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Geographical patterns of phenotypic diversity and structure of Kenyan wild sorghum populations (*Sorghum* spp.) as an aid to germplasm collection and conservation strategy

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Abstract

Kenya lies within sorghum centre of diversity. However, information on the relative extent of diversity patterns within and among genetically defined groups of distinct ecosystems is lacking. The objective was to assess the structure and phenotypic diversity of wild sorghum populations across a range of geographical and ecological conditions in the country. Sixty-two wild sorghum populations (30 individuals per population) sampled from four distinct sorghum growing regions of Kenya and covering different agroecologies were characterized for ten qualitative traits. Plant height, number of tillers, panicle sizes and flag leaf dimensions were also recorded. Frequencies of the phenotypic classes of each character were calculated. The Shannon diversity index (H') was used to estimate the magnitude of diversity. Principal component analysis was used to differentiate populations within and between regions. Wild sorghum is widely distributed in Kenya, occurring in sympatric ranges with cultivated sorghum, and both have overlapping flowering windows. All characters considered displayed great phenotypic diversity. Pooled over characters within regions, the mean H' ranged between 0.60 and 0.93 in Western and Coast regions, respectively. Wild sorghum was found to show a weak regional differentiation, probably reflecting the importance of seed-mediated gene flow in shaping the wild sorghum population structure. Trait distribution was variable among regions, but there was no conspicuous distribution of the traits studied in any given region. Spontaneous hybridization and introgression of genes from cultivated to wild sorghum seems to be likely, and may already have occurred for a long time, although undocumented. Implications for *in situ* and *ex situ* genetic resources conservation are discussed.

Keywords: ecogeographical regions; gene flow; genetic resources; introgression; population structure; wild sorghum

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Introduction

Several wild sorghum species are recognized in Africa, but their morphological and ecological boundaries are not well defined. Species *Sorghum bicolor* (L.) Moench comprises the cultivated sorghum and its closely related wild relatives that have their natural range throughout Africa (De Wet, 1978; Duvall and Doebley, 1990). The three recognized subspecies of *S. bicolor* (L.) Moench in Africa are as follows: *S. bicolor* ssp. *bicolor* (L.) Moench (cultivated sorghum), *S. bicolor* ssp. *drummondii* (Steud.) De Wet and *S. bicolor* ssp. *verticilliflorum* (Steud.) De Wet. Four botanical ecotypes, corresponding to four of the Snowden's 'species' (Snowden, 1955), are recognized within *S. bicolor* ssp. *verticilliflorum* as follows: *S. aethiopicum*, *S. virgatum*, *S. arundinaceum* and *S. verticilliflorum*. Other wild sorghum species that exists in Africa include *S. almum* Parodi, *S. purpureo-sericeum* (Hochst. Ex A. Rich) Asch. & Schweinf, *S. halepense* (L.) Pers and *S. versicolor* Andersson (Price *et al.*, 2005).

The wild species of sorghum serve as a potential genetic resource for sorghum-breeding programmes (Rooney and Smith, 2000; Rosenow and Dahlberg, 2000). Many wild sorghum species contain resistances to major pests and diseases of cultivated sorghum such as shootfly, sorghum midges, sorghum ergot and downy mildew (Bapat and Mote, 1982; Karunakar *et al.*, 1994; Franzmann and Hardy, 1996; Sharma and Fransmann, 2001; Kamala *et al.*, 2002; Komolong *et al.*, 2002). *Striga* resistance mechanisms such as low germination stimulant production, germination inhibition and low haustorial initiation activity have been reported to occur in wild sorghum (Rich *et al.*, 2004). Good grain starch properties in wild sorghum could be used to improve feed or food digestion efficiency in cultivated sorghum (Dillon *et al.*, 2007).

More genes for desirable characters and higher biological yield are needed for progressive improvement of cultivated sorghum. The availability of such genes depends on identification of geographical regions with a concentration for various characters of agronomic value. The identification of such sites is of paramount importance for designing appropriate sampling strategies for germplasm collection and for selecting appropriate *in situ* sites to complement *ex situ* conservation efforts. Choice of sites for *in situ* conservation may depend on high diversity estimates based on markers or knowledge of adaptive traits linked to certain ecological conditions (Workeye, 2002), for example co-evolving host–pathogen systems and adaptation to other stress conditions.

The genetic diversity existing in wild sorghum in centres of origin represents one of the world's most important natural resources for future plant-breeding efforts and thus for global food security. On the other hand, gene flow between cultivated sorghum and their wild relatives is an important process that has strong implications for conservation of biodiversity and plant breeding. Conserving crop wild relatives *in situ* ensures that both the inherent genetic variability and very evolutionary processes that generate variability are conserved.

Kenya is a diverse country in terms of altitude, temperature, rainfall and soil types. Such diversity of ecological conditions is expected to cause existence of diverse vegetation, crop species and their wild relatives in many regions. In addition, the country lies within the broad geographical range where sorghum is believed to have been domesticated (De Wet, 1977; Mann *et al.*, 1983; Doggett, 1988). In Kenya, cultivated and wild sorghums grow sympatrically, which raises concerns on the extent and implications of crop-to-wild gene flow. Information on the relative extent of diversity patterns within and among genetically defined groups of distinct ecosystems is lacking. A number of genetic diversity studies have been carried out on cultivated sorghum in Kenya (Mutegi *et al.* unpublished data; Rabbi *et al.* unpublished data); however, information on wild sorghum is limited. Hence, this study was carried out to assess the structure and phenotypic diversity of wild sorghum populations across a range of geographical and ecological conditions in Kenya.

Materials and methods

Geographical distribution of wild sorghum populations

A field survey was conducted between June and August 2006 in four main sorghum-growing regions in Kenya (Fig. S2, available online only at http://journals.cambridge.org). In each region, the survey was conducted along an east–west transect, stopping at every 50 m fall in altitude. The latitude, longitude and elevation of each sampling site were recorded using a geographic positioning system. A questionnaire and direct observations were used to record additional data on wild sorghum: habitat and dispersal of wild sorghum. At each sampling site, 30 panicles of wild sorghum were collected. A total of 62 populations were collected consisting of 17, 12, 19 and 14 populations from Turkana, Western, Coast and Eastern regions of Kenya, respectively. A random sample of ten plants per population growing in the field was used to obtain data on plant height, number of tillers, panicle length and width, and flag leaf length and width. Ten qualitative traits, i.e. panicle compactness and shape, inflorescence exertion, awn at maturity, glume colour, glume hairiness, glume hair colour, grain cover, grain colour, grain plumpness and shattering, were evaluated using published sorghum descriptors (IBPGR/ICRISAT, 1993; Table 1).

Analysis of phenotypic diversity

Phenotypic frequency distributions of the characters within regions were worked out for all populations. The H was computed using phenotypic frequencies to assess the diversity for each character for the entire 62 populations and the populations of each region by Hutchenson (1970) as follows:

$$H = -\sum_{i=1}^{n} P_i \log_e P_i,$$

where P_i is the proportion of populations in the ith phenotype class and n is the number of classes for a given character. The standardized H' ranging from zero to one was obtained by dividing H by the $\log_e$ of the total number of phenotypic classes as follows:

$$H' = \frac{H}{\log_e n}.$$

Principal component analyses (PCA) of the phenotypic data were conducted using pertinent SAS procedures (SAS Institute, 2004).

Results

Geographical distribution of wild sorghum populations

Our survey revealed that wild sorghum is widely distributed in Kenya (Fig. S2, available online only at http://journals.cambridge.org), ranging in altitudes from 0 to 1480 m above sea level. Large wild sorghum populations were frequently observed in the surveyed regions, and occurred frequently in sympatric ranges with cultivated sorghum with which it shares overlapping flowering windows. Wild sorghum occurs in cultivated sorghum fields, fallow lands, crop margins, other crop fields and crop fields abandoned due to severe drought, pests, weeds or extreme nutrient deficiencies. It is also found in protected natural habitats such as national parks.

Various wild sorghums were observed in our study. Wild sorghum types with a closer resemblance to cultivated sorghum occurred mainly in crop habitats.

Table 1. Codes and description of traits recorded for wild sorghum populations

Trait	Code	Description	Code	Description
Panicle compactness and shape	1	Very lax panicle	5	Loose drooping primary branches
	2	Very loose erect primary branches	6	Semi-loose erect primary branches
	3	Very loose drooping primary branches	7	Semi-loose drooping primary branches
	4	Loose erect primary branches		
Inflorescence exsertion	1	Slightly exserted	3	Well-exserted
	2	Exserted		
Awn at maturity	1	Absent	2	Present
Glume colour	1	White	6	Purple
	2	Sienna	7	Black
	3	Mahogany	8	Grey
	4	Red		
Glume hairiness	1	Absent	2	Present
Glume hair colour	1	White	6	Black
	2	Sienna	7	Grey
	3	Mahogany	8	Cream
	4	Red	9	Brown
	5	Purple	10	Pink
Grain cover	1	25% grain cover	7	Grain fully covered
	3	50% grain cover	9	Glumes longer than grain
	5	75% grain cover		
Phenotypic grain colour	1	White	4	Brown
	2	Yellow	5	Buff
	3	Red		
Grain plumpness	1	Dimple	2	Plumb
Shattering	1	Very low	7	High
	3	Low	9	Very high
	5	Intermediate		

In contrast, wild types with a closer resemblance to true wild sorghum were found in crop margins, while 'true-to-type' wild sorghum was found mainly in national parks and roadsides away from farmland. Hybrid plants (intermediate types) were frequently observed in sorghum fields, fallow, other cereals fields, along the roads, river banks and water canals. Hybrids include plants showing phenotypic characteristics intermediate between cultivated andwild sorghums such as tallness, vigour, multiple tillers, compact to semi-compact panicle shape, absence of awn on the spikelet, seed shattering, open to semi-open glumes on the grain and medium to large seeds size.

Phenotypic diversity

Great diversity was observed in the field for both cultivated and wild sorghums. Apparently, there was high-level diversity for all traits analyzed (Table 2). Pooled over characters within regions, the mean of H' ranged from 0.60 in Western to 0.93 in Coast region.

The PCA did not differentiate wild sorghum populations strictly according to regions (Fig. 1). Turkana and Western populations were well differentiated, whereas Western populations were partly overlapping with others. Coast and Eastern populations were not differentiated. The first three principal components accounted for 58.03% of the total variation observed (Table 3). The first principal component (PC1) accounted for 25.76% of the total variance, and had high contributing factor loadings from glume hair, glume hair cover, awn, glume colour and shattering. The second principal component (PC2) accounted for 21.02% of the total variation, and had high contributing factor loadings from panicle compactness and shape, inflorescence exsertion, awn, shattering and glume cover. The third principal component (PC3) accounted for 11.24% of the total variation, and had high factor loadings for grain colour, glume colour, glume cover, shattering and inflorescence exsertion.

Character distribution pattern of wild sorghum

Plants with a very lax panicle were more frequent in the Coast region (Table S1, available online only at http://journals.cambridge.org). A very loose panicle type with erect primary branches dominated among Turkana's populations, while panicles with loose erect primary branches were only found in Coast populations. Generally, the majority of inflorescences were well exserted in all regions except Turkana where majority of the inflorescences were only slightly exserted.

The extent to which grains were covered by glume ranged from 50 to 100% with some populations having individuals whose glumes were longer than the grain. Individuals with mahogany glume hair colour types were found only in the Coast region, whereas individuals with grey and pink glume hair colour types were found only in Western and regions, respectively. Red glumes were found in all except in the Western region. The most frequent grain colour was brown. Furthermore, glume hairiness was expressed in all regions. White seeded populations were only reported in Turkana, whereas red seeded populations were reported in Coast and Eastern regions. Yellow seeds were predominantly found in the Coast region. Most populations exhibited plumb grains, with dimple occurring only in the Western region. The extent of shattering varied across regions, but majority of the populations across regions showed intermediate levels of shattering.

Coast populations had the most variable plant height, number of tillers, panicle length and width (Fig. S3, available online only at http://journals.cambridge.org). Turkana populations had the most variable flag leaf length. Generally, Western populations had taller plants, while Turkana populations had smaller panicles and the lowest variation in terms of plant height. Eastern populations had the lowest number of tillers.

Discussion

Our survey showed that wild sorghum co-exists with cultivated sorghum, either intermixed with crop plants

Table 2. Estimates of the standardized Shannon diversity index (H') for ten phenotypic traits in 62 wild sorghum by region of origin

Region	PCS	IE	GLC	GLCV	GLH	GLHC	Awn	GC	GP	S	Mean ± SE
Turkana	0.85	0.80	0.79	0.86	0.84	0.44	0.85	0.85	0.89	0.88	0.81 ± 0.04
Western	0.53	0.63	0.60	0.60	0.62	0.58	0.60	0.60	0.62	0.60	0.60 ± 0.01
Coast	0.78	0.96	0.94	0.97	0.94	0.85	0.95	0.96	1.00	0.98	0.93 ± 0.02
Eastern	0.63	0.73	0.66	0.70	0.70	0.50	0.69	0.72	0.74	0.70	0.68 ± 0.02
Overall	0.80	0.94	0.91	0.95	0.94	0.73	0.94	0.96	1.00	0.94	0.91 ± 0.03

PCS, panicle compactness and shape; IE, inflorescence exsertion; GLC, glume colour; GLCV, glume covering; GLH, glume hairiness; GLHC, glume hair colour; GC, grain colour; GP, grain plumpness; S, shattering.

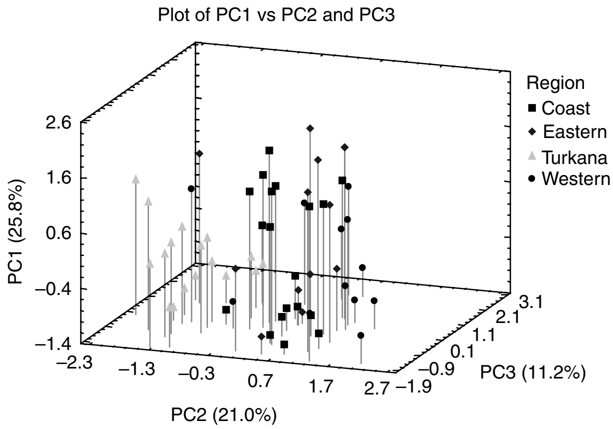

Fig. 1. Principal component analysis (PCA) based on ten qualitative phenotypic traits in 62 populations of wild sorghum collected from four regions of Kenya. Regions are identified by a different symbol.

or in adjacent habitats. Wild and cultivated sorghums have overlapping flowering windows and are known to be interfertile. This synchrony between cultivated and wild sorghums allows for crop-to-wild gene flow. Furthermore, seeds from wild plants could disperse into nearby farmers' fields, facilitating crop-to-wild gene flow in subsequent seasons. The abundance of intermediate types in the field is clear evidence that spontaneous hybridization between wild and cultivated sorghums is a common phenomenon in Kenya.

The great diversity of wild sorghum populations could be attributed to differences in the adaptation of different wild types to different habitats, human interference via selective rouging and presence of segregating populations derived from wild × crop hybridization. We frequently observed intermediate types in the fields, reflecting past hybridization and resultant introgression with cultivated sorghum. Under traditional sorghum farming systems, weeds including those of wild sorghum are removed manually from crop fields. Only those wild types difficult to distinguish from cultivated types at the vegetative stage are able to grow and produce an inflorescence. Some farmers leave some advanced segregating populations to mature and harvest their seeds for food. Though they do not directly replant such segregating populations, these hybrids do contribute to the next generation through pollen- or seed-mediated gene flow. While the control of wild sorghum is quite intensive in sorghum fields, this is not the case on the field edges or along irrigation canals partly because farmers use them for animal feeding, thatching houses, making baskets and traditional seats among others. Therefore, agricultural practices may have resulted in either depletion or build-up of a seed bank of wild types. A further study on the ecology, population genetics and phylogeography of wild crop sorghum co-existence is needed. There is also need to investigate wild sorghum status as an agronomic weed, and the extent to which they are sustained as genetically diverse genotypes.

Individual characters showed different levels of diversity in different regions. Although the highest phenotypic diversity of cultivated sorghum was reported in Turkana (Field observations; Mutegi, pers. commun. 2009), wild sorghum diversity was lower in Turkana than in the Coast region, which may be explained by the type of agricultural system practised. Turkana is a very dry region of Kenya, and crop production is only possible either under irrigation or on river banks. In either case, farmers cultivated sorghum in small family plots, and are able to apply highly selective rouging of wild weedy sorghum at very early stages of growth, usually before seed set. This may have resulted in the reduction of the wild sorghum seed bank and ultimately the lower diversity observed. As a consequence, this may reduce the probability of crop gene introgression into the wild gene pool.

The distribution of wild sorghum traits could be explained in two ways. Firstly, the pattern of morphotypes may be attributable to the specific climatic conditions in different regions, which may in turn lead to different evolutionary pathways. Secondly, the distribution pattern may reflect the distribution of different wild sorghum types found in Kenya. At least, five wild sorghum types are known to exist in Kenya (National Genebank of Kenya, NGBK; Kenya arboretum). However, these wild types have not been well characterized. Two or more wild races and/or species may be found in the same region, but may slightly differ from the same wild race and/or species in another region due to differential selection pressure. The majority of traits

Table 3. Factor loadings of the ten phenotypic traits for the first three principal components of a PCA and percentage variance accounted for 58.03% of the total variation observed

Trait	PC1	PC2	PC3
Panicle compactness and shape	−0.35	0.72	0.11
Inflorescence exsertion	0.38	0.67	−0.27
Glume colour	0.41	0.45	0.56
Glume cover	0.36	0.47	−0.38
Glume hair	−0.87	0.30	−0.04
Glume hair colour	0.86	−0.05	0.10
Awn	−0.52	0.56	0.17
Grain colour	0.17	0.17	0.62
Grain plumpness	−0.26	−0.09	−0.18
Shattering	0.38	0.51	−0.36
Percentage	25.76	21.02	11.24

studied here were not conspicuously unique to any single region. This could be attributed to gene flow as farmers move fodder and wild-cultivated sorghum seed admixtures from one region to another, thus overcoming regional boundaries. Nevertheless, the predominance of some phenotypic classes might indicate the adaptive role of certain traits such as panicle shape, seed colour and grain covering. Several studies indicated that phenotypic variation is apparently the result of an adaptive response to the environment (Bruschi *et al.*, 2003). In our study, a correlation between phenotypes and environmental conditions was not performed, as it was problematic to obtain reliable environmental data. Thirdly, crop-to-wild gene flow may also explain the distribution of morphotypes observed. Wild plants that acquire crop genes will continue to evolve, subject to natural selection pressure, resulting in new morphotypes.

Wild sorghums have previously been classified by phenotypic traits, e.g. panicle shape and size, plant height and leaf size (De Wet and Harlan, 1971; Harlan and de Wet, 1972; Doggett, 1988). Here, we tried to classify wild sorghum populations using mainly the panicle compactness and shape, panicle size and plant height. Turkana populations showed two groups of panicle compactness and shape (Table S1, available online only at http://journals.cambridge.org). The predominant group displayed very loose erect primary branches and large open panicles, and may be classified as *S. arundinaceum*. A further group had very lax panicles with spreading primary branches, and may be classified as *S. verticilliflorum*. According to De Wet (1978), *S. arundinaceum* is characterized by a large and open inflorescence, with flexible branches that are undivided at the base, while *S. verticilliflorum* has large inflorescences with spreading branches that are usually divided near the base.

Western populations consisted of four groups according to panicle compactness and shape. The first two most predominant groups were characterized by very lax panicles and very lose erect primary branches, and they may be classified as *S. verticilliflorum* and *S. arundinaceum*, respectively (Table S1, available online only at http://journals.cambridge.org). The third group was characterized by loose erect primary branches, variable but generally large panicles, and tall plants, and may be classified as subspecies *drummondii* (Smith and Frederiksen 2000). The fourth group was characterized by semi-loose erect primary branches and small and short panicles, and may be classified as *S. aethiopicum*. De Wet (1978) characterized *S. aethiopicum* by a relatively small, contracted inflorescence with sub-erect branches that are strongly divided.

Coast populations consisted of five groups according to panicle compactness and shape (Table S1, available online only at http://journals.cambridge.org), probably suggesting the existence of five wild races and/or species. The first and predominant group was characterized by very lax panicles with variable panicle sizes, and may be classified as *S. verticilliflorum*. However, within this group, we observed small and narrow leaved wild sorghum, which could belong to *S. aethiopicum*. The second group was characterized by very loose erect primary branched panicles, large leaves and glumes with inconspicuous awns. This group may be classified as *S. arundinaceum*. The third group was characterized by very loose drooping primary branches, with glumes longer than grains, small panicles, absence of awns and very low shattering ability. This population (our identification number: 36) occurred mainly on Manda Island. This may be a different wild sorghum species, probably *S. purpureo-sericeum*. An inventory of the NGBK also showed that a similar population (genebank accession number: GBK-044827) had earlier been collected in Eastern Kenya and classified as *S. purpureo-sericeum* (NGBK, pers. commun.). The fourth group was characterized by loose erect primary branched panicles, and it may be classified as subspecies *drummondii*. In Coast region, we found a conspicuous population, which was grown for fodder by a large-scale dairy farmer. This population was identified as *S. almum*, and was characterized by very lax panicles, large panicle sizes and very tall plants (>3 m).

Eastern populations consisted of four groups according to panicle compactness and shape (Table S1, available online only at http://journals.cambridge.org). The first two groups were characterized by very lax panicles and very loose erect primary branched panicles, and may be classified as *S. verticilliflorum* and *S. arundinaceum*, respectively. The third group was characterized by semi-loose erect primary branches and small and short panicles, and may be classified as *S. aethiopicum*.

Thus, the survey revealed that three of the four ecotypes within the subspecies *verticilliflorum* exist in Kenya. These are, according to Snowden 'species' classification, S. *verticilliflorum*, *S. arundinaceum* and *S. aethiopicum*. The survey excluded *S. virgatum*, which can easily be distinguished from the other ecotypes by its narrowly linear leaf blades that are rarely more than 2 cm wide (De Wet and Harlan, 1971) and its perennial nature (Murty *et al.*, 1967). It is worth noting that the ecotypes of subspecies *verticilliflorum* are morphologically and ecologically so closely related that they do not deserve a formal taxonomic status (De Wet, 1978; Dahlberg, 2000). The presence of subspecies *drummondii* was evident in the Western, Coast and Eastern regions where occurrence of shattercane-type weeds frequently occurred in abandoned sorghum fields. Though only the phenotypic traits have been used to classify wild sorghum, such traits, especially the quantitative traits (e.g. plant height and panicle sizes), generally are not reliable in taxonomy. This is because the environmental effects are unknown, just as in the case with herbarium samples.

Conclusion

Wild sorghum is widely distributed in major sorghum-growing regions in Kenya and displays great phenotypic diversity. Wild sorghum populations studied in these regions show a weak regional differentiation, probably reflecting the importance of seed-mediated gene flow in shaping the population genetic structure of wild sorghum. Generally, the high phenotypic diversity observed highlights the importance of *in situ* wild sorghum populations as reservoirs of genetic variability. There is need to systematically conserve these genetic resources as a safeguard against possible widespread genetic erosion. The findings in this study could help in planning and establishing priorities for future germplasm collection in the country. For example, areas such as the coast where relatively large variation was found could be targeted for broadening the genetic base of the existing *ex situ* sorghum collections in the country. Presently, *in situ* conservation of crop wild relatives including those of sorghum is presumably done in protected lands such as wildlife sanctuaries and forests. There is need toconduct extensive surveys in such protected areas with a view of mapping and characterizing the amount and patterns of variation in such populations. Depending on the outcome of such studies, new areas may be established in order to encompass more diversity. Spontaneous hybridization and introgression of genes from cultivated to wild sorghum and vice versa thus seems to be very likely. However, further characterization of the direction and level of such introgression is needed.

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