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Core Collection of Sorghum: I. Stratification Based on Eco-Geographical Data

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ABSTRACT

ICRISAT conserves a large (36 719 entries) collection of sorghum [*Sorghum bicolor* (L.) Moench] accessions in India. This collection comprises cultivated and wild sorghums acquired over the past 25 years from 90 countries. However, it is difficult to characterize and assess a large collection with limited time and resources. To facilitate maintenance, assessment, and utilization of the collection, we considered the establishment of a core collection using stratified sampling strategies. Results from a study of the morpho-agronomic diversity were used to describe the genetic structure of the collection. Morphological traits, including days to flowering and plant height, can be affected by daylength variation. These two characters were highly correlated with latitudinal and racial distributions of landraces. Thus, stratifying the entire collection for response to photoperiod, estimated by flowering date and plant height, was indicative of a major source of specific adaptation within the collection. This stratification resulted in four clusters, which described the sensitivity of genotypes to photoperiod within the latitudinal range where selection was carried out by farmers. These four clusters may serve as the basis for a random stratified sampling to establish cores in this collection.

SORGHUM is the fifth most important cereal crop in the world based on total grain production and is an essential component of the cropping systems of subsistence farmers and the diets of millions of people in the semiarid tropics. The continued improvement of this important crop depends upon the utilization of genetic variability in landraces originally maintained by traditional agricultural practices. Taxonomically, *Sorghum bicolor* (L.) Moench subs. *bicolor* has 15 races: the 5 basic races of bicolor, durra, caudatum, kafir, and guinea, and their 10 intermediates (Harlan and de Wet, 1972). The large set of cultivated sorghums, presently maintained at ICRISAT Asia Center (IAC), Patancheru, India, has been assembled from 40 countries in Africa, 24 in Asia, 11 in Europe, 13 in the Americas, and several entries from Russia and Australia.

To facilitate the use of such a large collection, establishing core collections is recommended in order to prioritize maintenance and evaluation on subsets that retain a large part of the diversity encompassed in the entire collection (Brown, 1989a). Different sampling strategies are proposed including sampling based on random procedures applied on a stratified collection (Brown, 1989b). The choice of criterion to stratify the collection depends on the data set available and the objectives for establishing a core. Several studies have shown that phenotypic divergence among and within landrace populations is related to geographical distance between countries of origin (Spagnoletti Zeuli and Qualset, 1987; Peeters and Martinelli, 1989; Schoen and Brown, 1993; Spagnoletti Zeuli and Qualset, 1993).

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Abbreviations: FL, days to 50% flowering; IAC, ICRISAT Asia Center; PHT, plant height.

Therefore, eco-geographical information can be used to stratify the phenotypic diversity of the entire collection.

Sorghum landraces are known to respond differently to daylength and temperature according to their specific geographical adaptation. Temperature and photoperiod responses have often formed the basis for traditional cropping systems (Chantereau et al., 1998). Several studies have reported the impact of photoperiod on the development of tropical sorghum genotypes (Quinby, 1966; Miller et al., 1968a; Miller et al., 1968b; Caddel and Weibel, 1971; Major et al., 1990; Vaksmann et al., 1998). Accessions that originated from different photothermal environments show variation in the growing-degree-days required for floral initiation due to differences in inherent earliness rather than responsiveness to temperature (Craufurd et al., 1998). Moreover, a genetic component in floral initiation and panicle differentiation of the sorghum plant in response to photoperiod variation was observed by Miller et al. (1968b). During the long-day season, flowering was reported to be under the control of a few major genes, while a different set of genes controlled flowering under tropical conditions with short daylengths. An experiment based on a variable set of maturities indicated that sorghum varieties tend to flower at about the same time in short days, but not in long days (Miller et al., 1968b).

Farmers from West Africa preferentially sow highly adaptive landraces to match the diversity of local environmental conditions (Kouressy et al., 1998). They select landraces that will guarantee a maturity corresponding to the end of the rainy season, thereby limiting damage from predatory birds and weather-induced pathological conditions (Trouche et al., 1998). Thus, photoperiod sensitivity in the sorghum crop has been subjected to selective pressure through natural and artificial means. Adaptation of sorghum to diverse environments is determined largely by maturity differences and photoperiod sensitivity based on latitude (daylength) (Craufurd et al., 1999). For tropical areas, the calendar year is divided into two major seasons defined by the monsoons. Days are longer during the rainy season than during the post-rainy season except at equatorial latitudes. Consequently, when introduced into other areas during the long days of the rainy season, equatorial and tropical landraces adapted to shorter daylength may experience delayed flowering or may fail to flower because of a non-optimal photoperiod. Photoperiod-sensitive landraces attain flowering earlier during the post-rainy season when days are shorter, and consequently have a reduced plant stature. Therefore, photoperiod sensitivity could be defined both by days to flowering and plant height in both rainy and post-rainy seasons.

To improve access and use of the sorghum genetic resources maintained at ICRISAT, core collections are being established. As a first step in this process, we conducted a study of the morpho-agronomic diversity, including days to flowering and plant height, to stratify the collection before sampling. Thus the objective of this study was to use photoperiod sensitivity as a means for hierarchical stratification of accessions of sorghum landraces to form a core collection representing the ICRISAT germplasm collection.

MATERIALS AND METHODS

Initially, the entire ICRISAT sorghum collection was reduced to landraces from a latitude range of 40° N lat to 40° S lat, with complete passport information and characterization data. Beyond this geographical range, few accessions were expected to be original landraces but introduced material. This reduced collection consisted of 22 473 landraces from 76 countries, constituting 62% of the collection conserved at ICRISAT. Geographical groups were established by stratifying the latitudes into four ranges of 20° lat each: latitude range 1 (LR-1) = 10° S lat to 10° N lat; latitude range 2 (LR-2) = 20° S lat to 10° S lat and 10° N lat to 20° N lat; latitude range 3 (LR-3) = 30° S lat to 20° S lat and 20° N lat to 30° N lat; latitude range 4 (LR-4) = 40° S lat to 30° S lat and 30° N lat to 40° N lat. For proper interpretation of our results, we designated LR-1 and LR-2 to the latitudinal range of equatorial and tropical areas, respectively. A two-way table was constructed that placed the landraces into 60 groups according to their taxonomic race classification (row entries in Table 1) and latitudinal range (column entries in Table 1).

Table 1. Percentage of sorghum landraces cross-classified according to race (rows) and latitudinal range (columns).

	Latitudinal range				
Race	**LR-1: 10° S lat to 10° N lat**	**LR-2: 20° S lat to 10° S lat and 10° N lat to 20° N lat**	**LR-3: 30° S lat to 20° S lat and 20° N lat to 30° N lat**	**LR-4: 40° S lat to 30° S lat and 30° N lat to 40° lat**	**All**
	%				
Bicolor, B	**0.9**	**1.2**	**0.3**	**0.8**	**3.2**
Caudatum, C	**14.6**	**5.6**	**0.8**	**0.8**	**21.8**
Durra, D	**5.9**	**11.7**	**2.3**	**0.3**	**20.2**
Guinea, G	**7.0**	**9.7**	**0.4**	**0.2**	**17.4**
Kafir, K	**0.0**	**0.3**	**0.9**	**1.1**	**2.3**
Caudatum-bicolor, CB	**0.9**	**1.6**	**0.4**	**0.5**	**3.4**
Durra-bicolor, DB	**2.8**	**2.2**	**0.5**	**0.1**	**5.6**
Guinea-bicolor, GB	**0.6**	**0.3**	**0.0**	**0.0**	**1.0**
Kafir-bicolor, KB	**0.0**	**0.1**	**0.1**	**0.0**	**0.2**
Durra-caudatum, DC	**3.0**	**8.3**	**0.6**	**0.3**	**12.1**
Guinea-caudatum, GC	**3.7**	**5.3**	**1.1**	**0.5**	**10.7**
Kafir-caudatum, KC	**0.0**	**0.2**	**0.4**	**0.2**	**0.9**
Guinea-durra, GD	**0.1**	**0.4**	**0.1**	**0.0**	**0.6**
Kafir-durra, KD	**0.0**	**0.2**	**0.2**	**0.1**	**0.5**
Guinea-kafir, GK	**0.0**	**0.0**	**0.1**	**0.0**	**0.1**
All races	**39.7**	**47.1**	**8.2**	**5.0**	**100.0**

Morpho-agronomic data were collected on accessions grown on vertisol soils at Patancheru, India (17°25′ N, 78° E). Data were collected for several years from 1975 to 1996 in both the kharif (rainy, higher average daily temperature of 27°C, long-day) and the rabi (post-rainy, lower average daily temperature of 22°C, short-day) seasons. Kharif typically extends from June to December, while rabi usually extends from September to April. These two different environmental conditions are typical of most of the semiarid tropics (Appa Rao et al., 1996). Data were recorded on the following quantitative characters: days to 50% flowering (days), plant height (cm), peduncle exertion (cm), panicle length (cm), panicle width (cm), number of basal tillers, grain size (mm), and 100-seed weight (g). To stratify the sorghum collection according to photoperiod sensitivity, we based our analyses on days to flowering and plant height data collected during two crop seasons. Days to 50% flowering were recorded as the date when 50% of the plants had started flowering (i.e., 15 of the 30 plants per row per accession). Plant height was observed at maturity and recorded as the length (cm) of the main stalk recorded on 10 random plants from the base of the stalk to the tip of the panicle. These two characters were recorded in both kharif and rabi seasons. Photoperiod response was defined by the relative differences in number of days to 50% flowering (FL) and plant height (PHT) during the long-day rainy season and the short-day post-rainy season. Days to 50% flowering was calculated as the difference in days to flowering between kharif (FLK) and rabi (FLR), whereas PHT was calculated as the difference in plant height between kharif (PHTK) and rabi (PHTR). Methods for measuring other quantitative characters used for data validation and principal component analysis are as described in Appa Rao et al. (1996).

Before using the data recorded during the 21 yr of characterization held at IAC, data validation was performed with 642 accessions selected to represent all 15 races and 43 countries. From 1996 to 1998, field trials were conducted on these 642 accessions plus a check (IS 1054) that was replicated within each field trial and between seasons and years. For quantitative characters, the records from 1996 to 1998 showed positive and significant ($P < 0.05$) correlations with those found in the database (data not shown).

Thus, from the original data file on 22 473 landraces, FL and PHT data were calculated and the collection was divided into four classes of the same size according to their quartiles (Table 2). A character scored as FL1 or PHT1 corresponded to one-quarter of the collection where landraces have the smallest reaction to the daylength variation and were classified as photoperiod-insensitive. In the same manner, FL2 and PHT2, FL3 and PHT3, and FL4 and PHT4 corresponded to mildly photoperiod-sensitive, photoperiod-sensitive, and highly photoperiod-sensitive sorghum groups, respectively. A disjunctive table was obtained with the 22 473 accessions and the eight variables (four variables for FL and four variables for PHT). Then the frequency distribution within the 60 race-latitudinal groups for each of the eight variables was calculated. The matrix formed by the 60 groups and the eight variables was subjected to a cluster analysis using Ward's linking procedure based on the Euclidean distance between clusters (StatSoft, 1997). Once the number of clusters was determined, we used the K-means procedure (StatSoft, 1997) to define the clusters and their constitution. The K-means method is compared to an ANOVA in reverse, which minimizes within-cluster variability while maximizing variability between clusters, and requires an a priori number of clusters before classifying the accessions into clusters. Thus the clustering of the sorghum collection performed on variables relating to photoperiod reaction provides a number of clusters that stratified the entire landrace collection and gives a biological meaning to the structure.

Table 2. Ranges and quartiles established for differences in measurements between rainy (kharif) and post-rainy (rabi) seasons for flowering date (FL) (days), and for plant height (PHT) (cm) in the sorghum landrace collection.

	Quartiles established	
Ranges†	**Flowering (FL = FLK − FLR‡)**	**Plant height (PHT = PHTK − PHTR§)**
	d	**cm**
Min–Q1	**[−58, 4] ≡ FL1**	**[−170, 65] ≡ PHT1**
Q1–Q2	**[4, 23] ≡ FL2**	**[65, 130] ≡ PHT2**
Q2–Q3	**[23, 43] ≡ FL3**	**[130, 180] ≡ PHT3**
Q3–max	**[43, 139] ≡ FL4**	**[180, 425] ≡ PHT4**

† Q1, Q2, Q3 are the first, second, and third quartiles.

‡ FLK and FLR: Flowering date recorded in the kharif and the rabi season, respectively.

§ PHTK and PHTR: Plant height recorded in the kharif and the rabi season, respectively.

In addition, the diversity of the entire landrace collection was assessed by a principal component analysis of the standardized data of the 10 same variables recorded during the 21 yr of field observations at IAC. Scores were calculated for individual landraces from the first two components. Fifty landraces were taken at random within each of the four clusters. These were plotted according to their first two principal component scores.

RESULTS AND DISCUSSION

Classification of the landrace collection into four latitudinal origins (Table 1) grouped the greatest number (86.8%) of accessions into equatorial and tropical areas, that is, LR-1 and LR-2. Classification of the landrace collection into the 15 taxonomic races resulted in 82.2% of the accessions assigned to caudatum, durra, guinea, durra-caudatum, and guinea-caudatum forms.

Ranges and quartiles established for the differences in FL and PHT between seasons are described in Table 2. The distribution of the landraces within the latitudinal classes and the four frequency classes of FL and PHT are shown in Fig. 1. For the lower latitudes (LR-1, i.e., equatorial areas), the distribution of the accessions was skewed toward the highly photoperiod-responsive class for both variables. Close to one-half (47.1%) of the landraces from the total collection belonged to LR-2 and was evenly distributed over the four frequency classes for both variables. Conversely, a higher frequency of accessions from the LR-3 and LR-4 belonged to FL1 and PHT1, where 25% of the total collection was photoperiod-insensitive.

Similar results were found for the distribution of FL and PHT within the 60 groups (Fig. 2). These results illustrate the relationship between racial classification, geographical adaptation, and photoperiod response. Generally, the frequency of photoperiod-insensitive accessions increased with the latitudinal class from equatorial (LR-1) to temperate (LR-4). The proportion of photoperiod-insensitive landraces was about 9% for LR-1 and more than 70% for LR-4, based on both flowering and plant height. However within the same latitudinal class, races reacted differently to daylength variation. Both for FL and PHT, the frequency distributions of guinea and its intermediate forms within any latitudinal

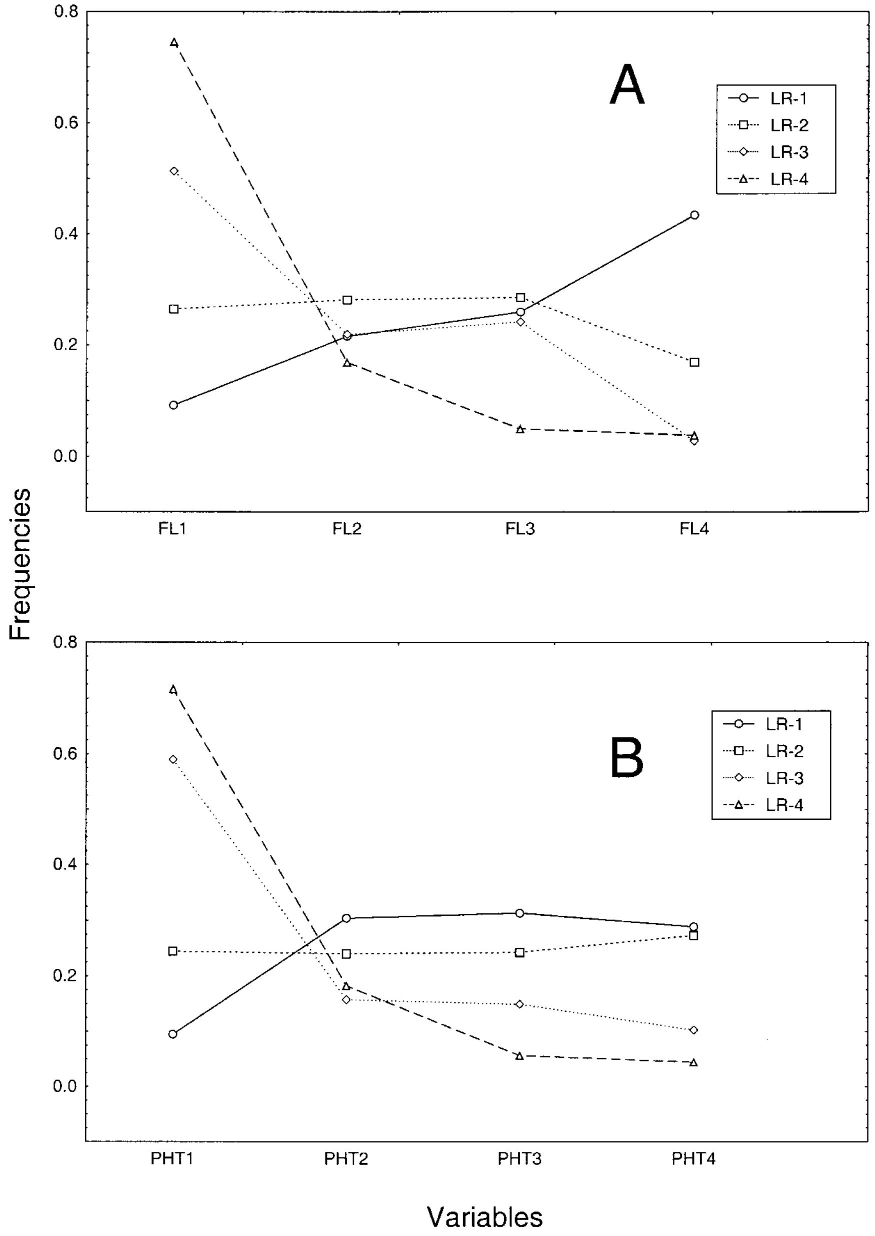

Fig. 1. Frequency distribution according to latitudinal ranges (LR) for differences between the kharif and rabi in (A) flowering date (FL), and (B) plant height (PHT) in the ICRISAT sorghum landrace collection. Variables were divided according to their quartiles (Table 1). Each variable representing 25% of the total collection characterizes a photoperiod-sensitive class.

class were skewed toward the most photoperiod-sensitive response, even at the temperate latitude (LR-4). Less than 5% of the landraces showed high sensitivity to daylength variation in LR-4. Among these highly sensitive accessions, a fairly high frequency belonged to the guinea race and its intermediates (35.7% based on FL and 22.0% based on PHT). These results agree with other studies defining West African guinea landraces as having highly sensitive photoperiod reactions (Chantereau et al., 1998; Trouche et al., 1998; Vaksmann et al., 1998).

Conversely, more than 90% of the accessions of the kafir race were photoperiod-insensitive (FL1 and PHT1). While equatorial landraces are generally highly photoperiod-sensitive, a large proportion of kafir landraces was photoperiod-insensitive (83.3% based on FL and 66.7% based on PHT). In LR-4, about 30% of the landraces showed insensitivity to daylength variation, and 22.7% of these accessions belonged to the kafir race and its intermediates. Other studies have shown the same photoperiod insensitivity of accessions of the kafir race originating from temperate areas (Chantereau et al., 1998). This distribution of race-latitudinal groups into different classes for photoperiod response suggests that photoperiod sensitivity represents a complex interaction between environmental and genetic components.

With the K-means clustering, 95% of the race-latitudinal groups was classified similarly to the Ward's clustering, validating the partitioning of the 60 groups into four clusters. The constitution of each cluster is given

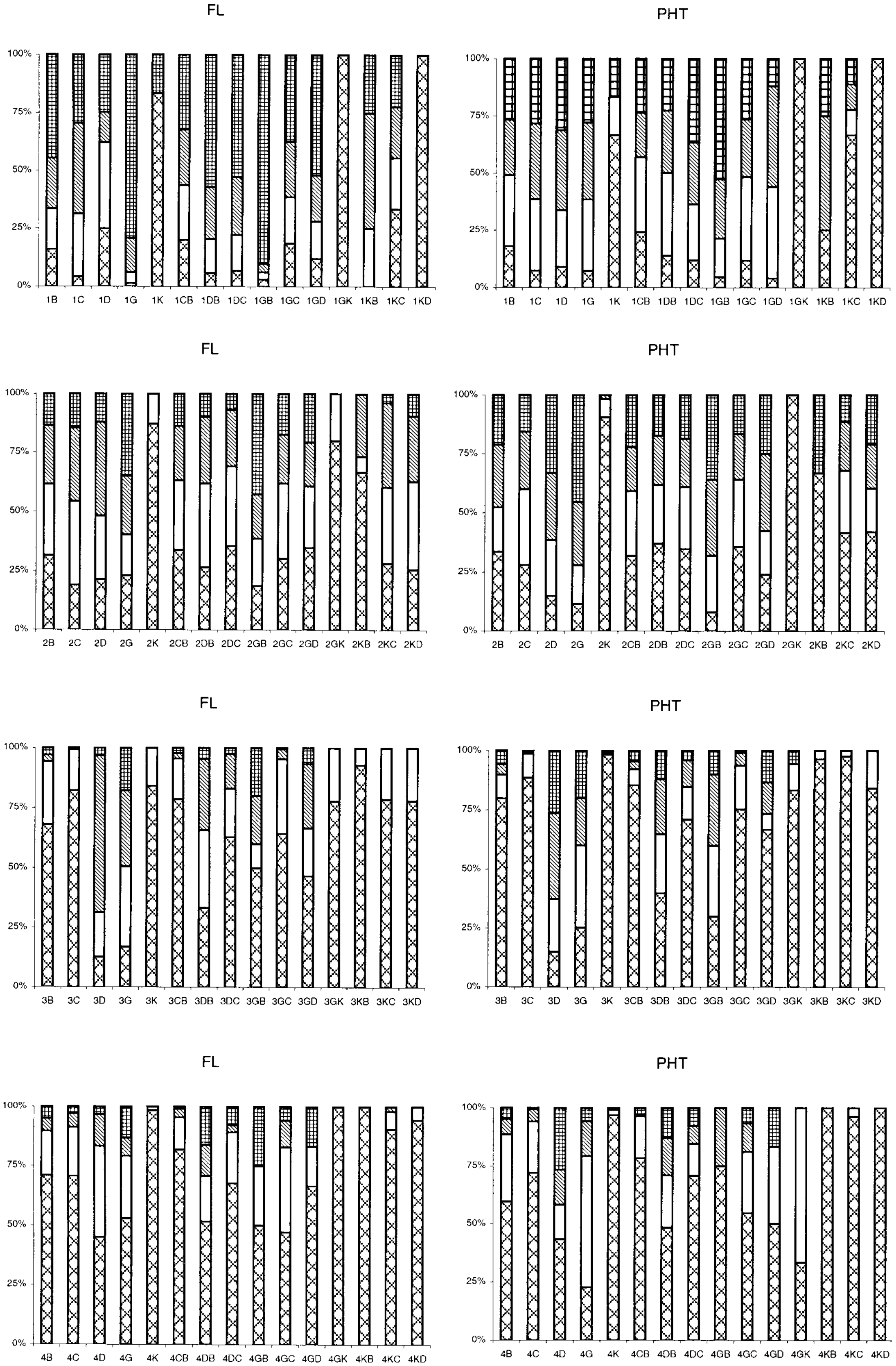

Fig. 2. Photoperiod-sensitivity distribution of frequencies for days to flowering (FL) or plant height (PHT) classes according to latitudinal range and racial classification for the ICRISAT sorghum landrace collection. Races are designated by the first letter of their names: B for bicolor, C for caudatum, D for durra, G for guinea, K for kafir; and intermediate races are coded with two letters, for example, CB for caudatum-bicolor. A number preceding the letter race name indicates the latitudinal range: 1, LR-1; 2, LR-2; 3, LR-3; and 4, LR-4. FL1 and PHT1 are represented with lozenges, FL2 and PHT2 with blank, FL3 and PHT3 with dashes, FL4 and PHT4 with pattern of squares.

Table 3. Constitution of each cluster of photoperiod reaction defined from the K-means clustering performed on the sorghum landrace collection.

Photoperiod reaction			
Insensitive	Mildly sensitive	Sensitive	Highly sensitive
Latitudinal range and race†			
1GK	1K	1D	1B
1KD	1KC	1CB	1C
2GK	2KB	1KB	1G
2K	3B	2B	1DB
3C	3DC	2C	1GB
3K	3GC	2D	1DC
3CB	3GD	2CB	1GC
3KB	4B	2DB	1GD
3KC	4C	2DC	2G
3KD	4DB	2GC	2GB
3GK	4GB	2GD	
4K	4DC	2KC	
4CB	4GC	2KD	
4KB	4GD	3D	
4KC	4GK	3G	
4KD		3DB	
		3GB	
		4D	
		4G	

† For latitudinal ranges, 1 = 10° S lat to 10° N lat, 2 = 20° S lat to 10° S lat and 10° N lat to 20° N lat, 3 = 30° S lat to 20° S lat and 20° N lat to 30° N lat, 4 = 40° S lat to 30° S lat and 30° N lat to 40° N lat; for races, B = bicolor, C = caudatum, D = durra, G = guinea, K = kafir, CB = caudatum-bicolor, DB = durra-bicolor, GB = guinea-bicolor, KB = kafir-bicolor, DC = durra-caudatum, GC = guinea-caudatum, KC = kafir-caudatum, GD = guinea-durra, KD = kafir-durra, GK = guinea-kafir.

in Table 3. In general, each cluster was associated with a particular latitudinal class. Landraces that originated from LR-3 and LR-4 mainly belonged to clusters that included the photoperiod-insensitive and mildly photoperiod-sensitive groups, respectively. The third cluster, mostly composed of groups from tropical latitudes (LR-2), was designated as photoperiod-sensitive. The fourth cluster of highly photoperiod-sensitive groups consisted of landraces mainly from equatorial latitudes (LR-1).

Race groups from the same latitude mainly clustered together. Nevertheless, some exceptions were noted. Equatorial groups that contained landraces known to be highly photoperiod-sensitive were sometimes clustered with photoperiod-insensitive temperate landraces. This was the case for accessions from the kafir race and its intermediate forms and was consistent with the results shown in Fig. 2. As an example, the guinea-kafir intermediate from equatorial latitudes (1GK) was clustered with the kafir race from temperate latitudes (4K) (Table 3). Within the entire landrace collection, 16 race-latitudinal groups (1160 accessions) were classified as photoperiod-insensitive. A second cluster with 15 race-latitudinal groups (1062 accessions) was classified as mildly photoperiod-sensitive. The third cluster (10 630 accessions) included 19 race-latitudinal groups of photoperiod-sensitive landraces. Finally, the fourth cluster (9621 accessions) consisted of 10 race-latitudinal groups of highly photoperiod-sensitive landraces. Generally, the accessions in the ICRISAT sorghum landrace collection can be classified according to photoperiod sensitivity into clusters consistent with the evolution of the crop and the fit of landraces in cropping systems of the semiarid tropics.

Principal component analysis of the 10 morpho-agronomic variables explained 48.8% of the variance with the first two axes. The first axis accounted for 29.6% of the variance and the principal component scores were positively influenced by days to flower and plant height in the rainy season (factor loading 0.84 and 0.85, respectively) and in the post-rainy season (loading 0.70 for both variables). The second axis explained 19.2% of the variance and was positively correlated with grain size (loading 0.85) and 100-seed weight (loading 0.80). Fifty landraces were randomly chosen within each cluster and the first two principal component scores were plotted (Fig. 3). Although four well-differentiated and non-overlapping clusters were obtained from the race-latitudinal groups, great intra-cluster diversity was found. The

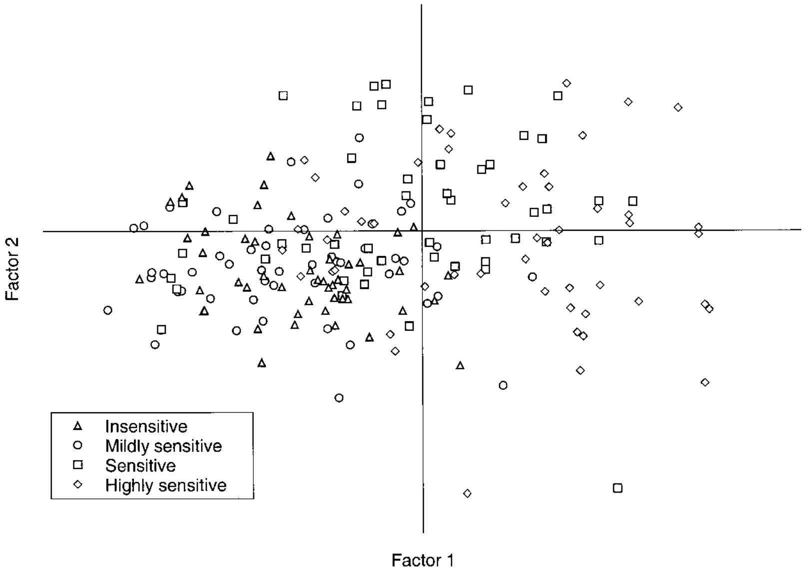

Fig. 3. Principal component analysis for 10 morpho-agronomic variables in the ICRISAT sorghum landrace collection. Bi-plot is shown for the rotated (Varimax) factor-scores for 50 accessions randomly selected within each cluster of photoperiod sensitivity. Cluster membership was defined from the eight photoperiod variables using the K-means procedure.

photoperiod-sensitive and highly photoperiod-sensitive landraces had a wider distribution of morpho-agronomic diversity, as described by the first two component scores. There was variability for the characters that described the first two components, although the distribution of the accessions within the photoperiod-insensitive and mildly photoperiod-sensitive clusters was reduced. For example, there were accessions within these two clusters that flowered early and had a shorter plant height with both small and large seed size. Conversely, large-seeded accessions had a smaller range of days to flowering and plant height. Thus there was no evidence of sharply reduced diversity within the two clusters and their value for breeding in the temperate regions was not limited. This result meets the objectives of the study since a stratification of the entire landrace collection was found that maintained morpho-agronomic diversity within each cluster. Hence, random sampling could be performed within each cluster to establish a core collection.

In conclusion, with the analysis of photoperiod response, race classification, and latitudinal range, we found clear structure to the diversity within the landrace collection of sorghum maintained at ICRISAT. For establishing a core collection, stratification according to photoperiod sensitivity is most efficient for sampling strategies, especially since the clusters are of unequal size (the largest cluster represents about 1/10 of the smallest one). Such unbalanced representation of clusters will prevent loose or defective sampling of small clusters. The use of a hierarchical stratification based upon an estimate of photoperiod sensitivity simplified the diversity among the entire landrace collection into four well-defined clusters. There was evidence that both natural selection for adaptation to environment and farmers' selection for specific use or specific cropping systems accounted for most of the morpho-agronomic diversity. The results of this study should enhance utilization of the sorghum landrace collection by allowing breeders to concentrate their evaluation on variation within the clusters as an initial focus. This will also assist in establishing core collections that can be used to facilitate the maintenance, evaluation, and use of the collection by curators, breeders, and farmers, respectively.

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