

Pearl Millet

Gilles Bezançon

Pearl millet is, along with sorghum, the staple food for a significant part of the population in Africa and the Indian subcontinent. It is the cereal most tolerant to drought; it is cultivated in the Sahel, in zones where rainfall is no more than 200 mm. For these reasons, the conservation, evaluation, and commercialization of genetic resources of pearl millet constitute a considerable task. Pearl millet is mostly cultivated in arid and semi-arid areas in Africa, where it covers 11.5 million ha, and in India, where it covers 14.7 million ha (FAO, 1996).

Three quarters of the African production comes from the western part of the continent, and the major producer countries, in decreasing order, are Nigeria, Niger, Burkina Faso, Chad, Mali, and Mauritania. In East Africa, the Sudan and Uganda are the primary producers, while in southern Africa this traditional crop has nearly disappeared. In Africa, the local varieties, early or late, are tall and put out many suckers. They are not highly productive: planted in poor soils, they do not benefit from tilling and only rarely get inputs in the form of organic manure from livestock. Seeds are planted during the beginning of the rains and must be planted several times in case of poor rainfall.

In India, pearl millet is cultivated on a large scale in Rajasthan, Gujarat, and Haryana. The use of animals for ploughing allows the soil to be worked and seeding is done by means of traditional seeders. The traditional varieties are late-yielding and short-strawed, and they put out few suckers. But here also, because chemical fertilizers are rarely used, grain yields are not high. Yields remain low, 0.6 to 0.8 t/ha, compared with those of other cereals cultivated in the tropics, such as rice and maize. Pearl millet can be intercropped, with cowpea, for example. Finally, in the United States, pearl millet is cultivated on more than 150,000 ha to produce fodder and grain: the yields are over 1.2 t/ha (FAO, 1996).

The primary product of the plant is the grain, which has greater nutritive value than wheat and rice. It is consumed in the form of dough, porridge, couscous, or pancakes, and in certain regions is used to make alcoholic beverages (pearl millet beer). The straw can also be used as forage or in construction of roofs and fences for traditional houses.

TAXONOMY AND GENETIC RESOURCES

Botany and Taxonomy of the Genus *Pennisetum*

Pearl millet, *Pennisetum glaucum* (L.) R. Br., belongs to the genus *Pennisetum* (family Poaceae, subfamily Panicoideae, tribe Paniceae). The species of *Pennisetum* (numbering about 60) are distributed in tropical and subtropical zones across the world. The genus is divided into five sections and pearl millet belongs to the section *Penicillaria*, which is characterized by the presence of a tuft of hairs on the apex of the stamen. In this section, van der Zon (1992) recognized three subspecies within the species *P. glaucum* ($x = 7$, $2n = 2x = 14$): *P. glaucum* ssp. *glaucum*, cultivated pearl millet, found in Africa; *P. glaucum* ssp. *violaceum*, the wild form, widely distributed in Africa in the Sahelian and sub-desert zone, in a discontinuous manner from the Atlantic to the Red Sea and in varied ecological situations; and *P. glaucum* ssp. *sieberianum*, which combines the intermediate forms resulting from natural hybridizations between the cultivated and wild forms.

On the model of Harlan and de Wet (1971), the species complex of the genus *Pennisetum* can be structured in three gene pools. The primary pool, monospecific, combines the three subspecies of *P. glaucum*. In certain regions of cultivation, the importance of intermediate forms has led local people to give them a particular name: *shibra* in Haoussa in Niger and *n'doul* in Wolof in Senegal. The secondary pool is composed of two species, *P. purpureum* and *P. squamulatum*, which can easily hybridize with *P. glaucum* (Hanna, 1987). *Pennisetum purpureum* is a perennial species, allotetraploid ($x = 7$, $2n = 4x = 28$), sexual, and allogamous. *Pennisetum squamulatum* is a perennial species, tetraploid ($x = 9$, $2n = 4x = 36$) and apomictic. These two species are used in improvement of pearl millet by apomixis (Hanna, 1987, 1990). The tertiary pool comprises the other species of the genus, including species of the section *Brevivalvula*. Widely represented in Africa, where they occupy various ecological niches, *Brevivalvula* are either annual or perennial with varied systems of reproduction (sexual, apomictic, vegetative). For these reasons, they can be used in genetic improvement of cultivated pearl millet.

Genetic Resources

Around 1960 the Rockefeller Foundation and the Indian Agricultural Research Institute undertook the establishment of a world collection of pearl millet cultivars. This first attempt fell through. A relatively large number of traditional cultivars disappeared partly because of desertification in zones particularly exposed to climatic fluctuations and partly because of socioeconomic transformations in some countries. This led the Food and Agriculture Organisation of the United Nations and then the IBPGR (International Board for Plant Genetic Resources) to undertake, around the

1970s, the collection and conservation of genetic resources of pearl millet and sorghum in the Sahelian zone. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), mandated by the CGIAR (Consultative Group for International Agricultural Research), coordinated these collections in collaboration with IBPGR, ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération), now IRD (Institut de Recherche pour le Développement) and national institutes for agricultural research. A world collection of close to 24,000 samples—traditional cultivars and wild forms together—originating from 44 countries is presently conserved, for the long and medium term, in the Indian centre of ICRISAT at Patancheru. Other sites of conservation are, notably, the GeneTrop laboratory of the IRD at Montpellier, in France—for medium-term conservation of around 3200 samples, 11% of them are wild species—and the Sahelian centre of ICRISAT of Sadore, in Niger. Doubles of these collections were established at the Centre for Conservation of Genetic Resources of Ottawa, in Canada, as well as at the National Seed Storage Laboratory in Fort Collins, United States, for long-term conservation.

For each of these collections the samples were accompanied by a profile comprising 11 descriptors, which gives information on the original situation of the sample.

ORGANIZATION OF GENETIC DIVERSITY

Agromorphological Variability

The large size of the collections makes it difficult to evaluate the diversity they contain. Several evaluation studies conducted by ICRISAT have been done on specific collections of some countries, including Ghana, Malawi, Cameroon, and the Central African Republic, and of several states in India. The results for 1939 and 2458 samples from the world collection, evaluated for 20 and 18 characters respectively, are presented in a catalogue published by the NBPGR (National Bureau of Plant Genetic Resources, India) and ICRISAT (NBPGR and ICRISAT, 1993). These data are reported only for cultivated forms. There are no studies that include the wild forms, which would make it possible to describe the genetic diversity of the entire collection and to compare the data with enzymatic electrophoresis data obtained elsewhere.

Apart from these purely descriptive studies conducted in India, various analyses have been done. They have resulted in classifications, notably for the cultivated forms, that are consistent with the classification of cultivars into large regional groups established from observations during various expeditions (Clément, 1985). Portéres (1950, 1976) recognized 16 species distributed in four groups on the basis of their geographic distribution: far West Africa group, West and Central Africa group, Nile-Sudan group, and

East Africa and Angola group. For francophone West Africa, Bono (1973) constituted two groups essentially on the basis of characters of false ears: group I, divided into two subgroups (the forms found in Mali, Côte d'Ivoire, and Mauritania, and some forms of Niger, on the one hand, and the forms found in Burkina Faso, on the other), and group II, also divided into two subgroups (pearl millets of Niger and of Senegal). On the basis of grain shape, Brunken et al. (1977) defined four races: *typhoides*, *nigritarum*, *globosum*, and *leonis*. The notations made on the length of the cycle as well as on about 10 characters of the ears and grain for some 1500 ears collected in Mali and Senegal have indicated a regional differentiation in each of these countries (Marchais, 1982).

Marchais et al. (1993) studied 267 accessions of cultivated pearl millet and 118 wild pearl millet using 14 morphological characters. The results obtained (Fig. 1) show a marked distinction between cultivated and wild pearl millets on the basis of just a few characters: length of ears, density of ears, length of pedicel of the involucre, grain size, stem diameter, tiller number, and leaf width.

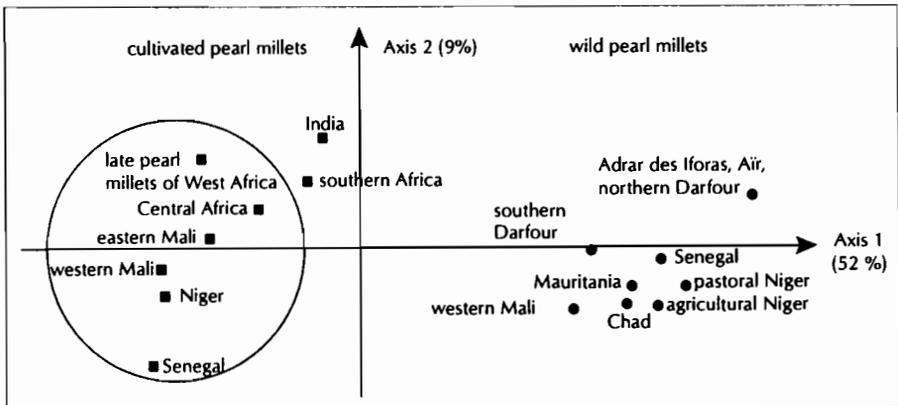


Fig. 1. Position of means of major morphological families of pearl millet on the 1-2 plane of a principal components analysis of 14 botanical characters with high heritability (Marchais et al., 1993). The pearl millets cultivated in West Africa in the wider sense are circled.

Within the cultivated pearl millets, there are five groups for West Africa, one for Central Africa, one for India, and one for southern Africa, the two last being more homogeneous. Discrimination among the wild pearl millets is less marked because of their greater morphological homogeneity.

Phenological Diversity of Cultivated Pearl Millets

Data on the flowering phenology of more than 12,000 cultivars obtained by ICRISAT (Marchais et al., personal communication) indicated two phenomena

that concur with the triggering of flowering in pearl millet: the need for a minimum number of degree-days and sensitivity to day length. Figure 2 compiles the results observed for two cultivation cycles, one completed in long days and the other in short days. It was observed that, for each of the regions studied, there is a range of varieties that, during long days, flower between 45 and 140 days. This diversity can be imputed to differences in the duration of the rainy season in each region.

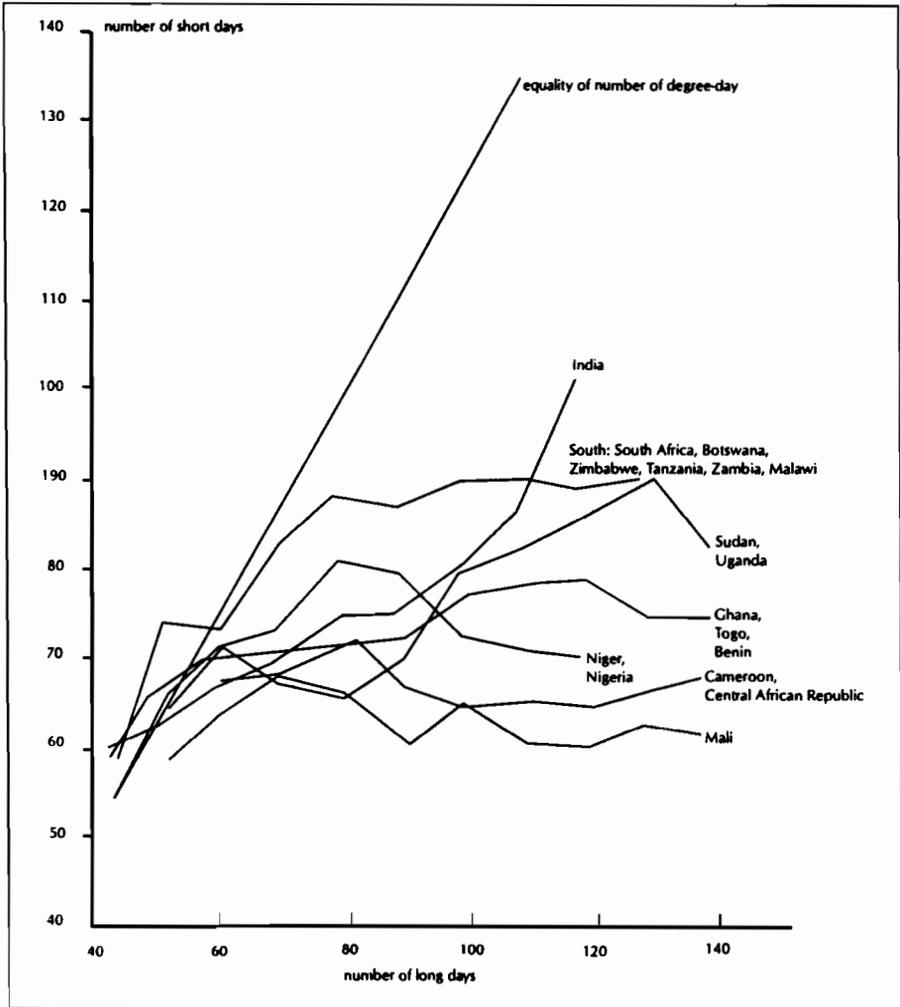


Fig. 2. Comparative evolution of flowering in long and short days according to the geographic origin of the pearl millets observed (Marchais et al., personal communication).

On the other hand, during short days, the cycles do not go beyond 90 days, except for cultivars of southern India. The cultivars that flower between 40 and 60 days for a long-day cultivation flower during a period that is equivalent in number of degree-days when cultivated during short days. These cultivars can thus be considered heat-sensitive, but not photosensitive. In cultivars that flower beyond 60 days for a long-day cultivation, behaviour during short days varies according to the region.

Overall, there are three possible behaviours. The first pertains to cultivars of the South group: up to about 80 days, the increase in the cycle of long days is accompanied by an increase in the cycle of short days, then the length of the cycle of short days does not increase further, which could be explained by a maximal thermoperiodic demand with the appearance of photosensitivity. The second is represented by cultivars of West Africa: the traditional early pearl millets that flower in less than 80 days and can be called thermoperiodic (but with a lower demand in degree-days than pearl millets of the South group) are distinguished from the traditional late pearl millets that flower after 80 days, which can be called photosensitive and have a minimal thermoperiodic demand. The third behaviour pertains to the Indian varieties, which represent an intermediate situation, in which the elongation of the long-day cycle is accompanied by an elongation of the short-day cycle, in a continuous fashion. There is a north-south gradient here, the longer cycles characterizing the cultivars of southern India. In this situation, it is difficult to talk of photosensitive and non-photosensitive pearl millets.

The other groups shown in the figure are more or less close to one of the major groups that we have just described.

Overall, in this phenological analysis of flowering of cultivated pearl millets, we find groups close to those that have been observed with other descriptors of diversity. The distinction between early and late pearl millets is obvious only in West Africa. The most characteristic are very early and non-photosensitive cultivars from Ghana, Togo, and Benin, the photosensitive and long-cycle pearl millets of Mali, and the peculiar pearl millets of Sierra Leone that have a very long cycle.

Biochemical and Molecular Variability

Most of the results on enzymatic polymorphism of pearl millets come from the studies of Tostain (1994) on 549 accessions, of which 361 were cultivated pearl millets and 188 were wild pearl millets. For the eight enzymatic systems studied, 12 loci proved polymorphic, for a total of 46 alleles, or an average of 3.8 alleles per locus.

The results obtained show that, in their zone of origin, wild and cultivated pearl millet cannot be differentiated at the loci studied by alleles that would be fixed in one group and absent from the other. The two groups differ only by the allelic frequencies at these loci.

The analyses done on the wild pearl millets indicate five groups, which correspond to well-defined geographic entities. The 'west' group (I) comprises the populations of Senegal, Mauritania, and western Mali; the 'centre' group (II) corresponds to the populations of Adrar des Iforas and from Gourma to Mali, Oudalan in Burkina Faso, the Azawak and Ader Douthi valleys to Niger; the 'Air' group (III) is made up of the population from the Air massif to Niger; the 'Chad-west' group (IV) comprises the populations located south of Lake Chad; and the 'Darfour' group (V) comprises populations east of Lake Chad and from Darfour to Sudan.

For the cultivated pearl millets, various partial enzymatic analyses have led the author to distribute the set of samples into seven groups, on a geographical as well as physiological basis (length of cycle): group A (early pearl millets presently found in Senegal and western Niger), group B (early pearl millets of western Mali), group C (early pearl millets found from Niger to Sudan), group D (early pearl millets of Togo and Ghana), group E (late pearl millets of West Africa), group F (early and late pearl millets of East Africa and southern Africa), and group G (early and late pearl millets of India). The multivariate analyses on the whole do not confirm the entire classification, since certain groups, notably A, C, and E, partly overlap. Discriminant analysis gives 72% to 76% individuals well classified for these three groups, against 83% to 94% for the other groups.

A global analysis was done on 188 samples of the wild form from the entire area of distribution and 123 samples of the cultivated form belonging to four groups A, B, C, and D. It shows, for the wild pearl millets, a genetic diversity comparable to that of cultivated pearl millets: the Nei index of diversity is equal to 0.249 for the wild pearl millets and 0.256 for the cultivated pearl millets. On the other hand, the structuration of wild pearl millets is weaker than that of cultivated pearl millets ($G_{ST} = 0.13$ against 0.17). It is the cultivated pearl millets of groups A and B (early cultivars of West Africa) that are the closest to the wild pearl millets (Fig. 3a), while the pearl millets of group C (early forms found from Niger to Sudan) are in a less central position. In sum, two major sets can be distinguished: the first contains the wild and cultivated forms of groups A, B, and D; the second contains the rest of the cultivated pearl millets (late pearl millets of West Africa, pearl millets of East and southern Africa, pearl millets of India). A peculiar case is the Tiotande variety, originating in Senegal and cultivated in the off season, which stands apart from the rest (Fig. 3b).

Samples that represent only a limited part of the genetic diversity of wild and cultivated pearl millets were analysed using other molecular descriptors of polymorphism (sequencing, RFLP, RAPD). The comparison of some samples of pearl millet by RFLP showed that chloroplast DNA probe is very poorly polymorphic and that ribosomal DNA is polymorphic only in wild pearl millet (Gepts and Clegg, 1989). An RFLP analysis on the *ADH-1* region indicates genetic variability within and between populations as well

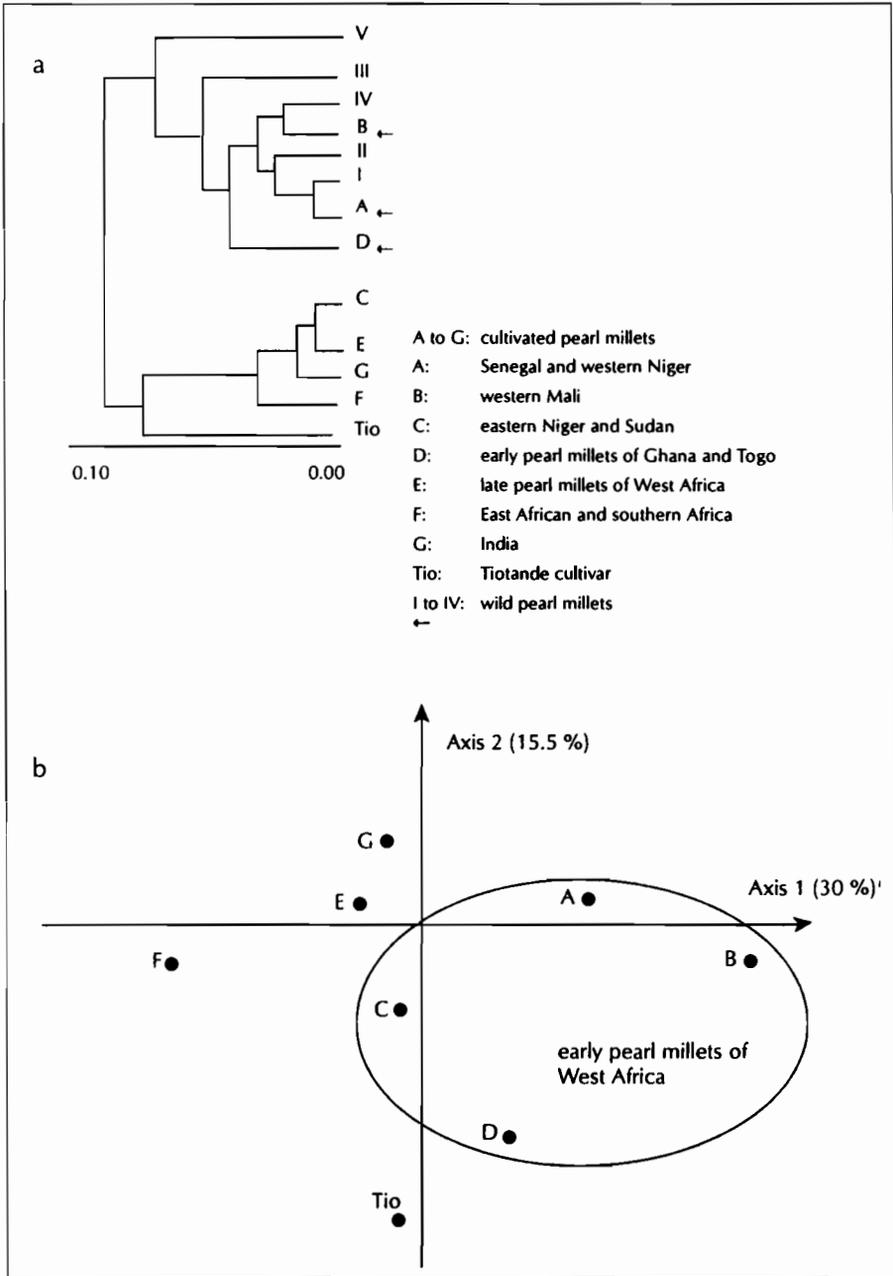


Fig. 3. (a) Dendrogram of Nei distances between groups of cultivated and wild pearl millets (Tostain, 1998). (b) Principal components analysis of 361 accessions of cultivated pearl millet. Only the projections from the centres of gravity of 7 groups of cultivated pearl millets and the Tiotande cultivar are represented (Tostain, 1998).

as the specificity of certain restriction profiles of wild forms (Pilate-Andre et al., 1993). The sequencing of alleles of the *ADH-1* gene of these samples showed no significant difference between wild and cultivated pearl millet (Gaut and Clegg, 1993). Tostain (1996) studied the diversity of 14 populations of pearl millet (4 wild, 9 cultivated, and 1 accession of Tanzania that is intermediate between wild and cultivated forms) using RAPD markers. The results confirm overall the classifications obtained with enzymatic markers but, there also, the RAPD markers reveal a very low diversity within populations and do not enable a clear separation between wild and cultivated forms. All the results obtained using different descriptors of polymorphism, whether biochemical (isozymes) or molecular (RFLP, RAPD sequencing), are consistent in terms of difficulties in differentiating the wild and cultivated pearl millet.

Relationships between Levels of Variability

Classification of wild and cultivated pearl millets obtained from data of enzymatic polymorphism was similar to classifications established on the basis of morphological characters. A good correspondence was observed with the classification of Marchais et al. (1993).

In the particular case of Niger pearl millets, a comparative analysis was done on a sample of 21 cultivars representative of the cultivated pearl millets in Niger using 12 quantitative characters and 3 qualitative characters (Siaka et al., 1996). The results (Fig. 4a) show a structuration of the diversity into three groups: cultivars of group 1 originate in the desert zone, cultivars of group 2 are cultivated in the eastern part of countries between longitudes 8°E and 13°E, and cultivars of group 3 are cultivated in the western part of countries between longitudes 1°E and 8°E. This structuration corresponds to three groups (Fig. 4b) indicated by Tostain (1994) on the basis of enzymatic polymorphism: late pearl millets (group 1), early pearl millets with short ears (group 2), and early pearl millets with long ears (group 3).

Other criteria have also been used to describe the diversity of pearl millets. L. Marchais (personal communication) tested close to 200 cultivars for their capacity to restore male fertility on the male-sterile cytoplasm described by Marchais and Pernes (1985). The results indicate a geographic differentiation: the pearl millets of India and southern Africa constitute two homogeneous groups, which have a very low rate of restoration, while in West Africa early pearl millets, which show a high variability for restorative ability, are distinguished from late pearl millets, which for the most part maintain sterility.

The results taken together—morphological, phenological, biochemical, and cytoplasmic data—tend to confirm the information collected by the researchers with respect to the geographic differentiation of pearl millets. This differentiation results first in natural selection and adaptation of wild pearl millets and cultivars to various environments and, second, in

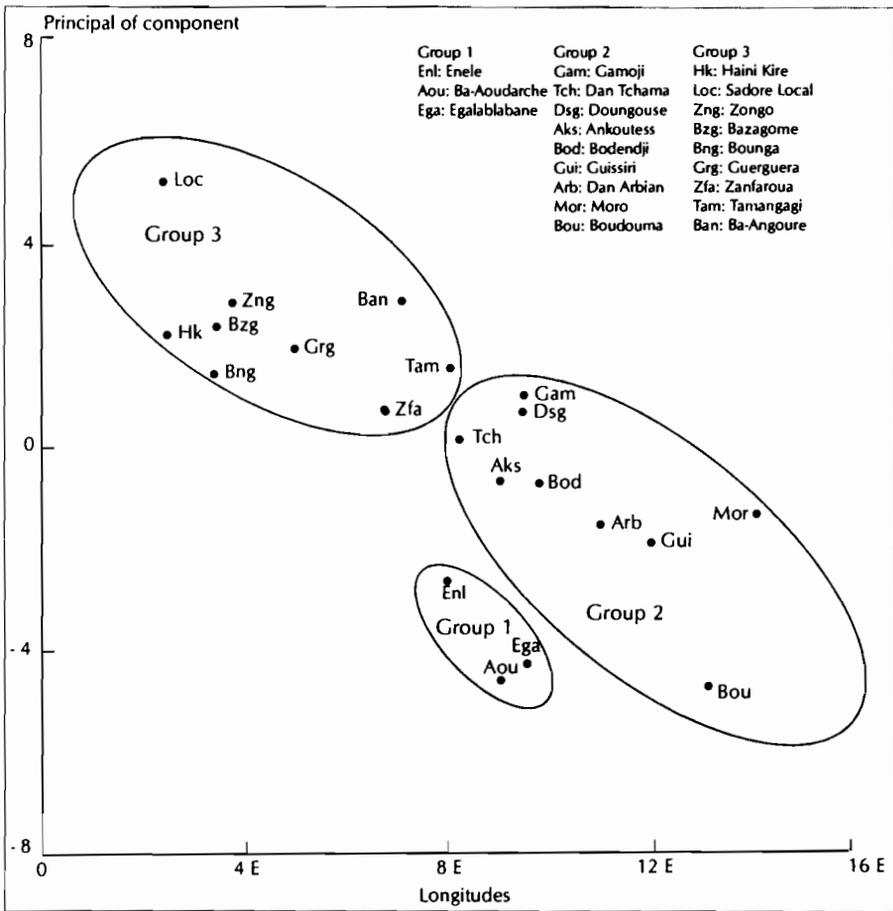


Fig. 4a. Projection according to longitude and the primary axis of the principal components analysis of 21 local cultivars of Niger (Siaka et al., 1996)

domestication, a process in which the role of the farmer is critical. This geographic structuration of the diversity of wild and cultivated pearl millets must thus be taken into account on a priority basis in the elaboration of new methods of conservation, management, and commercialization of genetic resources.

The origin of pearl millet domestication can be more precisely defined only through new information gained from supplementary studies based on descriptors of genetic polymorphism that are less sensitive than isozymes to the actual gene flows, such as chloroplast DNA. Moreover, it would be desirable to extend the sample to the entire area of distribution of wild pearl millet, up to Sudan and Ethiopia. This region is extremely important for understanding the domestication of pearl millet. It corresponds to the centre of origin of cowpea and sorghum, which, like pearl millet, are also cultivated

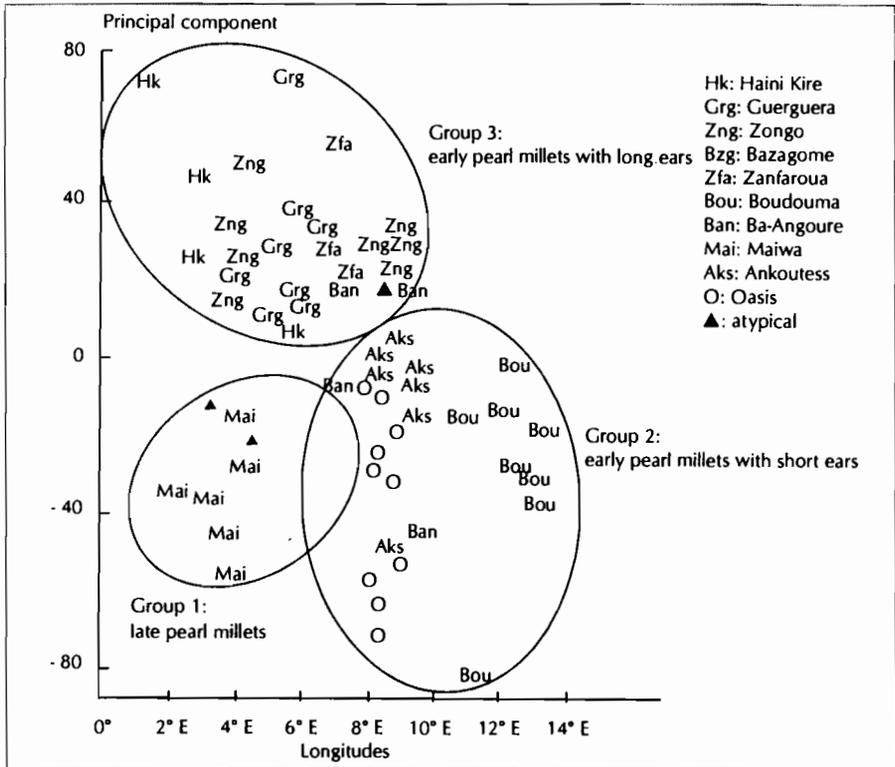


Fig. 4b. Projection according to longitude and the primary axis of the principal components analysis of 66 accessions of Niger (Tostain, 1994).

in India, unlike species such as rice *Oryza glaberrima* and yams of the *Dioscorea cayenensis*-*D. rotundata*, which were domesticated in West Africa.

DOMESTICATION AND MANAGEMENT OF GENETIC RESOURCES

The geographic distribution of wild pearl millet, limited to Sahelian Africa, suggests that it was domesticated here to give us the cereal we know today. The oldest vestiges of cultivated pearl millet in contact with wild pearl millet were found in Mauritania and are more than 3000 years old (Amblard and Pernes, 1989), while imprints of wild pearl millet were discovered on pottery dating around 5000 years ago in the centre of the Sudan (Stemler, 1990). Various genetic analyses have shown that the phenomenon of domestication depends on a small number of linked genes—length of pedicel and involucre, senility of ear at maturity, size of seed envelope, and presence or absence of hairs—the recessive alleles of which enable the expression of the cultivated phenotype (Pernes et al., 1984), which could explain a rapid domestication.

In pearl millet, an allogamous species, there are gene flows between cultivated and wild forms, which are more or less controlled by barriers to reproduction before and after the zygote stage. They give rise to viable hybrid forms that the farmer must eliminate during domestication to maintain the cultivated phenotype, as is done even today. But such selection remains flexible, and the hybrids can be harvested if needed. These constant exchanges blur the traces of a possible genetic structuration arising directly from domestication. In these conditions, the calculations of genetic distance from enzymatic polymorphism data are difficult to use to locate the centre of domestication of the cultivated form. The differences in genetic distance could reflect mainly variations in the efficacy of barriers to reproduction between wild and cultivated forms. The hypothesis of domestication accompanied by reinforcement of these barriers to gene exchanges between the ancestral and cultivated forms can not be ruled out and thus goes against the association of a centre of domestication with the shortest genetic distance between populations of the present wild form and those of the cultivated form (Bezancon et al., 1997). This is why, rather than look for a centre of domestication of pearl millet in a region delimited by Mauritania, Senegal, and western Mali (Tostain, 1992), it is preferable to conserve the idea of a non-centre in the sense of Harlan (1971). The domestication of pearl millet, associated with migratory phenomena, could have occurred in different geographic zones, simultaneously or in different eras, each agrarian civilization selecting a specific morphotype particularly well adapted to the local conditions—climate, soil, and cultivation practices. Long-distance migrations, on the continental scale in southern Africa and on the intercontinental scale in India, led to the constitution of groups more homogeneous and well-differentiated from the original forms.

At ICRISAT, several techniques have been recommended to maintain the diversity of the world collection. The technique of intercrosses between a defined number of plants (100) of the same cultivar (Appa-Rao, 1980) presents constraints related to the mechanisms needed to isolate breeding fields. These problems can be overcome by making controlled crosses with pollen mixtures, which increases the work involved. The technique of self-fertilization (Burton, 1983) saves time and labour. Self-fertilization is done on plants that serve to characterize the cultivars and enables conservation of dominant and recessive genes that are used to classify the cultivars. In this case, however, the plants produced are smaller and less vigorous and produce smaller and fewer grains. The technique of pools favours gene exchanges and can be used to increase adaptability. It relies on the constitution of pools from a mixture of grains from closely related cultivars—those from the same region or those having identical characteristics—the mixture being cultivated in conditions of isolation.

The technique of intercrosses and that of pools seem particularly suitable for pearl millet. In contrast, the technique of self-fertilization has major disadvantages, particularly problems of genetic drift.

The objective of ICRISAT is to produce enough grains for evaluation, selection, exchange, and conservation. There are two ways of conserving grains: long-term conservation (temperature -18°C and 5% relative humidity) designed for basic collections and medium-term conservation (temperature $+5^{\circ}\text{C}$ and 20% relative humidity) in collections for evaluation, multiplication, and distribution. It is clear that such methods applied to pearl millet collections are costly and labour-intensive.

The structuration of the genetic diversity of pearl millets, such as it has been indicated, serves as a basis for other projects of genetic resource conservation. In this context, the constitution of core collections is advisable.

Usually, to constitute a core collection, after stratification on the basis of taxonomic, geographic, sometimes morphological, enzymatic, or agronomic data, it is recommended that a sampling of 10% of the initial collection be drawn by random selection in each group of a number of samples proportionate to the logarithm of the group size (Brown, 1989). In cases where intragroup data are available, Marchais (1996), in the framework of a study on relative parental contributions that maximize the average value of certain characters such as grain yield for creation of a synthetic variety, proposed a method that enables the exact—rather than random—identification of samples that will constitute the core collection as well as their proportions. Such selection is done by maximizing the total Nei diversity (1973) of weighted bulk.

The algorithm follows the rationale used in population genetics for panmictic populations over several generations, with a constant selective value (Crow and Kimura, 1970). It establishes a relationship between allelic frequencies to generations n and $n + 1$ and the selective value of different genotypes. The method has been applied to a collection of 95 samples of wild pearl millet collected in Niger, which were described for 8 enzymatic systems—12 loci and 46 alleles—by Tostain (1992). This set presents a relatively homogeneous enzymatic diversity in relation to other geographic groups. A state of equilibrium was reached after 700 iterations and the results showed that the Nei diversity for the entire collection is equal to 3.58 in cases where all the samples are represented in equal proportions, while it is 6.48 after application of the algorithm. This level of diversity is obtained with only eight accessions.

The method has thus proved highly effective in increasing diversity while eliminating redundancies in this group of wild pearl millets of Niger. The same procedure could be applied to the average of allelic frequencies of each of the groups, in order to maximize the diversity of a core collection for the entire collection. Finally, this procedure of creating core collections can be used for qualitative as well as for quantitative characters, the latter being divided into classes.

The main objection that has been raised against the method is that, in most cases, the accessions are not sufficiently analysed before the constitution

of a core collection. The procedure could thus be put into place on samples taken randomly according to the principles of Brown (1989), after the samples are analysed.

The application of this methodology to the world collection of pearl millet described on the basis of enzymatic and molecular markers would enable us to uncover the numerous redundancies, notably among the cultivars, while increasing the overall level of diversity.

On the regional scale, perfection of a methodology of *in situ* conservation, associated with management and participatory improvement of genetic resources of pearl millet would also be a solution. The IRD presently conducts research of this type in the southwestern region of Niger. The dynamic aspect of *in situ* conservation contrasts with all the other methodologies, which enable the conservation of rigid structures. Here, the evolution of traditional cultivars is not prevented: the gene flows with the wild forms, if they are present, continue, exchanges continue to occur between traditional cultivars (exchanges between farmers, migrations) and with genetically improved cultivars sometimes provided by agricultural research institutes. The overall diversity evolves under the influence of environmental factors, physical and human, and closely approaches the method used by farmers to maintain their traditional cultivars. The knowledge and control of the mechanisms that govern these different factors could enable better management of genetic resources.

APPENDIX

Agromorphological Studies

The latest evaluations of cultivated pearl millets were done on 1938 samples originating from 33 countries observed for 20 descriptors during the first round, and then on 2458 samples originating from 38 countries observed for 18 descriptors during the second round (NBPGR and ICRISAT, 1993).

The study of Marchais et al. (1993) was done on 267 cultivated plants and 118 wild plants from samples representative of the whole collection. They were grown in Niger during the rainy season (planted 25 June). Each sample was represented by a line of 10 plants. The notations were done on 14 morphological characters: 12 quantitative characters (height of main stem, length and width of third leaf below the ear of the main stem, length of ear on the main stem, diameter of rachis of the ear of the main stem, length of the pedicel of the involucre, length of hairs on the involucre, length of internodes, length of glumules of hairs on the involucre, number of ears per involucre, length and width of grain) and two qualitative characters (pilosity of foliar limb and vitreousness of albumen).

Phenological Analyses

More than 12,000 cultivars were evaluated on their flowering (time from seed to flowering) in two conditions of cultivation: rainy season (planted 25 June, long days) and off season (planted 25 November, short days). Each sample was cultivated on a line of 4 m (around 20 plants) and the flowering was noted when 50% of the plants had produced an ear in female flowering (L. Marchais et al., personal communication). This experiment was done at the ICRISAT station in Patancheru, India.

Biochemical and Molecular Analyses

In total, 549 samples were analysed: 361 represented cultivated forms originating from 29 African countries and India and 188 were collected in 8 sub-Saharan African countries, representing populations of the wild form in almost its entire area of geographic distribution. Eight enzymatic systems were used: ADH, CAT, EST, GOT, MDH, PGD, PGI, and PGM (Tostain, 1994).

Data Analysis

The methods of statistical analysis used were principal components analysis and discriminant analysis, done with Stat-ITCF software. Parameters of biochemical polymorphism were calculated using Biosys 1-7 software. Different genetic distances were also calculated: Rogers, Cavalli-Sforza, Wright.

REFERENCES

- Amblard, S. and Pernes, J. 1989. The identification of cultivated pearl millet (*Pennisetum*) amongst plant impressions on pottery from Oued Chebbi (Dhar Oualata, Mauritania). *African Archeological Review*, 7: 117-126.
- Appa-Rao, S. 1980. Progress and problems of pearl millet germplasm maintenance. In: *Trends in Genetical Research on Pennisetum*. V.P. Gupta and J.L. Minocha, eds., Ludhiana, India, Punjab Agricultural University, pp. 279-282.
- Bezançon, G., Renno, J.F., and Anand Kumar, K. 1997. Le mil. In: *L'Amélioration des Plantes Tropicales*. A. Charrier et al., eds., Montpellier, France, CIRAD-Orstom, collection Repères, pp. 457-482.
- Bono, M. 1973. Contribution à la morphosystématique des *Pennisetum* annuels cultivés pour leur grain en Afrique occidentale francophone. *L'Agronomie Tropicale*, 28(3): 229-356.
- Brown, A.H.D. 1989. Core collections: a practical approach to genetic resources management. *Genome*, 31: 818-824.
- Brunken, J.N. de Wet, J.M.J., and Harlan, J.R. 1977. The morphology and domestication of pearl millet. *Economic Botany*, 31: 163-174.
- Burton, G.W. 1983. Breeding pearl millet. In: *Plant Breeding Reviews*, vol. 1, J. Janik, ed., Westport, USA, AVI Publishing, pp. 162-182.
- Clement, J.C. 1985. Les mils pénicillaires de l'Afrique de l'Ouest: prospections et collectes. Rome, IBPGR, 231 p.
- Crow, J.F. and Kimura, M. 1970. *An Introduction to Population Genetics Theory*. New York, Harper and Row, 591 p.
- FAO, 1996. *Annuaire Production: 1995*. Rome, FAO.
- Gaut, B.S. and Clegg, M.T. 1993. Nucleotide polymorphism in the ADH-1 locus of pearl millet (*Pennisetum glaucum*, Poaceae). *Genetics*, 135(4): 1091-1097.
- Gepts, P. and Clegg, M.T. 1989. Genetic diversity in pearl millet, *Pennisetum glaucum* (L.) R. Br., at the DNA sequence level. *Journal of Heredity*, 80: 203-208.
- Hanna, W.W. 1987. Utilization of wild relatives of pearl millet. In: *International Pearl Millet Workshop*. J.R., Witcombe ed., Patancheru, India, ICRISAT, pp. 33-42.
- Hanna, W.W. 1990. Transfer of germplasm from the secondary to the primary gene pool in *Pennisetum*. *Theoretical and Applied Genetics*, 80: 303-308.
- Harlan, J.R. 1971. Agricultural origins: centers and non-centers. *Science*, 14: 468-474.

- Harlan, J.R. and de Wet, J.M.J. 1971. Toward a rational classification of cultivated plants. *Taxon*, 20(4): 509-517.
- Marchais, L. 1982. La diversité phénotypique des mils pénicillaires cultivés au Sénégal et au Mali. *L'Agronomie Tropicale*, 37: 68-80.
- Marchais, L. 1996. Parental proportion maximizing the mean value of a parameter in a panmictic population can be useful in plant breeding. *Agronomie*, 16: 257-264.
- Marchais, L. and Pernes, J. 1985. Genetic divergence between wild and cultivated pearl millets (*Pennisetum typhoides*). 1. Male sterility. *Zeitschrift für Pflanzenzüchtung*, 95: 103-112.
- Marchais, L., Tostain, S., and Amoukou, I. 1993. Signification taxonomique et évolutive de la structure génétique des mils pénicillaires. In: *Le Mil en Afrique*. S. Hamon, ed., Paris, Orstom, Colloques et séminaires, pp. 119-128.
- NBPGR and ICRISAT, 1993. *Evaluation of Pearl Millet Germplasm: part 1 and part 2*.
- Nei, M., 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences of the United States of America*, 70: 3321-3323.
- Pernes, J., Combes, D., and Leblanc, J.M. 1984. Le mil. In: *Gestion des Ressources Génétiques des Plantes*. 1. Monographies, J. Pernes, ed., Paris, ACCT, pp. 159-210.
- Pilate-Andre, S., Lamy, F., and Sarr, A. 1993. Diversité génétique des mils détectable par RFLP au niveau de la région du gène *ADH-1*. In: *Le Mil en Afrique*. S. Hamon, ed., Paris, Orstom, Colloques et séminaires, pp. 67-75.
- Porteres, R. 1950. Vieilles agricultures de l'Afrique intertropicale: centres d'origine et de diversification variétale primaire et berceaux de l'agriculture antérieurs au XVI^e siècle. *L'Agronomie Tropicale*, 5(9-10): 489-507.
- Porteres, R. 1976. African cereals: *Eleusine*, fonio, black fonio, teff, *Brachiaria*, *Paspalum*, *Pennisetum* and African rice. In: *Origins of African Plant Domestication*. J.R. Harlan et al. eds., The Hague, Mouton, pp. 409-452.
- Siaka, S., Ouendeba, B., and Anand Kumar, K. 1996. Caractérisation des cultivars locaux du Niger. In: *Premières Journées Biologiques et Agronomiques du Niger*, 20-25 sept. 1996.
- Stemler, A. 1990. A scanning electron microscopic analysis of plant impressions in pottery from the sites of Kadero, El Zakiab, Um Direiwa and El Kadada. *Archéologie du Nil Moyen*, 4: 87-105.
- Tostain S. 1992. Enzyme diversity in pearl millet (*Pennisetum glaucum* L.). 3. Wild millet. *Theoretical and Applied Genetics*, 83: 733-742.

- Tostain, S. 1994. Evaluation de la diversité génétique des mils pénicillaires diploïdes, *Pennisetum glaucum* (L.) R. Br., au moyen de marqueurs enzymatiques: étude des relations entre formes sauvages et cultivées. Paris, Orstom, Travaux et documents microédites no. 124, 331 p.
- Tostain, S. 1996. Genetic diversity of pearl millet (*Pennisetum glaucum*) estimated by random amplified DNA markers and compared with isoenzymatic diversity. In: *Réunion sur les Plantes Tropicales*. Montpellier, France, EUCARPIA-CIRAD, p. 255.
- Tostain, S. 1998. Le mil, une longue histoire: hypothèses sur sa domestication et ses migrations. In: *Plantes et Paysages d'Afrique: une Histoire à Explorer*. M. Chastanet, eds., Paris, Karthala-CRA, pp. 461-490.
- van der Zon, A.P.M. 1992. *Graminées du Cameroun, 2. Flore*. Wageningen, Netherlands, Agricultural University, Papers no. 92-1, 557 p.

Bezançon Gilles.

Pearl millet.

In : Hamon P. (ed.), Seguin M. (ed.), Perrier X. (ed.),
Glaszmann J.C. (ed.). Genetic diversity of cultivated
tropical plants. Montpellier (FRA), Enfield : CIRAD,
Science Publ., 2003, p. 259-276.

(Repères). ISSN 1251-7224