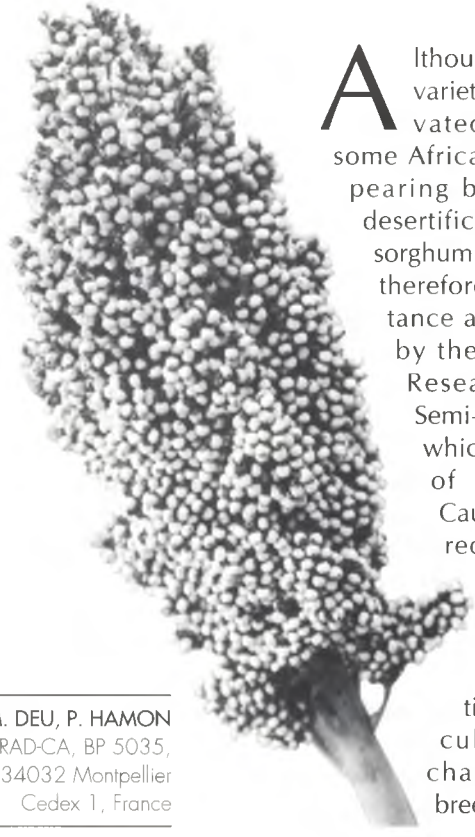
The genetic organization of sorghum

Hooked panicle of *durra* sorghum. Photo J. Chantereau

Today, collection, conservation and study of traditionally cropped sorghum varieties and related wild forms are of great importance. Cultivated sorghum diversity must be upheld. Local varieties and their wild progenitors represent a critical sorghum gene pool for breeding programmes.



Panicle of *caudatum* sorghum. Photo J. Chantereau

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Although traditional sorghum varieties are still widely cultivated in Africa and Asia, some African cultivars are disappearing because of increased desertification. Conservation of sorghum germplasm resources is therefore of paramount importance and currently overseen by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), which now has a repository of 30 000 accessions. Caution and skill are required in the maintenance, evaluation and use of these germplasm resources because of the size of the collection. Moreover, it is difficult to know now what characters will interest breeders in the future.

At the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), genetic diversity in sorghum is thus being analysed according to morphological traits, biochemical and molecular markers.

Sorghum taxonomy

The *Sorghum* genus belongs to the Poaceae (ex-Gramineae) family. High morphological variation has prompted botanists to increase the classification divisions within this genus — 712 cultivated sorghum taxa according to Snowden (1936). A simplified classification, first introduced by De Wet (1978) and slightly modified by Acheampong *et al.* (1984), is now in common use and recommended by the *International Plant Genetic Resources Institute* (IPGRI). *Sorghum* is thus classified in five botanical sections, but only the *Sorghum* section is presented here (Fig. 1).

The *Sorghum* section includes many species and two are diploid: *S. propinquum* (perennial) and *S. bicolor* (annual). These two species cross-pollinate but are completely geographically isolated.

S. bicolor is divided into three subspecies: ssp. *bicolor* (cultivated sorghum), ssp. *arundinaceum* (their wild relatives), and ssp. *drumondii* (weedy forms, obtained by hybridation of wild and cultivated forms).

Wild *S. bicolor* sorghum

Morphological and ecological diversity is high in wild sorghum of ssp. *arundinaceum*. They have been divided into four races[1] or ecotypes based on their inflorescence structure and geographic distribution (De Wet, 1978), i.e. aethiopicum, arundinaceum, verticilliflorum and virgatum, which only occur in Africa (Fig. 2a).

The aethiopicum race is widespread in the hottest and driest regions of the African savanna, from Mauritania to Sudan. The inflorescences are small and rather contracted.

The arundinaceum race is mainly limited to rain forest regions of western Africa, but populations have been found as far as southern Africa. The inflorescences are large and pendulous at maturity.

The verticilliflorum race is the most widespread and is commonly found in African savanna regions. The inflorescences are characteristically large and opened.

The virgatum race is present in northeastern Africa, along irrigation ditches and rivers (particularly the Nile Valley). It is quite close to the verticilliflorum race, but its inflorescence ramifications are more erect.

All of these wild sorghum races can readily cross even with cultivated forms. Fertile hybrids are commonly encountered in areas where two races occur together.

S. bicolor cultivated sorghum

Cultivated sorghum forms are monoecious, preferentially self-pollinating, with great phenotypic diversity. A simplified classification

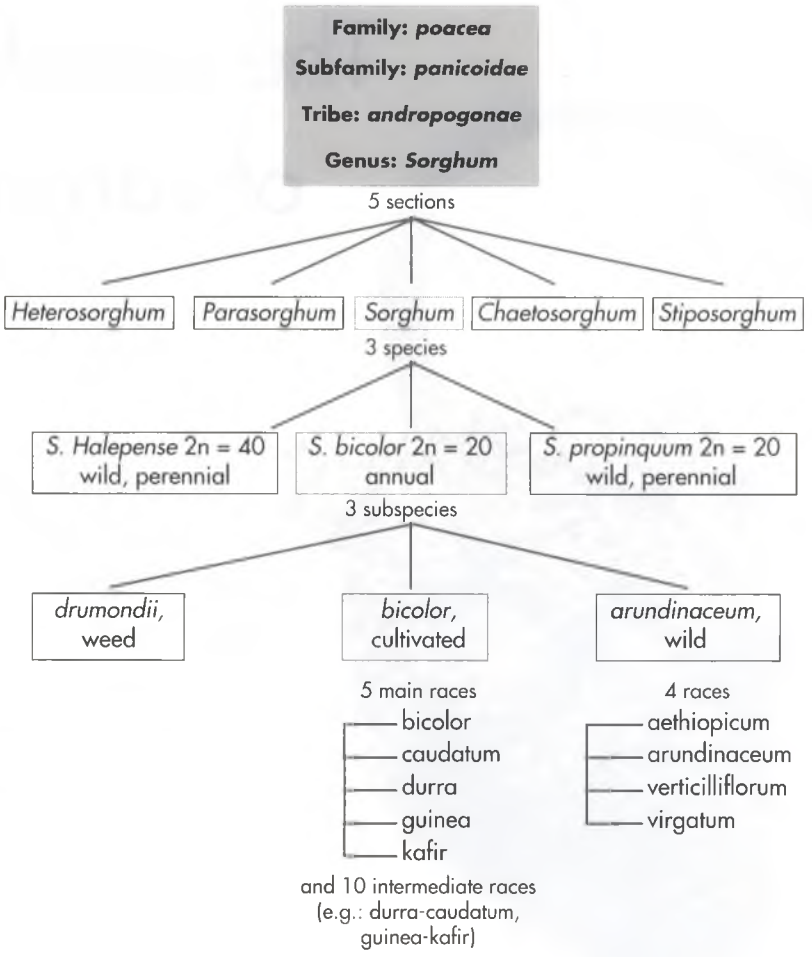


Figure 1. Taxonomy of the *Sorghum* genus.

was proposed by Harlan and De Wet (1972) according to morphological criteria (spikelet structure, panicle shape, since spikelet traits are considered to be highly stable and thus relatively unaffected by environmental stresses). Five basic races and ten intermediate races (representing crosses of the basic forms) have been defined. The ranges of these races overlap, although some races are more predominant in certain regions (Fig. 2b).

The bicolor race, the most primitive, is cropped throughout Africa and widely distributed in Asia. The grains are small, long and sheathed in a sticky glume; the panicles are loosely branched. These traits are close to those that characterize wild sorghum races.

The caudatum race is limited to central and eastern Africa. The grains are asymmetrical (turtle shell shaped). There is a variety of panicle shapes.

1. A race is defined as a set of varieties with common morphological traits and ecological adaptations. It forms a biological/genetic unit (Harlan & De Wet, 1971).

The durra race is the main cultivated sorghum race in India, and is also found in eastern Africa. It is well adapted to drought conditions. The grains are large and globular; the panicles are compact and often borne on a hooked stalk.

The kafir race, probably a recent sorghum race, is mainly distributed in southern Africa where farming was introduced later. The grains are symmetrical; the dense panicles are cylindrical shaped.

The guinea race is common in western Africa but is also found in southern Africa. This sorghum race is adapted to wet zones. The grains are symmetrical, with a rotation between glumes at ripeness; the panicles are loosely branched. There is high morphological variability in this race. Different classifications have been proposed based on grain size and the glume/grain ratio. Three or four subraces, including margaritiferum (small vitreous grains) have now been distinguished.

The economic and nutritional importance of cultivated sorghum

Sorghum is the fifth-ranking cereal in the world, based on grain production and surface area cropped. It is quite far behind the top-ranking cereal crops (wheat, rice and maize). In Africa, sorghum is in second position, with about half the output of maize (Chantereau & Nicou, 1991). Worldwide, the mean yield is 1.3 t/ha, but there is a very wide range (3.5 t/ha in USA and 0.7 t/ha in Africa).

In temperate regions, sorghum is currently cropped for animal feed, since syrup, sugar, alcohol and starch production is not cost-effective. In semiarid tropical zones, the whole plant is used by millions of people. The protein-rich grains are processed for human consumption; the stems are used for fuel and as building materials; crop residues (stems and leaves) provide a livestock fodder supplement.

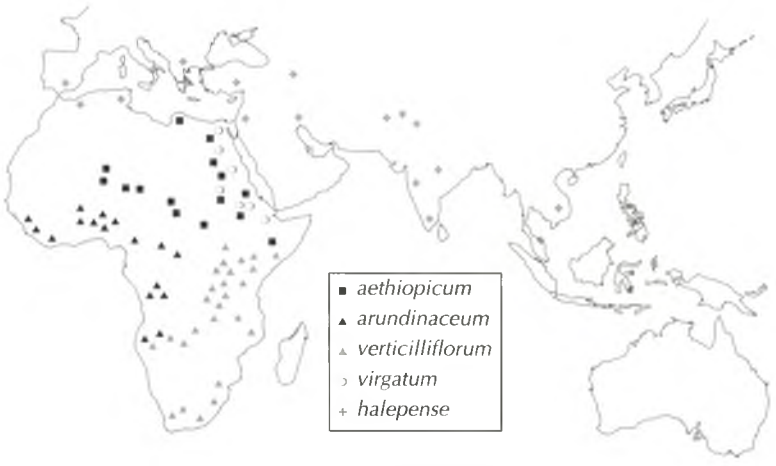


Figure 2a. Distribution of the main sorghum wild types.

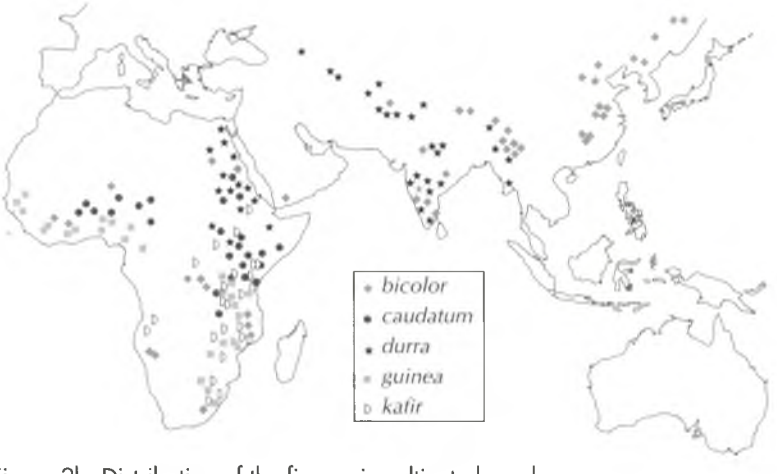


Figure 2b. Distribution of the five main cultivated sorghum races.

The genetic organization of cultivated sorghum

Three types of classification have highlighted this genetic organization.

Morphological classification

A quantitative study of 135 cultivated varieties involving 26 morpho-physiological traits (Chantereau *et al.*, 1989) led to a classification into three groups with different cropping performances:

– durra, hardy and adapted to dry zones;

– guinea and bicolor, hardy and adapted to wet zones;

– caudatum and kafir, high yielding, adapted to intermediate zones.

This organization is in line with the racial classification, but it is not as discriminating.

Enzymatic classification

Isoenzymatic markers do not allow discrimination of the sorghum races defined by Harlan and De Wet (1972).

Ollitrault *et al.* (1989), highlighted a sorghum organization centred around three geographically distinct areas: western Africa, southern Africa and eastern-central Africa.

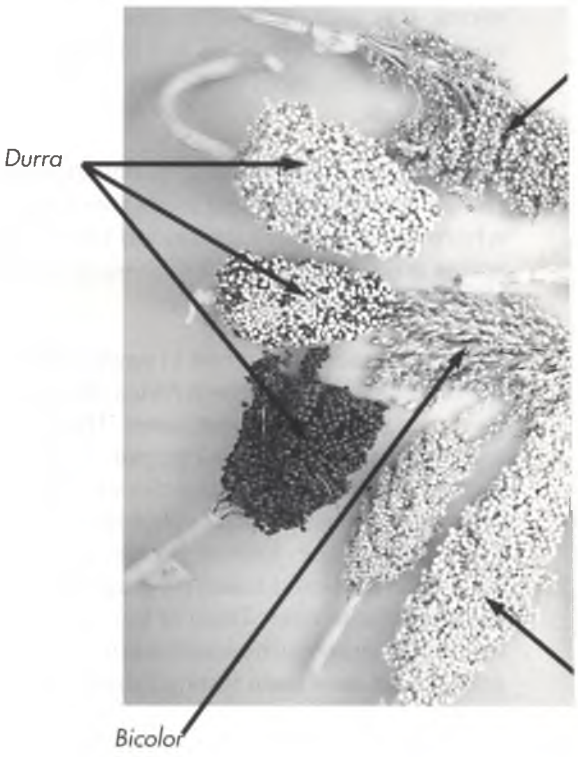
The five cultivated sorghum races: their uses and qualities

Culinary uses of the different sorghum races seem to be dictated by consumers' food habits and particularities of the local varieties.

The bicolor race is highly varied (broomcorn, sweet sorghum and fodder sorghum). Grain sorghum is rarely consumed directly by humans, it is mainly used in beer brewing.

Good quality flours can be produced from the caudatum, durra and kafir races, but this quality depends on the cultivars considered. Generally, white grain sorghum is very highly appreciated by consumers, while coloured grain is only used to produce beer (e.g. some kafir and caudatum forms).

The guinea race is particularly well adapted to wet zones and produces high quality grain that is resistant to mildew and local diseases. The guinea margaritiferum subrace produces an excellent quality grain which is prepared like rice in western Africa (boiled grain). Some guinea gambicum forms are considered tasteless and only used for human consumption at times of sorghum shortages, otherwise they are used in beer brewing. In Mali, couscous made with guinea gambicum is highly appreciated. White grain forms of guinea guineense are ground into flour, while red grain forms are mainly used in beer brewing. Flour made from guinea roxburghii is consumed by poor people in India, elsewhere this sorghum is appreciated as pop-sorghum. In southern Africa, forms of this subrace produce high quality grain for human consumption.



The variation noted in African cultivars typifies that of other sorghum cultivars grown throughout the world. This study confirmed that cultivated sorghum had a monophyletic origin and was domesticated in northeastern Africa. Indeed, domestication of a set of wild-types led to the first primitive sorghum forms, similar to the current bicolor race, then racial differentiation occurred in various geographical areas.

Finally, the results of an in-depth analysis of enzymatic diversity in the guinea race (Degremont, 1992) revealed three separate groups: a western African group, a southern African group and a guinea margaritiferum group.

Molecular classification

The molecular classification of sorghum is based on nuclear and cytoplasmic genome studies (chloroplastic and mitochondrial).

In the first case, DNA diversity was assessed in 100 cultivated sorghum varieties by a restriction fragment length polymorphism (RFLP) technique using heterologous nuclear genome probes. The results revealed racial differentiation in cultivated sorghum (Deu *et al.*, 1994).

Cultivated sorghum can be classified in six groups, excluding the bicolor race which does not form a specific group. The guinea race has been subdivided into three subclusters (western African, southern African, margaritiferum), while the caudatum, kafir and durra races constitute three subclusters groups. Guinea margariteferum seems to be the most differentiated cultivated sorghum race. These overall results are compatible with the monophyletic origin of cultivated sorghum.

Finally, these sorghum varieties and other guinea margaritiferum forms were investigated using chloroplastic and mitochondrial genome probes (Deu, 1993). The results did not reveal any geographic grouping. Most of the cultivated sorghum races were found to have a common mitochondrial background, except for the guinea margaritiferum forms.

Cultivated sorghum diversity: four races and intermediate forms.
Photo J.-L. Noyer

Traditional culinary uses

Dishes using boiled whole grain (China, India, Africa).

- Dishes requiring prior hulling and milling:
  - thick unfermented mash (*tô* in western Africa, *sankati* in India)
  - clear fermented mash
  - couscous (western Africa)
  - cakes and doughnuts
  - leavened bread (*injera* in Ethiopia) and flat bread (*roti* and *chapati* in India).
- Non-alcoholic and alcoholic beverages (homebrewed beer, such as *dolo* in Africa), alcohol (sorghum wine in China).
- Popped grain (*pop-sorghum* in India).
- Chewing sweet sorghum stalks.

The results also confirmed the genetic specificity of guinea margaritiferum and demonstrated the presence of two genetic entities within this sorghum subrace.

Relationships between cultivated sorghum and wild types

Studies on the mitochondrial genome have demonstrated that the genetic diversity observed in cultivated sorghum is encompassed within the related wild types, except for one of the two guinea margaritiferum groups.

Otherwise, there does not seem to be any particular affinity between wild and cultivated sorghum races: the three wild races, aethiopicum, virgatum and verticilliflorum, have mitochondrial genomes that are similar to those of most of the cultivated races, with the exception of both guinea margaritiferum groups. The guinea margaritiferum forms are therefore genetically isolated from the studied wild types, and from other cultivated sorghum races.

Conclusion: breeding applications

The traits and markers used have highlighted various structures and provided fresh data that will help in clarifying the genetic organization of the species *S. bicolor*.

Whereas the cropping performance is the same for all forms in the guinea race, it was found to be markedly differentiated in analyses using biochemical and molecular markers (i.e. three or four groups were distinguished by isoenzymatic and RFLP techniques respectively).

It is quite likely that these sorghum races were domesticated separately in at least two parts of Africa (western and southern). This diversity in the origins of the different races has promoted high between-race genetic variability which has not yet been exploited by breeders.

Studies using molecular markers have revealed very narrow-ranging genetic variability in the kafir race.

Moreover, molecular markers provide an estimate of parental divergence correlated with heterosis (Chantereau, 1993).

The information obtained in these studies can be readily used in the management and conservation of sorghum germplasm resources. A smaller collection with a wide range of variation should be set up and easily accessible to breeders.

The genetic assessment will help in choosing progenitors for breeding programmes (creation of lines or hybrids). Any breeding of the kafir race, for instance, will not lead to any significant genetic progress. Conversely, breeding guinea forms, choosing parents from different groups, will produce genetically interesting combinations, e.g. a western African guinea crossed with a guinea margaritiferum (Degremont, 1992). In wet regions of western Africa, attempts to directly introduce exotic non-guinea material (from USA and India) have failed. Caudatum, durum and kafir sorghum with compact panicles were found to be susceptible to mildew and local diseases. These races produced low quality grain that consumers rated poorly. In wet regions, hardy forms of guinea sorghum should thus be introduced in breeding programmes.

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Abstract... Resumen... Résumé

M. DEU, P. HAMON – **The genetic organization of sorghum.**

The collection, conservation and study of traditional cultivated varieties and related wild forms is of considerable importance today. Morphological, enzymatic and molecular classifications have been drawn up to provide understanding of the organization of cultivated varieties of the species *Sorghum bicolor* and the links with related wild forms. They provide complementary information which is of use in the management and conservation of sorghum germplasm resources and in breeding programmes.

Keywords: sorghum, *Sorghum*, genetic variability, classification, morphology, enzymatic analysis, molecular marker.

M. DEU, P. HAMON – **La organización genética de los sorgos.**

La cosecha, la conservación y el estudio de las variedades cultivadas tradicionales y las formas silvestres emparentadas revisten hoy una gran importancia. Para comprender la organización de los sorgos cultivados de la especie *Sorghum bicolor* y las relaciones con las formas silvestres emparentadas, se han establecido las tres clasificaciones morfológica, enzimática y molecular, que aportan informaciones complementarias que pueden ser utilizadas eficazmente en la gestión y la conservación de los recursos genéticos de los sorgos, así como en los programas de selección.

Palabras clave : sorgo, *Sorghum*, variabilidad genética, clasificación, morfología, análisis enzimótico, marcador molecular.

M. DEU, P. HAMON – **Diversité des sorghos : application à la gestion des ressources génétiques et à la sélection.**

La collecte, la conservation et l'étude des variétés cultivées traditionnelles et des formes sauvages apparentées revêtent aujourd'hui une grande importance. Pour comprendre l'organisation des sorghos cultivés de l'espèce *Sorghum bicolor* et les relations avec les formes sauvages apparentées, les trois classifications morphologique, enzymatique et moléculaire ont été établies. Elles apportent des informations complémentaires pouvant être efficacement utilisées dans la gestion et la conservation des ressources génétiques des sorghos ainsi que dans les programmes de sélection.

Mots-clés : sorgho, *Sorghum*, variabilité génétique, classification, morphologie, analyse enzymatique, marqueur moléculaire.