20
	Bazaomé	3	76 ± 10
	Ba-Angouré	3	75 ± 15
	Mean	30	78.3 ± 4.1
East	Ba-Angouré	4	38 ± 6
Early maturing	Ankoutess	7	29 ± 5
	Boudouma	7	23 ± 4
	Oases (Aïr)	11	12 ± 3
	Mean	29	25.5 ± 3.4
West and East Late maturing	Maiwa	7	74 ± 11

of differentiation (Gst) and the distance between groups (Dm) were estimated as described by NEI (1975).

The standard deviation of a group's diversity (composed by N accessions) was calculated using the expression:

$$\sigma = \sigma_{Hxi}/(1\text{-}Gst)\sqrt{N}$$

where H_{x_i} is the diversity H_x of the accessions i and σ_{Hx_i} the standard deviation of the diversity for accessions i computed from:

$$\sigma H_{x_i} = \frac{\sqrt{\Sigma_i (H_{x_i} - Hx)^2}}{(N-1)}$$

with $\overline{H}_x$, average diversity.

The diversity H_T of 66 accessions is calculated by: $H_T = \overline{H_t} + D_{st}$ with $\overline{H}_t$ being the average total group diversities and Dst the average inter groups distances. Gst for the 66 accessions from Niger is: $G_{st} = \frac{D_{st}}{H_T}$. The cluster analyses using the Euclidean distance method (hierarchical ascendant classification) and unweighted pair group method with modified Rogers distance coefficient were employed with STAT-ITCF and BIOSYS-1 softwares (ITCF 1987, SWOFFORD & SELANDER 1981).

Results

Differentiation of distinct groups in Niger. The projection of the 66 points in the plane defined by components 1 and 3 of the principal component analysis (52% of the total diversity) shows a diverse cluster of points (Fig. 2). Allele *Adh-A*^{6} is positively correlated to component 1, and *Adh-A*^{4} and *Pgm-A*^{1} are negatively correlated. Alleles *Adh-A*^{7} and *Cat-A*^{1} are highly and positively correlated to component 3. Alleles *Pgi-A*^{5} and *Est-A*^{7} are weakly and negatively correlated to component 3.

The results suggest that the first component identifies two morphological groups (Fig. 2). Group 1 consists of 28 accessions including millets from the oases of Aïr, cv. Boudouma and cv. Ankoutess, and three accessions from cv. Ba-Angouré (Ba-Angouré from east). Group 2 comprises 28 accessions from cvs Haini Kiré, Zongo, Guerguéra, Zanfaroua, Bazaomé, and three accessions from cv. Ba-Angouré (Ba-Angouré from west). The third component separates seven accessions of cv. Maiwa as group 3.

The groups 1 and 2, identified by principal component analysis, represent distinct geographic distribution (Figs. 1, 3). Apart from the 11 accessions from Aïr oases, the accessions of group 1 are cultivated in the eastern part of Niger between 8° and 13° E, and those of group 2 in the western part of the country between 1° and 8° E. The accessions of group 3 are distributed in the South-West and in the southern Maradi region near the border with Nigeria.

In the same locality (Kannaré, Badifa and Dan Boudoukou), accessions of late-maturing and early-maturing pearl millets are grouped with group 3 and group 2, respectively (Fig. 2). The Ankoutess and Ba-Angouré accessions from Baban Tapki village are grouped with groups 1 and 2, respectively (Fig. 2).

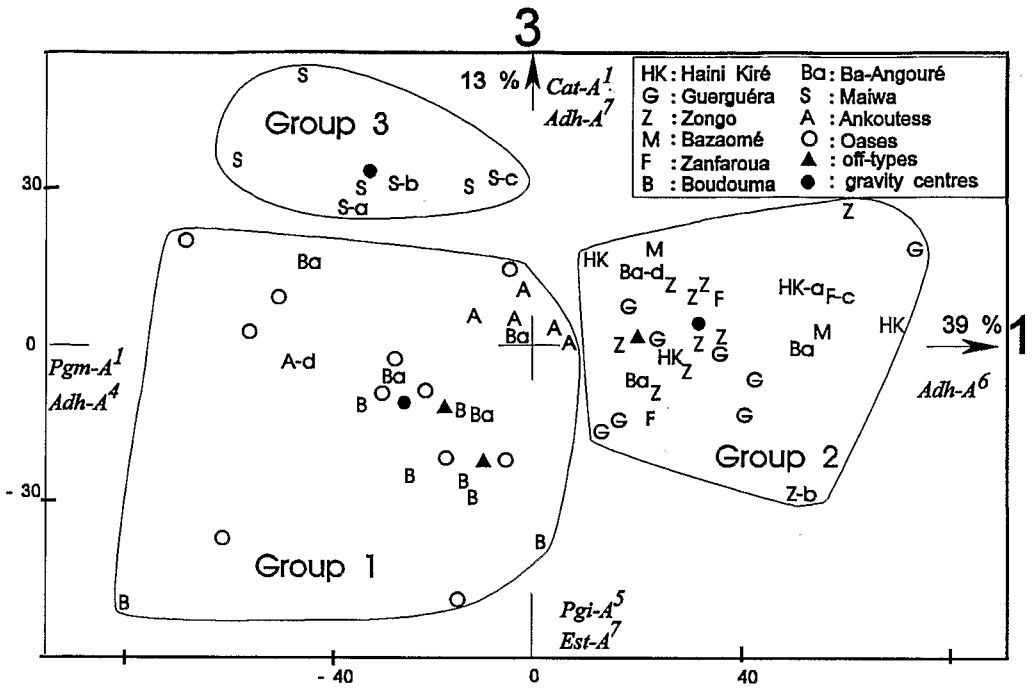

Fig. 2. Projections on axes 1 and 3 of principal component analysis of Niger accessions. Off-types are placed in supplementary elements. The variables correlated to component 1 and 3 are noted. ● Gravity centres for the three attested groups. Three pairs (late- and early-maturing millets) are from three respective villages: *a* Kannaré; *b* Badifa; *c* Dan Boudoukou. Two different cultivars with an identical cycle (early-maturing), Ba-Angouré and Ankoutess, were collected in Baban Tapki village (d)

Only three accessions are not explained by this rationalization of principal component analysis: an accession from the Bazaomé and one from the Haini Kiré cultivars are in group 1. An accession from cv. Ankoutess is in group 2.

The discriminant analysis confirms that 95% of these accessions are classified in groups 1, 2, and 3 (93, 100, and 86%, respectively). Five alleles allowed these groups to be distinguished (Table 2). The alleles *Pgm-A*^{1} and *Adh-A*^{4} have lower frequencies in group 2 (respectively 0.42 and 0.13) and the frequency of *Adh-A*^{6} from group 2 is the highest of the three (0.76). *Adh-A*^{7} has a higher frequency in the accessions from group 3 (0.20), and the accessions from group 1 have a lower frequency for *Cat-A*^{1} (0.72).

Six loci contribute about 95% of the total diversity (Table 3): *Est-A* (about 28%), *Adh-A* (20%), *Pgm-A* (16%), *Cat-A* (11%), *Pgi-A* (8%), and *Pgd-A* (8%). *Est-A* is a polymorphic locus in the 3 groups, but in group 3 the diversity of the locus *Adh-A* (0.71) is higher than in other groups, and in group 1, the loci *Cat-A* (0.41) and *Pgd-A* (0.29) have a higher diversity than others. The loci *Pgi-A* and *Pgm-A* have higher diversities (0.23 and 0.49) in group 2 than, respectively, in group 3 and in groups 1 and 3.

The lowest and highest diversities (Hx) were observed in accessions from Aoudéras (0.134 and 0.254) and Tabelot (0.145 and 0.296) oases. In the oases of

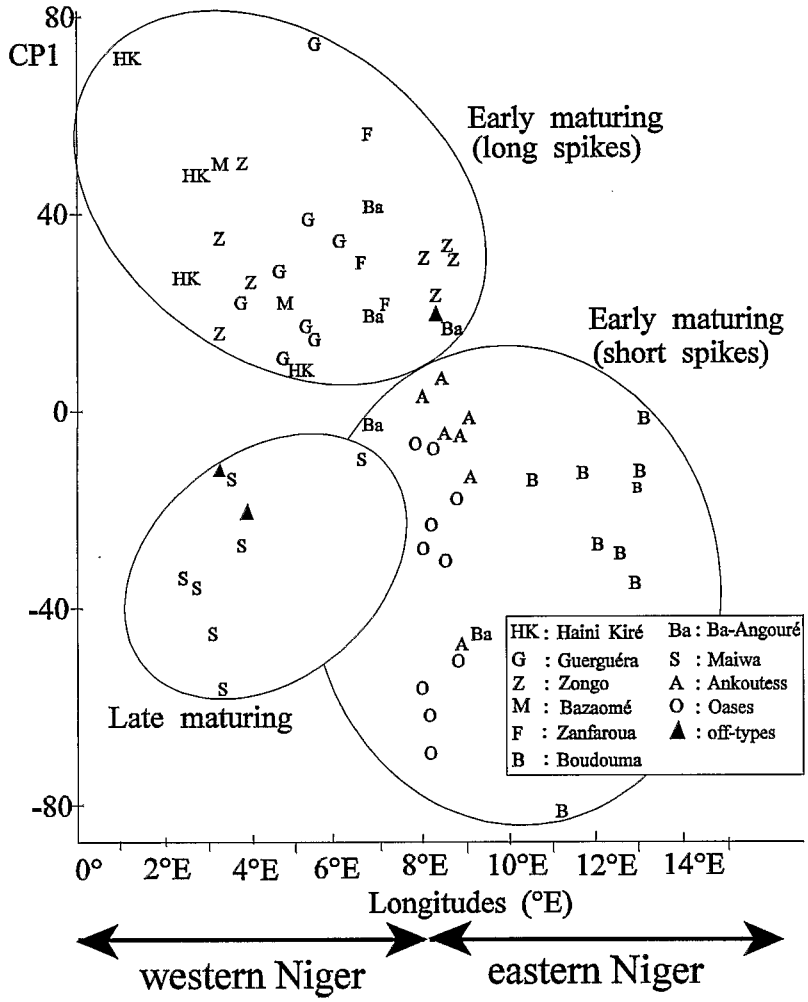

Fig. 3. Longitude of the 66 accessions (represented by symbols) from Niger. *CP 1* values on first component of principal component analysis

Table 2. Discriminant allele frequencies (mean ± S.D.) in the three pearl millet groups in Niger, and their average frequency. Number of accessions for each group in brackets

Groups Loci	1 (28)	2 (28)	3 (7)	1–3 (63)
Pgm-A^1	0.71 ± 0.13	0.42 ± 0.18	0.70 ± 0.15	0.58 ± 0.20
Adh-A^6	0.51 ± 0.19	0.76 ± 0.14	0.30 ± 0.14	0.60 ± 0.23
Adh-A^4	0.39 ± 0.19	0.13 ± 0.08	0.38 ± 0.08	0.27 ± 0.19
Adh-A^7	0.03 ± 0.07	0.03 ± 0.05	0.20 ± 0.12	0.05 ± 0.09
Cat-A^1	0.72 ± 0.13	0.80 ± 0.11	0.93 ± 0.03	0.78 ± 0.13

Table 3. Group diversities (H_t, mean ± S.D.; H_s; and Gst) for 9 polymorphic loci and the mean of diversities for 12 loci concerning the 3 cultivated pearl millet groups identified in Niger

N° groups Loci	1	2	3
Adh-A	0.573 ± 0.018	0.393 ± 0.041	0.714 ± 0.025
Cat-A	0.406 ± 0.029	0.323 ± 0.034	0.123 ± 0.062
Est-A	0.794 ± 0.012	0.784 ± 0.013	0.794 ± 0.022
Got-A	0.001 ± 0.003	0.001 ± 0.003	0.000
Got-B	0.008 ± 0.009	0.007 ± 0.008	0.006 ± 0.015
Mdh-A	0.068 ± 0.025	0.077 ± 0.026	0.034 ± 0.036
Pgd-A	0.287 ± 0.035	0.195 ± 0.035	0.166 ± 0.067
Pgi-A	0.247 ± 0.036	0.230 ± 0.036	0.125 ± 0.062
Pgm-A	0.410 ± 0.028	0.486 ± 0.011	0.418 ± 0.053
$\Sigma H_t/12$	0.234 ± 0.007	0.209 ± 0.005	0.198 ± 0.009
Hs	0.214	0.194	0.185
Gst	0.088	0.071	0.069

Aïr, grains are obtained for each season from the north (Algeria, Libya) and south (southern Niger, Nigeria). Significant genetic heterogeneity has already been observed in the Chad oases (VINCHON 1949), and exchange of grain between the Sahara and the southern Niger oases have been in existence for a long time (GAST & ADRIAN 1965).

The group diversities (H_t) are significantly different (Table 3): the diversity of group 1 is the highest (0.234 ± 0.007) and that of group 3 the lowest (0.198 ± 0.009). The major proportion of the observed genetic diversity is between accessions into each group (H_s from 91 to 93% depending on groups). Millets of oases caused the coefficient of differentiation of group 1 as the highest of the three (Table 3).

The diversity of 66 accessions, H_T, is equal to 0.224, inferior to group 1 diversity. Only 4.5% of the total diversity permits to distinguish the three groups of the Niger cultivars (Gst = 0.045).

The distance, Dm, between groups 1 and 2 is equal to 0.014 ± 0.003, and that between groups 1 and 3 to 0.009 ± 0.003. It is between group 2, and group 3, that the distance is important (0.022 ± 0.006).

The diversity of the early-maturing pearl millets (groups 1 and 2 pooled) is greater than that of late-maturing pearl millets (0.230 ± 0.004 versus 0.198 ± 0.009). The diversity of the loci *Cat-A, Pgi-A,* and *Pgm-A* is superior in early-maturing pearl millets (0.37 ± 0.02 versus 0.12 ± 0.06 for the first locus, 0.24 ± 0.02 versus 0.12 ± 0.06 for the second, and 0.50 ± 0.01 versus 0.42 ± 0.05 for the third). *Adh-A* diversity is inferior to that of the late-maturing pearl millets (0.53 ± 0.02 versus 0.71 ± 0.02). The minimum Nei's distance between these groups corresponds to 0.012 ± 0.004.

The cluster analysis of cultivars from Niger confirms the morphological observations (Fig. 4). The results obtained using few enzymatic markers show two main clusters. In the east, a group (1) of early-maturing pearl millets with short spikes

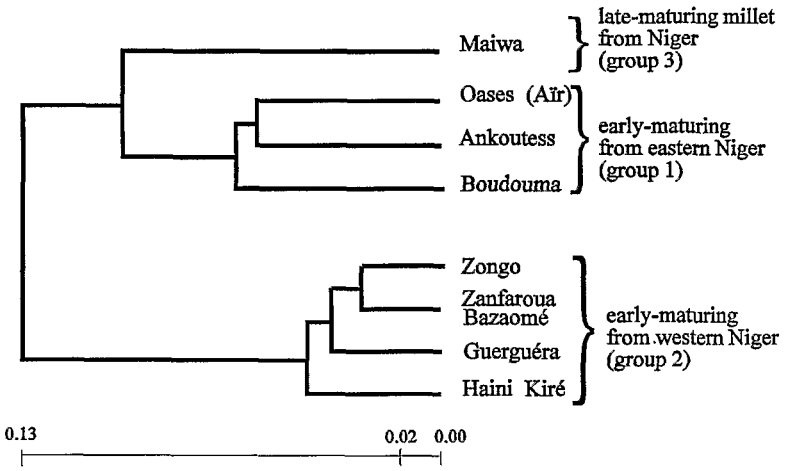

Fig. 4. Cluster analysis of main cultivars from Niger using unweighted pair group method. The coefficient used is the modified Rogers distance. The 46 alleles have been used for the calculation (software Biosys-1)

(millets from Aïr oases, Boudouma and Ankoutess landraces); a group (2) of early-maturing pearl millets in the west with long spikes (Haini Kiré, Guerguéra and Zongo landraces), and a small group (3) of late-maturing pearl millets in the south of the country. The late-maturing cv. Maiwa is closer to the early-maturing cultivars with short spikes from the east than to the early-maturing cultivars with long spikes from the west. This conclusion is also illustrated by the projection into the plane (1, 2) of the principal component analysis: in this axis system the groups 1 and 3 are confounded.

Comparison of Niger pearl millet cultivars with other West African cultivars. Additional analysis of relationships between 112 early-maturing and 74 late-maturing millets by principal component analysis and discriminant analysis identified five groups in West Africa: A: accessions of early-maturing pearl millets from Senegal, Mauritania, eastern Mali, Algeria, Tunisia and northern Burkina Faso; B: accessions of late-maturing pearl millet from Côte-d'Ivoire, southern Burkina Faso, Ghana, Togo, Benin and Nigeria; C: accessions of early- and late-maturing pearl millet from Cameroon, Central African Republic, Chad and Sudan; D: accessions of early-maturing pearl millet from Ghana and Togo; E: accessions of early-maturing pearl millets from western Mali.

In the plane formed by components 1 and 2 of the principal component analysis of 186 accessions and 63 Niger accessions (without the three offtypes) as additional data, the centre of gravity of accessions from group 1 is close to that one of group C (Cameroon to Sudan pearl millets), and the centre of gravity of group 3 is close to those of groups B (late-maturing millets) and C. Group 2 has its centre of gravity close to that of pearl millets from group A, particularly those of Senegal to northern Burkina Faso. The discriminant analysis with accessions of the 8 pearl millets groups gaven the following results (Table 4): 80.3% of accessions are well-classified. The distances between the 8 groups show that there is a small genetic distance between the accessions of groups 1 and C, 2 and A, 3 and B, C. The classification

Table 4. Discriminant analysis for 249 accessions of West African pearl millet. *A* Early-maturing pearl millets from Senegal, Mauritania, Algeria, Tunisia, eastern Mali, northern Burkina Faso; *B* late-maturing pearl millets from Ivory Coast, southern Burkina Faso, Ghana, Togo, Benin, Nigeria; *C* from Cameroon, Central African Republic, Chad, Sudan; *D* early-maturing pearl millets from Togo and Ghana; *E* from western Mali. 1, 2, and 3: Groups from Niger

Final groups	Other West African groups					Niger groups			Total
	A	B	C	D	E	1	2	3	
Initial Groups									
A	**49**	4	1	0	4	2	4	3	**67**
B	3	**39**	3	0	0	2	0	3	**50**
C	0	1	**30**	1	0	4	4	2	**42**
D	0	0	0	**7**	0	1	0	0	**8**
E	1	0	0	0	**17**	0	1	0	**19**
1	1	0	1	0	0	**24**	2	0	**28**
2	0	0	0	0	0	0	**27**	1	**28**
3	0	0	0	0	0	0	0	7	**7**
Total	54	44	35	8	21	33	38	16	**249**

by a hierarchical ascendant classification offers the summary of the table of distances and earlier results obtained by principal component analysis and discriminant analysis (Fig. 5). Such classification created five classes with groups C-1, B-3, A-2, D, and E.

These results, obtained by different methods of analysis, can be summed up as: Niger groups 1, 2, and 3 are close to groups C, A, and B, respectively.

The genetic diversity of the 112 West African early-maturing cultivated pearl millets (0.246 ± 0.003) is superior to that of early-maturing millets from group 1. The existence of early-maturing millets in Ghana and Togo (D) and in west Mali (E) explains this high diversity and coefficient of differentiation (0.184). The 74 late-maturing millets from the other countries of West Africa have a diversity (0.215 ± 0.003) and a coefficient of differentiation ($Gst = 0.143$) superior to those of late-maturing accessions from Niger.

The differences observed between groups 2 and 3 confirm the isolation within the species of two sympatric cultivated groups, early- (nearly photoperiod insensitive) and late-maturing (highly photoperiod sensitive) pearl millets observed within the geographic boundaries of each country and in all the pearl millets of West Africa (PILATE-ANDRE & al. 1986, TOSTAIN & al. 1987). This divergence has already been used in millet improvement (BHARDWAJ & WEBSTER 1971).

Discussion

The 1990 season when the collection was undertaken was characterized by drought throughout the country and thus permitted observations on shift in the distribution

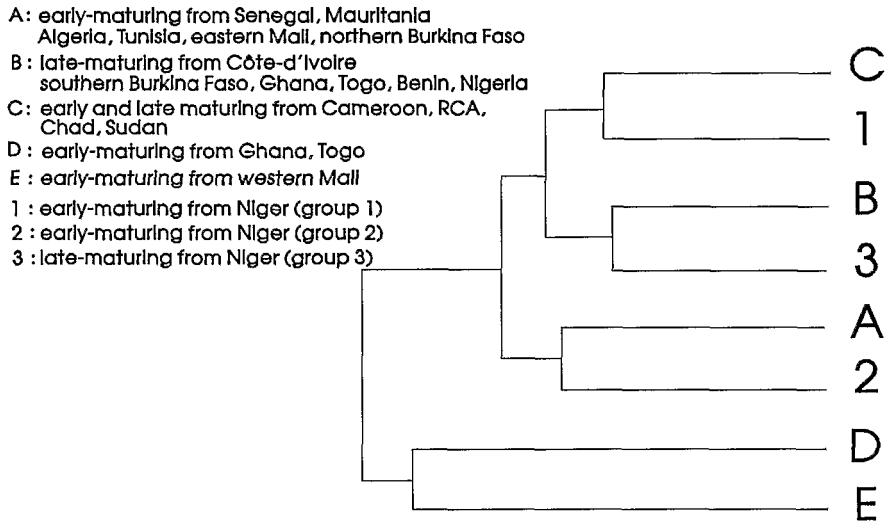

Fig. 5. Classification of the Euclidean distances (C.A.H.) between the 10 average discriminant allelic frequencies of the 3 Niger groups 1, 2, 3 and the five groups of other West African millets

of cultivated areas of important local cultivars (CLEMENT 1985): a decrease in cultivated area for cvs Maiwa, Ankoutess, and Zongo, and an expansion of area used for cv. Boudouma towards the centre of the country were noted.

Three enzymatic systems, ADH, CAT, and PGM, among the 8 studied, are sufficient to sort out the cultivated pearl millets of Niger as evidenced in this study. The polymorphism of ADH and PGM allows to separate accessions into groups 1 and 2; the polymorphism of ADH and CAT allows the separation of the accessions from groups 1 and 3.

The diversity within the accessions of the 3 groups is equal to about 90% of the total diversity, confirming the genetic variation of Niger pearl millets among the cultivated pearl millets (TOSTAIN & MARCHAIS 1989) and in similar species (HAMRICK & GODT 1990).

Similarity of the early-maturing millets from group 1 and late-maturing millets from group 3. The small genetic distance between the early-maturing pearl millets from group 1 and the late-maturing ones from group 3 has yet to be explained. The spikes exhibit a different morphology and differences in time of flowering and thus prevent introgression in their zone of contact in the south of Maradi (DUMONT 1966). The following scenario may explain this: around 5000 years B.P., drought forced the populations from east Niger and north-east Nigeria to migrate southward with their seeds of early-maturing millets (supposed not very different from enzymatic group 1), to the northern Cameroon fertile tablelands (DAVID 1980). Once in this region, these early-maturing pearl millets underwent a selection for photoperiod response, a secondary trait of domestication (BILQUEZ & CLEMENT 1969, PERNES 1985) resulting in the evolution of late-maturing plants. Selection within this late-maturing group of plants could have led to plants of cv. Maiwa with long and nearly conical spikes comparable to the spikes of pearl millets from group 2.

This hypothesis could be verifiable by investigation of the enzymatic polymorphism of the early-maturing pearl millets from Nigeria, called "Gero". The photoperiod-sensitive pearl millets could have led to the origin of pearl millets in the West Africa Sudanian zones (TOSTAIN & MARCHAIS 1989).

Similarity of the early-maturing millets from Senegal-Mauritania and Niger. The similarity of the early-maturing pearl millets from Senegal and Mauritania (A) to some from Niger (group 2) is the second finding that needs an explanation (Fig. 5). This genetic proximity, despite geographic distance, has been observed for the morphological characteristics of the spike (BONO 1973, MARCHAIS 1982) and the enzymatic characteristics (TOSTAIN & al. 1987). The pearl millets from Senegal, Mauritania and western Mali are considered to be the first to have been domesticated (TOSTAIN 1992), in the Senegalese-Gambian subcentre of the West African centre defined by PORTERES (1950). In this zone, where cereal cultivation from a steppe type is longstanding, two zones, Chadian (including Niger) and Senegalese-Gambian, have been demonstrated. In the Chadian sector, the subspp. *ancylochaete, gibbosum* and *maiwa*, described by STAPF & HUBBARD (1934), are found. In the second sector, a whole series of other subspecies are described; *P. nigritarum* DURAND & SCHINZ is common to the two sectors (PORTERES 1950, 1976), as proved by the observation of the ornamentation of the aristation ("inner silk") from the floral involucre (BONO 1973). These characteristics can be related to the enzymatic groups: pearl millets from group 1 correspond to subsp. *gibbosum*, millets from group 2 to subsp. *ancylochaete*, and those from group 3 to subsp. *maiwa*. Subsp. *nigritarum* can be associated with the millets from group 2. These facts explain the separation between the two early-maturing groups from Niger which does not correspond to observed ecologic differences.

Another description based on seed shape (BRUNKEN & al. 1977) discerns three races of pearl millets in Niger: *typhoides, nigritarum*, and *globosum*, but their areas of distribution are not well defined and cannot be compared with the enzymatic groups described here.

Conclusion

In conclusion, the study of the enzymatic polymorphism and grouping of pearl millets from West Africa, and in particular those from Niger, should help breeders to select traditional cultivars for intra- and inter-population improvement. The groupings described here should also help in a breeding program to select parents to combine complementary characters. It is also possible to exploit heterosis using early-maturing western Mali accessions or early-maturing pearl millets from Ghana-Togo with appropriate breeding methodology.

We thank the ICRISAT Sahelian Center, and the ORSTOM Centre in Niamey (Niger) for support during the collection in Niger. We thank Dr J. F. RENNO for his help during the collection mission, MAMADOU ISSA for his help in the electrophoretic analysis, and Drs K. ANAND KUMAR, G. BEZANÇON, G. SECOND, and L. MARCHAIS for suggestions on the manuscript.

References

BHARDWAJ, B. D., WEBSTER, O. J., 1971: Studies of F1 hybrids between photoperiod sensitive and non-sensitive *Pennisetum* millets. – Crop Sci. **11**: 289–291.

BILQUEZ, A. F., CLEMENT, J., 1969: Etude du mode d'hérédité de la précocité chez le mil pénicillaire (*Pennisetum typhoides* STAPF & HUBB.) II. Déterminisme génétique des variations de précocité des mils du groupe souna. – Agron. Trop. **24**: 258–262.

BONO, M., 1973: Contribution à la morpho-systématique des *Pennisetum* annuels cultivés pour leur grain en Afrique occidentale francophone. – Agron. Trop. **28**: 229–356.

BORGEL, A., SEQUIER, J., 1977: Prospection des mils pénicillaires et sorghos en Afrique de l'Ouest, Niger campagne 1976. – FAO/ORSTOM, Paris.

BRUNKEN, J., DE WET, J. M. J., HARLAN, J. R., 1977: The morphology and domestication of pearl millet. – Econ. Bot. **31**: 163–174.

CATHERINET, M. D., DUMONT, S., MAYAKI, A. A., 1963: Le mil et le sorgho dans l'agriculture de Niger. A) Cultures. Besoins. Sol et climat. Facteurs limitants. – Agron. Trop. **18**: 108–113.

CLEMENT, J. C., 1985: Les mils pénicillaires de l'Afrique de l'Ouest. Prospections et collectes IBPGR-ORSTOM. – IBPGR, Rome 85/15, ORSTOM.

DAVID, N., 1980: Early Bantu expansion in the context of Central African prehistory: 4.000-1 BC. – In BOUQUIAUX, L., (Ed.): L'expansion Bantoue, actes du Colloque International de CNRS, 4–16 Avril 1977, Viviers (France), pp. 609–647. – Paris: Selaf.

DUMONT, S., 1966: Mils et sorghos cultivés dans le Niger-Est. – Agron. Trop. **8**: 883–917.

GAST, M., ADRIAN, J., 1965: Mils et sorghos en Ahaggar: étude ethnologique et nutritionnelle. Mémoires du Centre de Recherches anthropologiques, préhistoriques et ethnologiques. – Conseil Recherche Scient. Algérie **4**: 1–80.

HAMRICK, J. L., GODT, M. J. W., 1990: Allozyme diversity in plant species. – In BROWN, A. H. D., CLEGG, M. T., KAHLER, A. L., WEIR, B. S., (Eds): Plant population genetics, breeding and genetic resources, pp. 43–63. – Sunderland, Massachusetts: Sinauer.

ITCF, 1987: STAT-ITCF software. Institut Technique des céréales et des fourrages. Boigneville F91720, France.

MARCHAIS, L., 1975: La variabilité naturelle connue chez les mils pénicillaires cultivés et sauvages: inventaire en vue d'une prospection en Afrique de l'Ouest. – Paris: ORSTOM.

– 1982: La diversité phénotypique des mils pénicillaires cultivés au Sénégal et au Mali. – Agron. Trop. **37**: 68–80.

MARCHAL, A., 1950: Les pénicillaires cultivés au Niger. – Agron. Trop. **5**: 582–592.

NEI, M., 1975: Molecular population genetics and evolution. – Amsterdam Oxford: North Holland.

PERNES, J., 1985: Le mil. – In ACCT, (Ed.): Gestion des ressources génétiques des plantes. Monographies, **1**, pp. 159–201. – Paris: Lavoisier.

PILATE-ANDRE, S., SANDMEIER, M., TOURE, A., PERNES, J., 1986: Evaluation du polymorphisme enzymatique des mils pénicillaires (*Pennisetum typhoides* STAPF et HUBBARD) de l'Afrique de l'Ouest. – In CNRS, Paris, (Ed.): Coll. nat. CNRS biologie des populations, Lyon, 4–6 Sept. 1986, pp. 352–356. – Paris: CNRS.

PORTERES, R., 1950: Vieilles agricultures de l'Afrique inter-tropicale. Centre d'origine et de diversification variétale primaire et berceaux d'agriculture antérieurs au XVI^{e} siècle. – Agron. Trop. **5**: 489–507.

– 1976: African cereals: Eleusine, Fonio, Black fonio, Teff, *Brachiaria, Paspalum, Pennisetum*, and African rice. – In HARLAN, J. R., DE WET, J. M. J., STEMLER, A. B. L., (Eds): Origins of African plant domestication, pp. 409–452. – The Hague, Paris: Mouton.

STAPF, O., HUBBARD, C. E., 1934: *Pennisetum*. – In THISTLETON, D. P., (Ed.): Flora of Tropical Africa. Dyer Gramineae 9 (6), pp. 954–1070. – London: Crown Agents for the Colonies Schroet.

SWOFFORD, D. L., SELANDER, R. B., 1981: Biosys-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. – J. Heredity **72**: 281–283.

TOSTAIN, S., 1992: Enzyme diversity in pearl millet (*Pennisetum glaucum*). 3. Wild. – Theor. Appl. Genet. **83**: 733–742.
– MARCHAIS, L., 1989: Enzyme diversity in pearl millet (*Pennisetum glaucum*). 2. Africa and India. – Theor. Appl. Genet. **77**: 634–640.
– RIANDEY, M. F., MARCHAIS, L., 1987: Enzyme diversity in pearl millet (*Pennisetum glaucum*). 1. West Africa. – Theor. Appl. Genet. **74**: 188–193.
VINCHON, R., 1949: Etude sur la génétique des *Pennisetum* cultivés. – Agron. Trop. **4**: 451–485.

Address of the author: S. TOSTAIN, Institut français de recherche scientifique pour le développement en coopération (Orstom), BP 5045, F-34032 Montpellier cedex 1, France.

Accepted March 21, 1994 by W. HAGEMANN