A global view of genetic diversity in cultivated sorghums using a core collection

M. Deu, F. Rattunde, and J. Chantereau

Abstract: We report here an analysis of the structure of genetic diversity in cultivated sorghums. A core collection of 210 landraces representative of race, latitude of origin, response to day length, and production system was analysed with 74 RFLP probes dispersed throughout the genome. Multivariate analyses showed the specificity of the subrace guinea margaritiferum, as well as the geographical and racial pattern of genetic diversity. Neighbour-joining analysis revealed a clear differentiation between northern and southern equatorial African accessions. The presence of Asian accessions in these 2 major geographical poles for sorghum evolution indicated two introductions of sorghum into Asia. Morphological race also influenced the pattern of sorghum genetic diversity. A single predominant race was identified in 8 of 10 clusters of accessions, i.e., 1 kafir, 1 durra, 4 guinea, and 2 caudatum clusters. Guinea sorghums, with the exception of accessions in the margaritiferum subrace, clustered in 3 geographical groups, i.e., western African, southern African, and Asian guinea clusters; the latter two appeared more closely related. Caudatum were mainly distributed in 2 clusters, the African Great Lakes caudatum cluster and those African caudatum originating from other African regions. This last differentiation appears related to contrasting photoperiod responses. These results aid in the optimization of sampling accessions for introgression in breeding programs.

Key words: sorghum, core collection, genetic diversity, RFLP.

Introduction

Sorghum is a major staple food and fodder crop in tropical and semi-tropical Africa and Asia (Doggett 1988). Cultivated sorghums (Sorghum bicolor subsp. bicolor) exhibit great phenotypic variability. Five major races (bicolor, caudatum, durra, guinea, and kafir) and 10 intermediate races, corresponding to the pairwise combination of major races, are identified according to panicle and spikelet morphology (Harlan and de Wet 1972).

Many studies have examined patterns of genetic diversity among sorghum accessions from ex situ germplasm collections using RFLP or RAPD markers (Aldrich and Doebley 1992; Tao et al. 1993; Deu et al. 1994; Cui et al. 1995; de...
Oliveira et al. 1996; Menkir et al. 1997) and more recently using SSR markers (Djé et al. 2000; Folkertsma et al. 2005). Most studies have indicated that geographic origin and (or) racial classification are associated with the organization of genetic diversity. However, RAPD markers alone failed to separate accessions into discrete racial or geographic groups in a large collection of sorghums (Menkir et al. 1997). This was probably due to different factors, such as the nature of evolutionary mechanisms underlying the variation measured by the different markers, the repetitive sequence revealed by some RAPD markers, the lack of allelism of RAPD bands of similar sizes, and their unequal distribution in the genome (N’Goran et al. 1994; Powell et al. 1996; Noli et al. 1997). Similarly, differentiation among races or geographic origins of sorghums was not revealed by Djé et al. (2000) using a limited number of SSR markers.

Thus, to date, there is no satisfactory assessment of the global structure of diversity of sorghums worldwide and based on a large number of markers. Previous studies were mostly based on relatively small numbers of accessions. Furthermore, sampling was not conducted on large collections appropriately stratified to assure representation of the full genetic diversity of cultivated sorghums worldwide. A useful approach to appropriately sample the diversity of world sorghum collections was recently developed by Grenier et al. (2001a). This approach relies on stratification of the world collection based on both a 2-way matrix of racial classification and latitude of origin and clustering on empirical assessments for photoperiod sensitivity, one of the principal determinants of adaptation. Knowledge of the major sorghum crop systems and the landraces prevalent in each could be used to further enhance the choice of accessions to best represent the full genetic diversity. For example, very contrasting sorghums, with contrasting adaptation are grown in the rainy season and post-rainy season within the same geographic region. In addition, knowledge of patterns of genetic diversity gained from previous studies could be considered to assure more complete representation of global diversity.

To enable a more comprehensive assessment of the structure of genetic diversity in tropical and sub-tropical landrace sorghums, this study established a large core collection based on the stratification technique developed by Grenier et al. (2001a) and complemented with knowledge of major crop systems and previously reported patterns of genetic diversity. A thorough analysis of the structure of global genetic diversity of cultivated sorghums was conducted using this worldwide core collection. A large number of RFLP markers have been applied to finely analyse the 210 accessions entering the core collection to (i) characterize the levels and patterns of diversity within and among clusters of accessions and (ii) examine the different factors (i.e., racial and geographical) involved in sorghum genetic differentiation. The manageable size of this core collection better permits the exploration of the range of variation of numerous and complex traits of agricultural interest, such as photoperiod sensitivity in trials conducted in different locations and (or) years owing to its reduced management and evaluation costs. Lastly, the characterization with molecular markers and the assessment of the extent and distribution of genetic diversity in such a collection permit a more relevant choice of the accessions suitable either to optimize a breeding program or to perform association studies between markers and traits based on linkage disequilibrium.

Materials and methods

Sampling and characterization of accessions

The 210 sorghum accessions assembled for this study were chosen to provide representation of cultivated landrace sorghums from the whole world, with sampling based on race classification, latitude of origin, response to day length, and form of cultivation. An extensive sampling exercise to develop core collections from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) sorghum collection was conducted by Grenier et al. (2001a, 2001b). Three core collections were obtained after stratification of the ICRISAT landraces collection into 4 clusters based on photoperiod sensitivity. The majority of sorghum accessions examined in this study were derived from the logarithmic sampling “L sorghum core” of 2247 accessions obtained by Grenier et al. (2001b). The L sorghum core was used because it best represented the full range of genetic diversity among the core collections. Subsequent random sampling (10%) within the L sorghum core resulted in a subset of 225 accessions (Grenier et al. 2000). We retained 128 of the 225 accessions, excluding the majority of the kafir race and intermediate kafir forms, which were over represented in the L subset and known for their low level of genetic and phenotypic diversities (Morden et al. 1989; Menkir et al. 1997; Djé et al. 2000). Supplementary accessions were added to this collection to provide more complete representation of diverse sorghum landraces, taking advantage of prior information on specific sets of germplasm and assuring appropriate representation of the variability of the guinea race, bicolor race, and transplanted sorghums of western Africa. Thus, 49 landrace accessions from a collection representing racial and geographical diversity (Deu et al. 1994), 16 from the ICRISAT world sorghum collection, and 17 from the CIRAD collection were added. Our final core collection, upon which this study is based, comprised 210 sorghum landrace accessions (with 179 and 31 accessions, respectively, from the ICRISAT and CIRAD collections).

Racial characterization based on panicle and spikelet morphology was performed in accordance to the Harlan and de Wet classification (1972). Additionally, the taxonomic characterization proposed by Snowden (1936) and recognised by de Wet and Harlan (1972) was used to distinguish the margariferum subrace from other guinea landraces. The accessions of the core collection were grown and independently observed for racial characterization in 3 different sites; ICRISAT Patancheru (1996–1998, India) for all except the 31 CIRAD accessions, ICRISAT Samanko, Mali, 2000, and CIRAD Montpellier, France, 2001.

RFLP analysis

A set of 90 probes was selected, according to their location on the CIRAD sorghum reference genetic map (Dufour et al. 1997; Boivin et al. 1999; Ventelon et al. 2001), to provide good coverage of the genome. These probes were rice (RZ prefix) and oat (CDO prefix) cDNA probes, maize genomic and cDNA probes (BNL, CSU, UMC prefixes),
Racial characterization

The racial classification of accessions was consistent for 168 accessions, but showed some discrepancies for the remaining 42 across the assessments in France, Mali, and India (Table 1). Most discrepancies were minor, for example, an accession characterized either as a basic race or a related intermediate form as in the case of IS 3771. When discrepancies did occur, accessions were classified according to the most consensual racial characterization. Major discrepancies occurred only for IS 7287, which did not conform to the ICRISAT grain description and was classified as X, and IS 9331 and IS 16186, for which interpretations of morphological characters by ICRISAT and CIRAD gene bank curators differed. The racial distribution of the accessions in this study, based on the consensual classification, was 24 bicolors; 62 guineas, of which 14 are margaritiferum; 44 caudatums; 29 durras; 19 kafirs; and 32 intermediate forms.

Marker polymorphism

Ninety probes were tested on the 210 accessions. A total of 16 probes were discarded because they provided either a poor level of polymorphism or a complex pattern of hybridization, suggestive of duplicated sequences. The 74 polymorphic probes yielded complete data for 205 accessions, revealing 219 RFLP bands for statistical analysis. Each band could be associated with one allele, since all but two of the selected probes revealed unique loci and unique bands in most of the accessions. The maximum number of RFLP alleles detected by a probe was 5 and the average number detected by polymorphic probes was 3.00, which is similar to values in previous sorghum studies (Deu et al. 1994; de Oliveira et al. 1996).

All races other than kafir exhibited similar levels of polymorphism, as indicated by the percentage of polymorphic loci, the total number of observed alleles, and Nei’s unbiased estimator of genetic diversity (Table 2a). The kafir accessions exhibited only 45% polymorphic loci, approximately half the frequency shown by other races, and only 110 alleles, in contrast to 169 to 176 in other races. The kafir accessions also present a very restricted genetic diversity with \( H = 0.14 \), as compared with values ranging from 0.33 to 0.37 found in other races.

A large number of alleles were rare (frequency \( \leq 1\% \)), totalling 31 out of 219 total alleles (Table 2a). Most of the rare alleles, 24 in total, occurred in a single accession. Rare alleles were encountered most often in bicolor and guinea accessions (11 in each race). The rare alleles in bicolor accessions were mostly found in 3 Ethiopian accessions (3 rare alleles) and in the Algerian and Turkish accessions (2 rare alleles each). The majority of rare alleles in the guinea accessions were detected in the margaritiferum subrace (4 alleles) and in the Asian (3 alleles) and Tanzanian (2 alleles) accessions. An intermediate number of rare alleles were observed in caudatum (4 alleles, 2 of which were from China) and durra (6 alleles, with 2 each from Cameroonian and Indian accessions) races. The kafir race, however, exhibited only one rare allele.
Table 1. List of the accessions of the core collection with comparative racial classification.

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**Note:** Bold font indicates missing RFLP data; italics indicate accession for which only RFLP data are available. Racial classification performed in accordance with Harlan and de Wet (1972); B, bicolor; C, caudatum; D, durra; G, guinea; Gm, Guinea margaritiferum; K, kafir; XY, intermediate between X and Y. Country codes are as follows: BEN, Benin; BDI, Burundi; BFA, Burkina Faso; BWA, Botswana; CAF, Central African Republic; CHN, China, CMR, Cameroon; DZA, Algeria; ETH, Ethiopia; GHA, Ghana; GMB, Gambia; IND, India; KEN, Kenya; KOR, Korea; LKA, Sri Lanka; LSO, Lesotho; MLI, Mali; MWI, Malawi; NER, Niger; NGA, Nigeria; NPL, Nepal; RWA, Rwanda; SDN, Sudan; SEN, Senegal; SLE, Sierra Leone; SOM, Somalia; SWZ, Swaziland; TCD, Chad; TUR, Turkey; TZA, Tanzania; UGA, Uganda; USA, United States of America; YEM, Yemen; ZAF, Republic of South Africa; ZAR, Democratic Republic of Congo (Zaire), ZMB, Zambia; ZWE, Zimbabwe.
Multivariate analysis

Considering all loci simultaneously, 194 genotypes were identified among the 205 accessions. The first FAC on 219 RFLP bands identified one distinct group composed almost entirely of guinea margaritiferum accessions (along with one guinea accession from Sri Lanka and one GC accession from Chad). A second FAC was conducted on 180 active RFLP bands (i.e., bands that were taken into account for the analysis), with the rare bands (≤1% frequency) and the specific bands of the previously identified, distinct, margaritiferum group of accessions set as inactive variables. However, this second FAC still resulted in a guinea margaritiferum group distinctly separated from all other cultivated sorghums (data not shown). A third FAC was performed on 175 active bands, with the guinea margaritiferum accessions as inactive, to examine the pattern of molecular variation in the rest of the cultivated sorghums.

The 3 main axes of the third FAC accounted for 12.9%, 8.7%, and 7.7% of the variation. The distribution of the accessions on the first 2 axes is shown in Fig. 1a. Differentiation based on geographic origin and racial classification is observed on this plane. The first axis separated the kafir accessions and southern African and Asian guinea accessions (negative coordinates) from other accessions. Axis 2 separated southern African accessions into 2 groups; a kafir group (lower) and a guinea race group (upper) with closely associated Asian guinea accessions. This axis also separated western African guinea accessions (upper right) from durra and caudatum accessions. The third axis (Fig. 1b) separated African caudatum accessions (lower right) from a mixed group composed primarily of durra and Asian caudatum accessions.

Discriminative markers and specific alleles

We examined the loading values of the 219 RFLP bands on the main axes for the first and third FACs. This could permit the identification of alleles exhibiting the highest power of discrimination between groups. The first FAC permitted identification of alleles (and consequently probes) that discriminate margaritiferum accessions from the rest of the cultivated sorghums, whereas the discriminative alleles within non-margaritiferum accessions were identified by the third FAC. Forty-eight discriminative probes were identified. They appeared scattered over the whole sorghum genome (Fig. 2). For example, alleles with strong negative contributions to axis 1 (mostly southern African guinea and kafir and Asian guinea accessions) were identified by probes located on linkage groups A, B, F, G, H, I, and J on our reference map (Boivin et al. 1999). Similarly, alleles with strong positive contributions to axis 2 (primarily guinea accessions

<table>
<thead>
<tr>
<th>Race (no. of accessions)</th>
<th>% polymorphic loci</th>
<th>Total no. of alleles</th>
<th>No. of rare alleles</th>
<th>Mean no. of alleles/polyorphic loci</th>
<th>H_exp^d</th>
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<tr>
<td>Bicolor (22)</td>
<td>0.92</td>
<td>175</td>
<td>11</td>
<td>2.38</td>
<td>0.37</td>
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<tr>
<td>Caudatum (43)</td>
<td>0.93</td>
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<td>4</td>
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<td>0.34</td>
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<td>Durra (29)</td>
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<td>Guinea (62)</td>
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<td>176</td>
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<td>2.38</td>
<td>0.35</td>
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<tr>
<td>Kafir (18)</td>
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<tr>
<td>Total (205)</td>
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<td>3.00</td>
<td>0.40</td>
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(a) Variation within races.

<table>
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<th>Cluster (no. of accessions)</th>
<th>% polymorphic loci</th>
<th>Total no. of alleles</th>
<th>No. of rare alleles</th>
<th>Mean no. of alleles/polyorphic loci</th>
<th>H_exp^d</th>
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<td>Cluster I (26), guinea from western Africa</td>
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<td>0</td>
<td>1.75</td>
<td>0.19</td>
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<tr>
<td>Cluster II (14), guinea margaritiferum</td>
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<td>106</td>
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<td>Cluster IV (12), Chinese sorghums</td>
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(b) Variation within clusters defined by NJ analysis.

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Fig. 1. Distribution of 205 sorghum accessions on the first planes of the FACs performed with 175 RFLP bands as active variables. The accessions are represented on plane (1, 2) in a and on plane (1, 3) in b, according to their morphological race and geographic origin. Each letter represents a race code designation (described in Table 1), and each number represents a geographic origin: 1, western Africa; 2, central Africa; 3, eastern Africa; 4, southern Africa; 5, Mediterranean basin; 6, Indian subcontinent; 7, eastern Asia; 8, America; 9, Middle East.

1: Western Africa (BEN, BFA, GHA, GMB, MLI, NER, NGA, SEN, SLE)
2: Central Africa (BDI, CAF, CMR, RWI, TCD, ZAR)
3: Eastern Africa (ETH, KEN, SDN, SOM, TZA, UGA)
4: Southern Africa (BWA, LSO, MWI, SWZ, ZAF, ZMB, ZWE)
5: Mediterranean basin (JDA, TUR)
6: Indian subcontinent (IND, LKA, NPL)
7: Eastern Asia (CHN, KOR)
8: America (USA)
9: Middle east (YEM)
**Fig. 2.** Location on the sorghum genetic map of the 74 probes used for sorghum core collection analysis. The genetic map was described in Boivin et al. (1999) and Ventelon et al. (2001). Linkage groups are named according to these authors. Discriminative probes detecting specific guinea margaritiferum alleles in the first FAC are noted in bold and italic. Discriminative probes identified in the third FAC are outlined by boxes; those probes for which alleles have a large contribution to axis 1, 2, and 3 are outlined by double lines, single lines, and dashed lines, respectively. + and – in the box indicates whether the contribution of alleles to each axis is positive or negative.
from western Africa) were revealed by probes on linkage groups B, C, D, E, F, G, and J. Alleles with positive contribution to axis 3 (primarily durra and Asian caudatum accessions) were identified by probes on linkage groups B, C, D, E, and F. Nevertheless, some alleles at linked loci (separated by fewer than 10 cM) contributed greatly to the discrimination between groups. One such example is the alleles detected by probes UMC53 and 5bRPG704 (linkage group B), for which the former differentiated western African guinea accessions from the other cultivated sorghums, while the latter differentiated all guinea accessions from the rest of the collection.

No allele appeared to be unique to a specific geographical or racial cluster of accessions. Nevertheless, some alleles were found to occur predominantly in specific clusters. The margaritiferums in this study exhibited 8 specific alleles, 5 of which were present in most of the margaritiferum accessions. The probes CDSR29, CDO590, CDO795, UMC104, and UMC164 revealed these 5 specific alleles. Alleles quasi-specific to most of the Chinese caudatum and bicolor accessions were revealed by probes UMC55, BNL 7.49, and SSCR194. No allele specific to the transplanted sorghum accessions was observed.

**Neighbour-joining analysis**

The dissimilarity values calculated between all pairwise accessions with the 219 RFLP bands ranged from 0 to 0.718 with an average of 0.196. The neighbour-joining (NJ) analysis (Fig. 3) permitted identification of the following 10 major clusters of accessions: cluster I, guinea accessions (not including the margaritiferum subrace) from western Africa; cluster II, guinea margaritiferum accessions; cluster III, durra accessions from Asia and Africa and durra–caudatum from Asia; cluster IV, Chinese accessions of mainly caudatum, bicolor, and caudatum–bicolor intermediate races; cluster V, caudatum accessions from diverse African countries; cluster VI, durra and caudatum accessions of transplanted sorghums from Chad and Cameroon; cluster VII, kafir and intermediate kafir varieties from southern Africa; cluster VIII, guinea accessions from southern Africa; cluster IX, guinea accessions from Asia; cluster X, caudatum accessions predominantly from the Great Lakes region of Africa.

These clusters formed 2 main geographical groups, with clusters I–VI primarily including accessions from north equatorial Africa and clusters VII–X containing accessions from south equatorial Africa. The Asian accessions were distributed among these two main geographical groups. A single predominant race could be identified in 8 of these clusters, with guinea accessions predominant in 4 clusters, caudatum accessions in 2 clusters, and durra and kafir accessions each in 1 cluster. Although the two remaining clusters appeared quite mixed at the racial level, they could be characterized by a specific geographic origin (cluster IV, composed of Chinese sorghums) or by a particular crop system carried out in a narrow geographic area (cluster VI, composed of transplanted sorghums). These transplanted sorghums are both durra and caudatum accessions cultivated in the post-rainy season on residual moisture in inundated clays from Chad and Cameroon after flood subsidence. Bicolor accessions were distributed widely across different clusters, although a portion of them was present in cluster IV.

Bootstrap values could confirm the consistency of some clusters, i.e., margaritiferum accessions (bootstrap value of 100% for cluster II) and Chinese accessions (bootstrap value of 98% for cluster IV). Relatively low bootstrap values observed for other clusters, i.e., durra (cluster III) or caudatum (cluster V), could be explained by the moderately strong structure observed in cultivated sorghums, the hybrid or intermediate origin of some accessions that could not be classified in a specific cluster, or the larger genetic variation in these clusters (as confirmed by the long branches found in these clusters compared with branches found in guinea margaritiferum and Chinese sorghums). Nevertheless, the high value found for the cophenetic correlation ($c_{coph} = 0.92$) indicated a good agreement between the tree and the original dissimilarity matrix, thus corroborating the consistency of the tree.

**Discussion**

This study provides one of the most detailed and comprehensive examinations of genetic diversity in tropical and sub-tropical landrace sorghums through analysis of a core collection, representative of geographic origin, race, photoperiod sensitivity, and production system, using a large number of markers (74 RFLP probes) dispersed over the entire genome. To evaluate the use of molecular markers for large-scale germplasm diversity analysis, Dillmann et al. (1997) have proposed several criteria that have been applied in this study: a large number of markers, a large repartition of these markers on the genetic map of the species, the selection of monolocus probes, and the use of a single enzyme per probe. These authors have reported that the precision of the estimation of the genetic distance calculated between all pairwise maize lines increases with the number of markers, as each marker can be considered as a sample of the genome.

The RFLP markers permitted the identification of 194 genotypes among the 205 accessions and 8 sets of accessions with identical RFLP patterns were found. They included 18 accessions. We could observe that each set was composed of 2 or 3 accessions originating from the same country or belonging to the same race and presenting a phenotypic similarity as shown by the analysis of morpho-agronomic traits in the field trials conducted in Mali and France. These identities could highlight the duplications of entries in the ex situ collections. These identities could be confirmed or weakened, since a large number of highly polymorphic SSR markers developed and mapped during these last years are now available for the sorghum research community (Bhattaramakki et al. 2000; Kong et al. 2000; Schloss et al. 2002). The characterization of this sorghum collection with a set of carefully selected SSR markers is now in progress.

Loci involved in the differentiation of the clusters were scattered over the whole sorghum genome. Furthermore, alleles at linked loci are also involved in discrimination between clusters. Interestingly, some of the discriminative loci mapped in genomic regions associated with morphology-related QTLs (plant height, panicle compactness, and length) identified by Rami et al. (1998) on linkage groups A, C1, and F. At least, the pattern of diversity revealed in this sorghum core collection permits investigation of genome-wide
LD owing to crop history (founder effect, genetic drift, and selection) and local LD owing to genetic linkage. We are engaged in an exploratory study on the extent and intensity of linkage disequilibrium useable for association studies in this species (Deu and Glaszmann 2004).

**Geographic and racial pattern of clustering**

The apparent first order differentiation between northern and southern equatorial African accessions indicated by the NJ analysis suggests 2 major geographic poles for sorghum evolution and differentiation. This observation is compatible with the postulated origin of this species in the northeast quadrant of Africa (Harlan and Stemler 1976; Doggett 1988; Wendorf et al. 1992). The absence of rare alleles (Table 2b) in southern equatorial accessions (kafir, guinea, and caudatum found in cluster VII, VIII, and X, respectively) fits also with the expectation that southern equatorial African sorghums evolved later from other African sorghums (Doggett 1988). The suggested bipolar evolution of sorghums also agrees with indications of ethnic divisions between northern (Nilotic and Sudanian) and southern equatorial Africa (Bantu) (de Wet and Huckabay 1967; Gourou 1970; Doggett 1988) that could have contributed to isolation of gene pools and divergent evolution. The presence of Asian accessions in both the north equatorial group (cluster IV, Fig. 3) and south equatorial group (cluster IX) suggests that sorghums from both pools could have been introduced to Asia as suggested by Harlan and Stemler (1976).

The NJ analysis indicated that morphological race also has substantial influence on the pattern of genetic diversity, with 8 of 10 clusters based on a single predominant race (Fig. 3). Previous studies have also shown associations between racial characterization and the pattern of genetic diversity as measured by RFLP (Deu et al. 1994; Cui et al. 1995) and RAPD (Tao et al. 1993) and by combining RFLP, RAPD, and ISSR molecular markers (de Oliveira et al. 1996). However, the racial differentiation observed in most of these studies was less clear than in this study. The stronger association of racial classification with pattern of diversity observed in this study could be due to many factors, including stratification of world germplasm and a greater number of accessions sampled for effectively sampling diversity, inclusion only of landrace accessions, and rigorous verification of racial classification.

**Genetic diversity within race**

The high diversity of the bicolor race, shown by its estimator of gene diversity, its mean number of alleles (Table 2a), and its presence in multiple clusters (Fig. 3), corresponds with expectations for this race, which is considered the most ancient with such wide geographic distribution and diversity of uses (forage, broom-corn, and sweet stems) (Doggett 1988).

The guinea race also exhibited high diversity, with 3 main and very distinct groups (western African (non-margaritferum), margaritferum, and southern African) (Fig. 3). These groups correspond to those identified previously with isozymes, RFLP, and SSR markers (Ollitrault et al. 1989; Deu et al. 1994, Cui et al. 1995; Folkertsma et al. 2005). The genetic distinctness of guinea margaritiferum sorghums from other guinea forms was previously discussed by Deu et al. (1994, 1995), de Oliveira et al. (1996), and Folkertsma et al. (in press). Our study showed that margaritiferums differed from other guineas not only by possessing rare and specific alleles, but also by having distinct genotypes at other loci, as indicated by the second FAC performed without the alleles specific to margaritiferums. The genetic distinctness of margaritiferums from other guinea sorghums from western Africa is remarkable, since both are interfertile and cultivated in sympathy in the same season by the same farmers. The only margaritiferum from southern Africa (IS 19455) included in this study did not cluster with the western African margaritiferums, but rather clustered with other southern African guinea accessions (Fig. 3), even though it was found to present a mitotype closely related to western African guinea margaritiferums (Deu et al. 1995). These results suggest that this southern African margaritiferum had a common ancestor with western African margaritiferums and that human selection and geographic isolation resulted in marked changes of its nuclear genetic background.

Our study has also revealed an additional small cluster of guinea accessions originating from Asia, not shown in previous studies. The close relationship between these Asian accessions and southern African guinea accessions suggests recent introduction of Asian forms from southern Africa. However, the presence of 3 alleles (frequency <10%) in both the Asian guinea and Asian durra accessions (data not shown) suggests weak gene flow between these races or limited introgression from wild local sorghums.

The differentiation of caudatum accessions into 3 groups (Fig. 3), although not previously reported as such, does correspond with previous studies. The 2 main groups, African Great Lakes (cluster X) and remaining African countries (cluster V), were clearly differentiated both in this study and in that of Deu et al. (2003) based on observations of 21 morphological traits. These 2 groups also showed considerable difference for photoperiod sensitivity when sown at 1-month intervals, with the Great Lakes accessions showing much higher sensitivity than that of the others (data not shown).

The third and smallest group of caudatums and caudatum–bicolor intermediates (cluster IV) was composed of Chinese accessions. This group showed very restricted genetic diversity (Table 2b), as was previously reported (de Oliveira et al. 1996). This group was not highly distinct from other cultivated sorghums in contrast to the finding of de Oliveira et al. (1996), although the small number of accessions involved in our study (n = 12) means that results could be influenced by sampling.

The observation of durra sorghums comprising 2 separate groups (Fig. 3) has not been previously reported. The main group (cluster III) consists of accessions of the most widely cultivated durra sorghums. These sorghums are known to have superior adaptation to droughty rain-fed conditions, and are considered to have originated in northeast Africa from where they migrated throughout Africa and on to Asia (Doggett 1988). The other dursas, belonging to the mixed group composed of durra and caudatum accessions (cluster VI), consist of particular transplanted sorghums from Chad and Cameroon, which are cultivated in the post-rainy season by transplantation in receding moisture systems. The cultivation of these 2 groups in different seasons would likely limit
Fig. 3. Neighbour-joining analysis based on RFLP data among 205 cultivated accessions using the Nei and Li similarity index. The numbers on the branches indicate bootstrap values (expressed in percentages) and are shown for all clusters with > 60% bootstrap support. Cl, cluster.
A low genetic diversity was observed in the kafir race as previously reported in studies using isozymes, RFLP, RAPD, or SSR markers (Ollitrault et al. 1989; Deu et al. 1994; Cui et al. 1995; Menkir et al. 1997; Djé et al. 2000). All but one of the kafir accessions constituted a specific cluster. This race exhibited the lowest number of alleles and the unique rare allele was encountered in the accession not included in the kafir cluster. These results are in agreement with the recent origin and restricted geographic distribution of this race (Doggett 1988).

Genetic resources management and crop improvement

The patterns of genetic relationships observed in this study should provide more detailed insights for genetic resource conservation and use of sorghum. The patterns of diversity within the guinea and caudatum races are particularly relevant to genetic base broadening efforts within those races. The association of level of photoperiod sensitivity with genetic differentiation observed within the caudatum race would have significant consequences for accessing the full range of genetic diversity in applied breeding programs, since they primarily use germplasm of similar photoperiod sensitivity. This is particularly critical in the guinea race, which is the most photoperiod sensitive (Grenier et al. 2001a), and any relationship between photoperiod sensitivity and genetic differentiation would have significant consequences for efforts to use genetic diversity within this race to develop guinea-race hybrids for western Africa.

Finally, the pattern of genetic diversity, as revealed in this study with RFLP markers, may offer new opportunities to relate that diversity to the structure of diversity for important agronomic traits, since this collection is being phenotyped and genetic differentiation would have significant consequences for efforts to use genetic diversity within this race to develop guinea-race hybrids for western Africa.

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