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RESEARCH ARTICLE

Geographical distribution of traits and diversity in the world collection of pearl millet [*Pennisetum glaucum* (L.) R. Br., synonym: *Cenchrus americanus* (L.) Morrone] landraces conserved at the ICRISAT genebank

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Abstract The genebank at ICRISAT conserves the largest collection of 23,092 pearl millet germplasm accessions originating in 52 countries. A total of 15,979 landraces originating in 34 countries and having geographic coordinates of the collection sites were selected to investigate the geographical distribution of pearl millet traits and diversity in the collection. Results revealed adaptation of pearl millet to latitudes ranging between 33.00°S and 36.91°N. Landraces with early flowering (33–40 days) were predominant in Pakistan, Ghana, Togo and India; with very late flowering (121–159 days) in Sierra Leone and the Central African Republic; with short plant height (80–100 cm) in India, Zambia and Sudan; with tallness (401–490 cm) in Chad, Burkina Faso, Nigeria and the Central African Republic; with high tillering (11–35) in India and Yemen; with high panicle exsertion (11–29 cm) in Ghana, Chad, India and Yemen; with long panicles (75–135 cm) in Nigeria and Niger; with thick panicles (41–58 mm) in Namibia, Togo and Zimbabwe and those with large seeds (16–19 g 1000 seeds^{-1}) were predominant in Togo, Benin, Ghana and Burkina Faso. Collections from Ghana for flowering (36–150 days), Burkina Faso for plant height (80–490), India and Yemen for total (1–35) and productive (1–19) tillers per plant, Niger for panicle exsertion (−45 to 21.0), panicle length (9–135 cm) and thickness (12–55 mm) and Zimbabwe for 1000 seed weight (3.5–19.3 g), were found as important sources for trait diversity. Launching collection missions for trait-specific germplasm is suggested to enrich the world collection of pearl millet at ICRISAT genebank for diversity.

Keywords Collection · Distribution · Diversity · Landrace · Latitude · *Pennisetum glaucum* · Variability

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Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br., synonym: *Cenchrus americanus* (L.) Morrone] is an

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important food and fodder crop. It is also used as poultry feed, animal feed and for alcohol extraction. It has great potential because of its ability to adapt well to the extreme limits of agriculture. It is assumed that it is cultivated in an area of about 30 m ha (Yadav and Rai 2013) mostly in Niger, Nigeria, Burkina Faso, Togo, Ghana, Mali, Senegal, the Central African Republic, Cameroon, Sudan, Botswana, Namibia, Zambia, Zimbabwe and South Africa in Africa and in India, Pakistan and Yemen in Asia. Its cultivation is being expanded into some non-traditional regions such as Brazil, USA, Canada, Mexico, West Asia and North Africa (WANA) and Central Asia.

Pearl millet was originated in a diffused belt stretching from western Sudan to Senegal and domesticated some 4000 years ago at its place of origin. It is endowed with enormous genetic variability for various morphological, yield, adaptation and quality traits and stress resistance (Brunken et al. 1977; Harlan 1971). Progressive adaptation to a wide range of environments responding to various selection pressures including human intervention has resulted in characteristic intra-specific diversity and differentiation represented by many landraces with specific eco-geographical origins (Teshome et al. 2001). The effects of changing climate on crops are complex because different species have different base and optimum temperature and photoperiod requirement for development. Within the species, the distribution and performance of trait-specific genotypes will be different. For example, flowering of pearl millet was delayed and less synchronized under dryland conditions (Pearson and Coaldrake 1983). Therefore, knowledge of the geographical distribution of different traits, particularly those of desirable traits of a species and the diversity available in the germplasm collections are critical to explore potential areas for targeted trait-specific germplasm and for enhanced utilization of large germplasm collections conserved in genebanks. Such studies are also useful for in situ conservation of germplasm, identification of suitable locations for pearl millet introduction and for evaluation of trait-specific germplasm. Researchers have found that when genetic resources are accompanied by geospatial data, they are more useful to study distribution and diversity of the species (Day Rubenstein et al. 2006). The availability of different domain specific tools such as diversity analysis and hot-spot analysis in geographic information systems have opened up avenues to assess the geographical distribution of different traits in large germplasm collections that are being conserved at national and international genebanks. Linking the genetic structure of landrace collections to geographical and environmental data will reveal valuable information to breed cultivars suitable for specific environments and farming practices. Preliminary morphological characterization of landraces reveals considerable variation between and within collection sites for many agronomically important traits. Such genetic variation in adaptive responses is little known and understood.

Systematic efforts were made at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) to collect and conserve the pearl millet diversity and thus 23,092 accessions including 809 accessions of wild relatives, originating in 52 countries, were assembled. Though the collection is large, studies on geographical distribution of traits in the world collection of pearl millet are meagre. Therefore, in this article, the geographical distribution of traits and diversity in the world collection of pearl millet landraces conserved at the ICRISAT genebank was studied.

Materials and methods

Geographical distribution of traits

The experimental material in the present study consists of passport and characterization data of pearl millet germplasm assembled at the ICRISAT genebank, India. By the end of year 2015, genebank at ICRISAT assembled 23,092 accessions of pearl millet germplasm from 52 countries, including landraces (19,885), breeding materials (2269), advanced cultivars (129) and wild relatives (809). Of the total landraces, 15,979 from 34 countries, having geographic coordinates were used to reveal the geographical distribution of trait-specific pearl millet. Georeferenced data for collection sites of landraces were validated and plotted using ArcGIS 10.1. Before plotting, landraces were grouped based on their agronomic performance, as early (33–40 days), medium (41–80 days), late (81–120 days) and very late (121–159 days) for days to 50 % flowering; and as short (80–100 cm), medium (101–200 cm), medium-tall (201–300 cm), tall (301–400 cm) and very tall (401–490 cm) for plant height. Total tillers per plant was grouped as low (1–5), moderate (6–10), high (11–15) and very high (16–35) and productive tillers per plant as low (1–5), moderate (6–10) and high (11–19). Landraces for panicle exsertion were grouped as low (−45 to 0 cm), medium (1–10 cm), high (11–20 cm) and very high (21–29 cm); for panicle length as very small (5–25 cm), small (26–50 cm), medium (51–75 cm), long (76–100 cm) and very long (101–135 cm); for panicle thickness as thin (10–20 mm), medium (21–40 mm) and thick (41–58 mm) and for 1000 seed weight as small (1–10 g), medium (11–15 g) and large (16–19 g).

Characterization of germplasm

The pearl millet germplasm landraces were characterized in batches of 500–1000 every year at ICRISAT farm, Patancheru (17.53°N latitude, 78.27°E longitude and 545 m.a.s.l.), in alfisols, during the rainy and postrainy seasons, from 1974 through 2013, for 21 morphoagronomic traits following descriptors for pearl millet (IBPGR and ICRISAT 1993). The rainy season crop was raised during June to October and the postrainy season crop during November to March of the subsequent year. At the Patancheru location, the monthly mean day length ranged from 11.7 to 13.20 h in the rainy season and from 11.10 to 12.0 h in the postrainy season. Minimum temperature during the crop period varied from 20.4 to 22.4 °C in the rainy season and from 11.4 to 19.4 °C in the postrainy season. Maximum temperature varied from 28.2 to 32.8 °C in the rainy and from 27.8 to 33.1 °C in the postrainy season. Fertilizers were applied at the rate of 100 kg ha^{-1} N and 40 kg ha^{-1} P_2O_5 in both the seasons. Every year, landraces were grown in augmented design using one of the three checks repeated for every block of 20 test accessions. Each landrace was sown in two 4 m long rows. The spacing between rows was 75 cm. The seed was sown using a tractor mounted four-cone planter. The crop was thinned 15–20 days after sowing to maintain approximately 10 cm spacing between plants thereby accommodating about 40 plants within a row. Life saving irrigation was provided during the rainy seasons while the crop was irrigated at regular intervals during the postrainy seasons to provide sufficient moisture to the growing crop. The crop was protected from weeds, pests and diseases to raise a good crop.

Excluding the countries (Ethiopia, The Maldives, Mauritania and Somalia) with less than five landraces, a final set of 15,969 from 30 countries were used to assess the diversity in the collection. Characterization data for eight important quantitative traits (days to 50 % flowering, plant height, total and productive tillers per plant, panicle exsertion, length and thickness and 1000 seed weight) and eight qualitative traits (panicle shape and density, bristle length, seed shape and color, endosperm texture, green fodder yield potential and seed yield potential) were retrieved from the ICRISAT pearl millet germplasm characterization database to assess the diversity in the collection. All observations, except seed traits were recorded in the rainy season. Observations on days to 50 % flowering, plant height, panicle length and thickness were recorded both in the rainy and postrainy seasons. Plant height, number of total and productive tillers per plant, panicle length, thickness and exsertion were recorded as the mean of five representative plants. Emergence of the stigma in 50 % of the plants in a plot (accession) was recorded as days to 50 % flowering (IBPGR and ICRISAT 1993). Height from the base to the tip of the panicle in centimeters was recorded as plant height. Number of total and productive tillers per plant was counted. Distance between the ligule of the flag leaf and the base of the panicle was recorded as panicle exsertion in centimeters. Length of the panicle was recorded in centimeters, while panicle thickness at maximum was recorded in millimeters. Panicle shape was recorded on a majority basis in a plot using descriptors for pearl millet. Panicle density, bristle length, green fodder yield potential and seed yield potential of the landraces were scored on a 1–9 scale, 1 being the poorest and 9 the best. Green fodder yield potential was recorded considering the plant height, tillering and leafiness of the landraces, while the seed yield potential was scored on the basis of the number of productive tillers, spikelet density, panicle length and thickness and seed size. For convenience, scoring on panicle density was further grouped; a score of 1–3 as loose, 4–6 as semi-compact and 7–9 as compact. Similarly, score on bristle length was grouped; a score of 1–3 as short, 4–6 as medium and 7–9 as long bristles. Score for green fodder yield and seed yield potential were recorded as low (score 1–3), moderate (4–6) and high (7–9). As the seed quality of harvests in the postrainy season was good, observations on all seed traits were recorded during the postrainy season. Weight of 1000 seeds drawn from the plot harvest was recorded in grams. Seed shape and color was recorded from the harvest of the plot in the postrainy season following descriptors for pearl millet. Endosperm texture was recorded by cutting five seeds per landrace and scoring corneous and starchy portions on a 1–9 scale. A score of 1–3 was recorded as mostly corneous, 4–6 as partly corneous and 7–9 as mostly starchy.

Data analysis

Quantitative data were analyzed using the residual maximum likelihood procedure in the GenStat 13.1 release (VSN International 2010). Range and means were calculated for eight quantitative traits and mean values of different traits were compared using Newman–Keuls procedure (Newman 1939; Keuls 1952). Mean values with different alphabets as suffix were considered as significant. The Shannon–Weaver diversity index (H′) calculated following GenStat 13.1, was used to measure and compare the phenotypic diversity for quantitative and qualitative traits in the collection from individual countries (Shannon and Weaver 1949). Frequencies were estimated for each group of all qualitative traits under study.

Climate data

Climatic data such as monthly mean (over the past 30 years) day length, minimum and maximum temperature and annual mean rainfall for each collection site, was downloaded from http://www.worldclim.org/current using the spatial analyst extension in ArcGIS® software in June 2014 (Hijmans et al. 2005) to study the spatial relationship between environmental variables and the type of material adapted at different locations. The lowest and highest monthly mean of minimum and maximum day length and temperature for each country were estimated. Association of climate and adaptation of trait-specific pearl millet and diversity in each country was discussed in this paper.

Results

Collection

The pearl millet collection under study includes 15,979 landrace accessions from 34 countries. India represented with a maximum number of landraces (5348) followed by Nigeria (1537), Namibia (1059), Mali (1040) and Zimbabwe (1015), while the remaining countries were represented with <1000 landraces. Ethiopia, The Maldives, Mauritania and Somalia were represented with less than five landraces. The collection under study was from a wide range of latitudes ranging between 33.00°S and 36.91°N indicating the wide adaptation of pearl millet.

Geographical distribution of traits

Knowledge of geographical distribution of traits is important for genebank curators to be able to plan future collections to fill trait-specific diversity gaps in the collection. Mapping of 15,979 landraces, using ArcGIS®, revealed interesting and useful information on the geographical distribution of pearl millet traits (Figs. 1, 2).

Quantitative traits

Plotting of landraces and frequency distribution of promising sources for different quantitative traits revealed relatively high frequency of early flowering (33–40 days) landraces in Pakistan (18 %) followed by Ghana (7.9 %) and Togo (2.7 %) (Table 1). Very late flowering (121–159 days) landraces were common in Sierra Leone (96.6 %), the Central African Republic (88.0 %), Benin (47.8 %) and Cameroon (41.0 %). Only 14 landraces from India and two each from Zambia (IP 8848 and IP 8853) and Sudan (IP 8014 and IP 10712) grew to a height of 80–100 cm. Very tall growing (401–490 cm) landraces were found at high frequencies in Chad (43.0 %), Burkina Faso (9.0 %), Nigeria (4.2 %), the Central African Republic (3.5 %) and Togo (1.6 %) (Fig. 1; Table 1). Twenty six landraces from India (0.5 %) and five from Yemen (1.9 %) had a very high number of total tiller per plant (15–35), while 25 landraces from India and three (IP 20266, IP 20348 and IP 20349) from Yemen produced more productive tillers per plant (11–19) (Fig. 1). Positive panicle exsertion was considered as a desirable trait for good quality seed and landraces showing high panicle exsertion (11–29 cm) were distributed at high frequencies in Ghana (20.9 %), Chad (15.1 %), India (14.3 %), Yemen (11.9 %), Pakistan (11.3 %) and Burkina Faso (10.4 %) (Fig. 2). A maximum of 47 landraces (3.1 %) from Nigeria and 40 (4.1 %) from Niger produced long panicles (75–135 cm), while 21

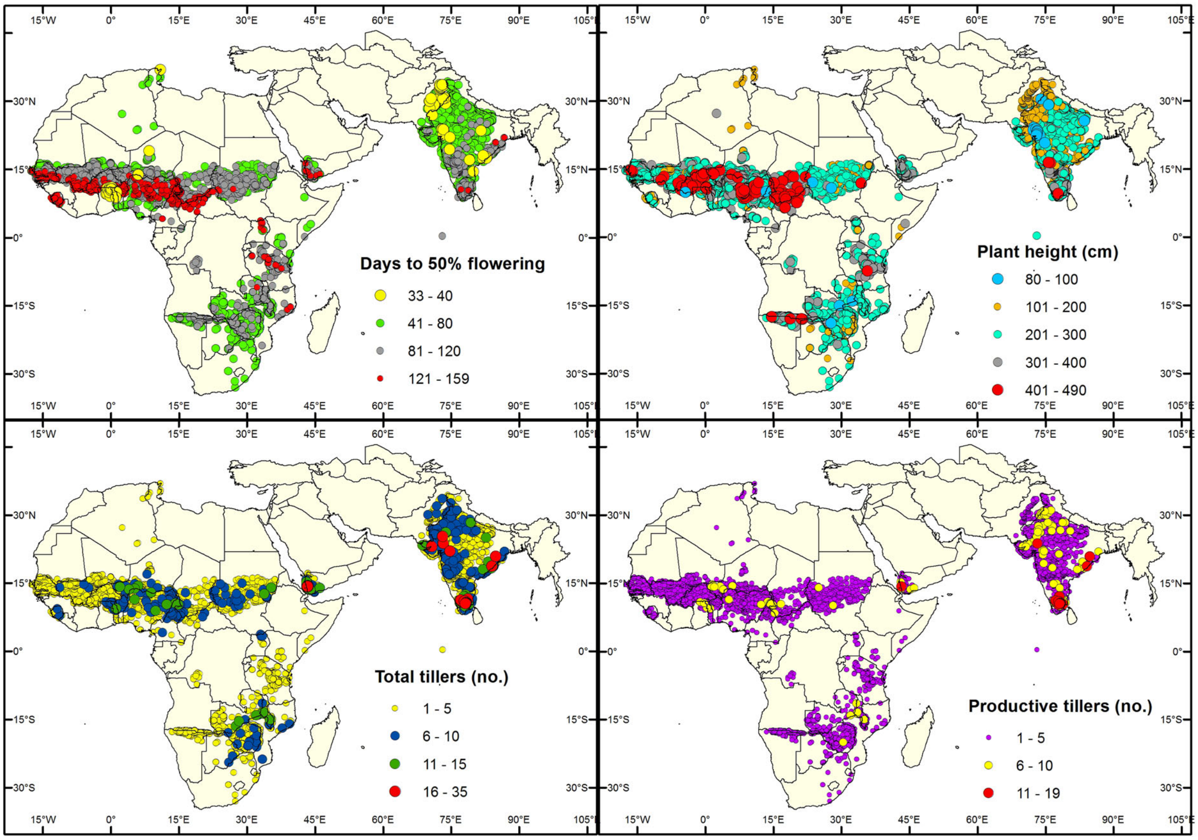

Fig. 1 Geographical distribution of pearl millet traits: Days to 50 % flowering, Plant height (cm), Total tillers per plant (no.) and Productive tillers per plant (no.)

(2.0 %) landraces from Namibia, 13 (2.7 %) from Togo and 12 (1.2 %) from Zimbabwe were the important source countries for thick panicle pearl millet (41–58 mm) (Fig. 2). Seed size is an important trait contributing to the seed yield per plant and a high frequency of landraces from Togo (20.2 %), Benin (13.0 %), Ghana (6.1 %) and Burkina Faso (3.3 %) produced larger seeds (16–19 g 1000 seeds^{-1}). Among the countries, India was identified as a promising source country for eight traits, followed by Niger (6), Burkina Faso (6), Ghana (5), Mali (5), Nigeria (5) and Yemen (5).

Qualitative traits

Panicle shape Panicle shape in pearl millet is useful in differentiating landraces. Nine panicle shapes (cylindrical, conical, club, candle, dumb-bell, lanceolate, spindle, oblanceolate and globose) were found in the collection under study (ESM Table 1). In the entire collection, 51 % landraces produced candle shaped panicles, 26 % produced cylindrical panicles, 12 % produced lanceolate panicles and 7.5 % landraces produced conical panicles. All other types were <2 % of the total collection. Frequency distribution of landraces for panicle shapes indicated that pearl millet producing candle shaped panicles is more common in Benin, Burkina Faso, Algeria, India, Kenya, Namibia, Niger, Nigeria, Pakistan, Senegal, Sierra Leone, Uganda, Yemen, Zaire and Zimbabwe. Conical panicles in Togo; cylindrical ones in Gambia, Mozambique, Malawi and Chad; lanceolate ones in South Africa, and spindle shaped ones in Tunisia were predominant (>50 %). Landraces from India, the Central African Republic, Cameroon, Sudan, Botswana, Tanzania, Zimbabwe, Burkina Faso, Ghana, Mali, Niger, Nigeria and Togo produced more than five panicle shapes. All nine panicle shapes were found in the collection from Zimbabwe indicating a high diversity for panicle shape in the collection from this country.

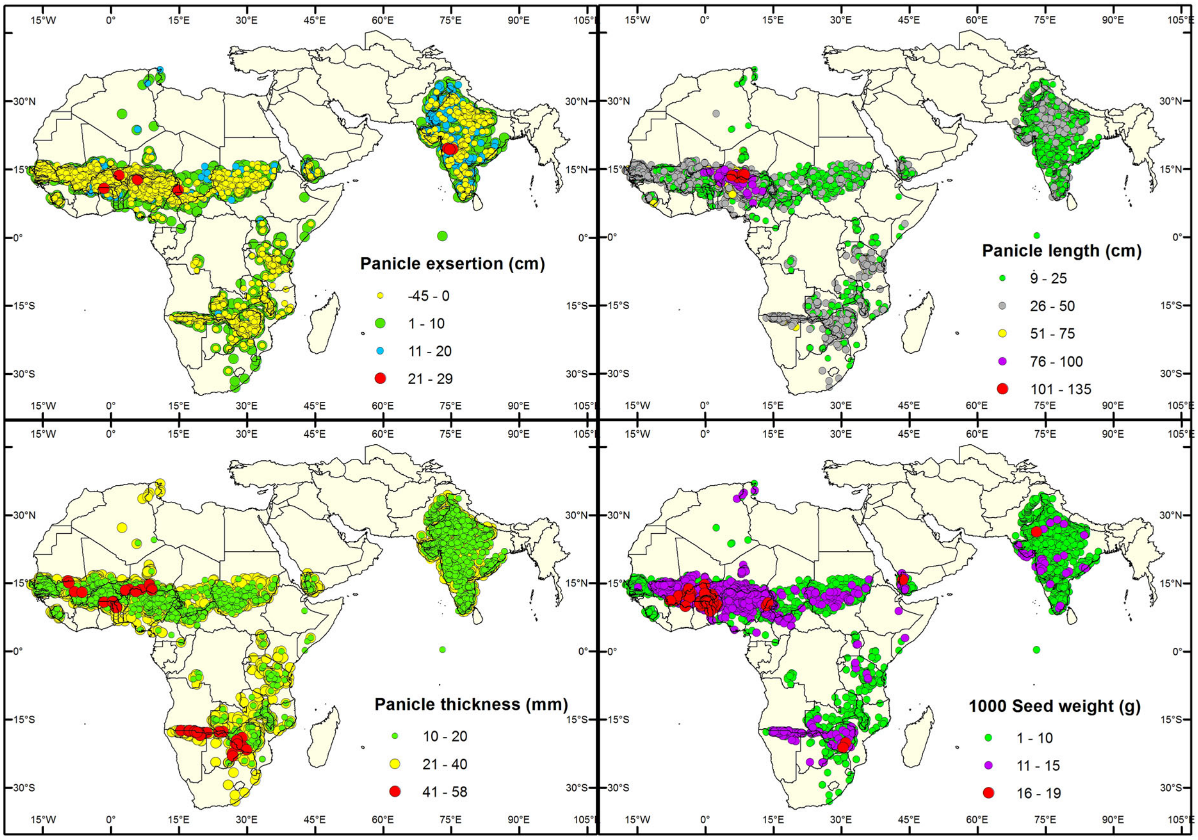

Fig. 2 Geographical distribution of pearl millet traits: Panicle exsertion (cm), Panicle length (cm), Panicle thickness (mm) and 1000 Seed weight (g)

Panicle density Panicle density is one of the important traits contributing to seed yield in pearl millet. The semi-compact panicle type was the most predominant type (83.7 %), and the remaining landraces had compact panicles. More than 60 % of the landraces from all countries, except Ghana, Mauritania, Tunisia and Yemen produced semi-compact panicles (ESM Table 1). A high frequency of landraces producing compact panicles were found in the collections from Ghana (55 %), Mauritania (75 %), Burkina Faso (20 %), the Central African Republic (35 %), Cameroon (32 %), Mozambique (32 %), Sudan (23 %), Senegal (27 %), Sierra Leone (25 %) and Somalia (25 %).

Bristle length Landraces with long bristles are useful in developing bird tolerant varieties. The long bristles of the panicle penetrate the eye of the bird therefore this serves as a self-defense mechanism to scare birds. A maximum of 15.9 % landraces from Botswana followed by 6.6 % from Zambia, 3.5 % from Senegal and 3.2 % landraces from Mozambique produced longer bristles (score 7–9) (ESM Table 1). A total of 96 % of the entire collection produced short bristled landraces (score 1–3), and these were predominant (>70 %) in all the countries (ESM Table 1).

Seed shape Five seed shapes [elliptical (23.8 %), globular (25.4 %), hexagonal (15.5 %), oblanceolate (18 %) and obovate (17.3 %)] were found in the collection (ESM Table 1). Landraces producing elliptical seeds (>50 %) were predominant in Yemen, Zaire, Chad, Sierra Leone and Tunisia; globular seeds in the Central African Republic Cameroon, Sudan, South Africa, Benin, Burkina Faso and Togo; hexagonal seeds in Ghana; oblanceolate seeds in Pakistan and Mozambique and obovate seeds in Kenya and Malawi. Twenty three countries represented all the five panicle shapes indicating high diversity for panicle shape in the collections from these countries.

Table 1 Geographical frequency (%) distribution of trait-specific pearl millet landraces in the world collection at ICRISAT genebank, India

Country	No. of accessions	1[a]	2	3	4	5	6	7	8	9	10
Asia											
India	5348	0.3	0.1	0.3	0.1	0.5	0.5	14.3			0.02
Pakistan	150	18.0						11.3			
Yemen	269		3.0			1.9	1.1	11.9			0.74
East Africa											
Kenya	18							5.6			
Malawi	296							0.3			
Sudan	586		0.5	0.3	0.2			4.4			
Tanzania	412		5.8		0.2			2.4			
Uganda	65		23.1					1.5			
South Africa											
Botswana	82									2.4	
Mozambique	31		6.5								
Namibia	1059				0.6			1.8		2.0	
South Africa	34										
Zaire	11										
Zambia	152		0.7	1.3				1.3			
Zimbabwe	1015			0.1				2.8		1.2	0.20
West and Central Africa											
Algeria	5							20.0			
Benin	46		47.8					4.3			13.0
Burkina Faso	512		24.4	0.2	9.0			10.4	0.2		3.3
C. African Rep.	142		88.0		3.5			1.4			
Cameroon	909		41.0	0.1				6.3			0.2
Chad	93		2.2		43.0			15.1			
Gambia	15							6.7			
Ghana	278	7.9	2.9					20.9		0.4	6.1
Mali	1040		9.3		0.7			4.9		0.3	0.4
Niger	970	0.2	0.1		0.6			3.7	4.1	0.6	
Nigeria	1537		14.4		4.2			3.0	3.1	0.1	
Senegal	339		9.4		0.6			1.2			
Sierra Leone	59		96.6								
Togo	490	2.7	12.4		1.6			9.2		2.7	20.2
Tunisia	6	16.7						33.3			
Total collection	15,969	0.5	7.4	0.1	1.2	0.2	0.2	8.0	0.5	0.4	0.9

[a] 1 = Early flowering (33–40 days), 2 = late flowering (121–159 days), 3 = short height (80–100 cm), 4 = tall (401–490 cm), 5 = high total tillers per plant (16–35), 6 = high productive tillers per plant (11–19), 7 = high panicle exsertion (11–29 cm), 8 = long panicle (75–135 cm), 9 = thick panicle (41–58 mm) and 10 = large seeds (>15 g 1000 seeds^{-1})

Seed color Ten different seed colors, brown (2.3 %), cream (4.3 %), deep grey (7.3 %), grey (49.6 %), grey brown (32.0 %), ivory (0.9 %), purple (0.8 %), purplish black (0.1 %), yellow (2.8 %) and a mixture of white and grey (0.2 %) were found in the collection (ESM Table 1). The collection from Sudan represented all ten colors indicating high diversity for seed color. Landraces from 13 countries produced more than five seeds colors. Landraces producing grey seeds were predominant (49.6 %) in the collection followed by those that produced grey brown seeds (32.1 %). As many as 11 countries were found as the predominant sources with more than 50 % of the landraces producing grey seeds. Landraces from Sierra Leone (76.3 %), Cameroon (30.7 %), the Central African Republic (27.5 %), Chad (15 %), Namibia (14 %) and Zamiba (11 %) produced farmer preferred cream color seeds. Similarly, considerable number of landraces from Ghana (5.8 %), Cameroon (5.4 %), the Central African Republic (4.9 %), and Namibia (2.3 %) produced ivory color seeds. Maximum number of landraces (39 %) from Sudan produced yellow seeds.

Endosperm texture Thirteen per cent of landraces in the collection produced mostly corneous, 63 % produced partly corneous and 24 % produced mostly starchy seeds (ESM Table 1). More than 50 % of landraces from 23 countries produced partly corneous endosperm. Mozambique (81 %) and Sierra Leone (78 %) are the important sources for pearl millet producing mostly corneous seeds. More than 50 % of the landraces from Benin, Burkina Faso and Sudan produced mostly starchy seeds.

Green fodder yield potential As many as 53.4 % of the landraces in the collection performed well and scored high (score 7–9) for this trait (ESM Table 1). Forty five per cent of the landraces performed moderately and 1.5 % performed poorly for green fodder yield. More than 50 % of the landraces from Burkina Faso, the Central African Republic, Cameroon, Gambia, Mali, Namibia, Nigeria, Senegal, Chad, Togo, Tanzania, Yemen, South Africa, Zaire and Zambia scored high (score 7–9) for green fodder yield potential.

Seed yield potential Eighty three per cent of the collection under study performed moderately for seed yield potential and fifteen per cent performed well with a high score for this trait (ESM Table 1). Pearl millet from Ghana (75 %), Botswana (27 %), Namibia (42 %) and Togo (26 %) had a high score (score 7–9) for seed yield potential.

Geographical distribution of diversity

Range

Wide variation was observed for all quantitative traits under study. The collection from Asian countries varied widely for total as well as productive tiller number (Table 2). On the other hand, collections from countries of Southern Africa varied widely for panicle thickness and seed weight, and the collections from West and Central African countries for days to 50 % flowering, plant height, panicle exsertion and panicle length. Among the countries, collection from Ghana for flowering (36–150 days), Burkina Faso for plant height (80–490), India and Yemen for total (1–35) and productive (1–19) tillers per plant, Niger for panicle exsertion (−45 to 21.0), panicle length (9–135 cm) and thickness (12–55 mm) and Zimbabwe for 1000 seed weight (3.5–19.3 g), were found as important sources for trait based variation.

Means

The Newman–Keuls test of significance for mean values indicated significant differences among the collections from different countries (Table 3). The landraces from Tunisia flowered significantly early (44 days). However, the collection from Tunisia did not differ significantly from the collection from Pakistan, Ghana, Algeria, India, Kenya, Togo, Botswana, Malawi and South Africa. Landraces from Chad grew tall (370.7 cm) and differed significantly from those originated in all other countries. Landraces from Burkina Faso, Namibia, the Central African Republic, Tanzania and Yemen also grew tall (more than 300 cm). On the other hand, landraces from Sierra Leone flowered significantly late, were short and produced more productive tillers with small seeds. Yemen found as an important source country for total tillers per plant had differed significantly from the collection of Namibia, Senegal and Tanzania. Significantly higher positive panicle exsertion was observed in landraces from Tunisia when compared to those from Zaire, Mozambique, Tanzania, Niger, Senegal, Nigeria, Sierra Leone and Gambia. Collections from Niger, Nigeria and Namibia were found to be significantly superior to the collections from other countries for panicle length. The longest panicles were found in

Table 2 Range of variation for different traits of pearl millet landraces from various countries, evaluated at ICRISAT, India

Country	No. of accessions	1[a]	2	3	4	5	6	7	8
Asia									
India	5348	33–139	80–416	1–35.0	1–19.0	−13 to 29	11–50	10–36	1.5–16.5
Pakistan	150	36–73	110–265	1.3–6.8	1–4.1	−9 to 13	13–35	15–26	5.7–9.9
Yemen	269	53–137	210–380	1–35.0	1–17.7	−10 to 15	15–50	18–35	4.0–15.8
East Africa									
Kenya	18	45–97	190–300	1–4.6	1–4.0	−10 to 13	17–30	19–32	4.8–8.8
Malawi	296	47–119	140–380	1–15.4	1–8.4	−18 to 11	16–42	16–36	3.3–9.7
Sudan	586	47–128	90–420	1–13.0	1–6.2	−15 to 17	13–42	13–37	2.9–14.9
Tanzania	412	47–135	190–401	1–4.3	1–4.3	−22 to 16	13–54	12–38	2.5–11.6
Uganda	65	45–143	115–330	1.4–5.8	1–5.0	−5 to 12	12–35	16–31	4.3–11.7
Southern Africa									
Botswana	82	43–105	160–300	1–6.8	1–3.0	−25 to 10	9–44	13–55	4.7–12.6
Mozambique	31	91–122	220–325	2.5–7.1	1.6–4.2	−8 to 8	15–36	15–40	3.3–7.0
Namibia	1059	47–87	170–430	1–3.5	1–3.0	−15 to 14	13–66	20–58	7.0–14.2
South Africa	34	50–71	170–310	1–4.3	1–3.0	−10 to 10	20–48	20–36	5.3–10.4
Zaire	11	81–91	270–340	1.4–2.8	1.2–2.4	−10 to 7	18–30	20–39	5.5–7.0
Zambia	152	45–121	94–380	1–14.6	1–6.2	−18 to 12	15–38	16–35	2.7–15.0
Zimbabwe	1015	44–98	90–380	1–9.4	1–5.8	−15 to 15	10–55	14–50	3.5–19.3
West and Central Africa									
Algeria	5	46–80	150–320	3–5.0	1.2–5.0	5–11	11–32	20–30	5.9–10.9
Benin	46	44–152	170–310	1–8.8	1–5.3	−15 to 11	14–60	19–33	6.8–19.3
Burkina Faso	512	43–146	80–490	1–5.0	1–4.3	−15 to 20	15–80	14–40	7.4–17.5
C. African R.	142	78–140	146–410	1.5–6.0	1.5–4.2	−6 to 13	11–32	14–32	4.8–12.8
Cameroon	909	56–146	100–400	1–10.5	1–9.5	−18 to 27	12–70	13–38	5.3–18.6
Chad	93	48–126	210–480	1–8.3	1–5.6	−17 to 20	16–45	16–30	5.5–11.5
Gambia	15	56–113	230–310	1–3.2	1–3.0	−10 to 12	23–46	19–30	5.0–8.8
Ghana	278	36–150	120–320	1–7.8	1–5.6	−11 to 22	12–36	17–42	5.5–18.6
Mali	1040	47–148	135–460	1–6.6	1–5.0	−18 to 20	15–56	17–44	5.0–16.4
Niger	970	39–122	110–440	1–14.3	1–8.6	−45 to 21	9–135	12–55	4.3–14.0
Nigeria	1537	45–144	140–470	1–13.3	1–7.0	−32 to 25	16–120	13–45	4.4–14.4
Senegal	339	47–134	141–420	1–5.0	1–5.0	−18 to 14	15–65	13–30	3.2–10.9
Sierra Leone	59	60–159	105–280	1–6.2	1–5.3	−11 to 10	17–70	16–33	3.2–5.3
Togo	490	36–149	108–460	1–11.7	1–6.5	−20 to 16	9–50	16–53	4.1–18.4
Tunisia	6	40–47	140–180	3.2–4.4	2.5–3.3	5–15	12–17	30–40	9.0–12.0

[a] 1 = Days to 50 % flowering, 2 = plant height (cm), 3 = total tillers per plant (no), 4 = productive tillers per plant (no), 5 = panicle exsertion (cm), 6 = panicle length (cm), 7 = panicle thickness (mm), 8 = 1000 seed weight (g)

the collection from Niger. Landraces from Tunisia, Togo and Namibia produced thick panicles, which differed significantly from those of all other countries. Landraces from Togo, Ghana and Benin were found to be good sources for large seeds, and differed significantly from those originated in all other countries.

Phenotypic diversity

Quantitative traits The Shannon–Weaver diversity index (H′) was calculated for all quantitative traits (Table 4) to measure allelic richness and evenness. A low H′ value indicates low diversity, while a high H′

Table 3 Mean* values for different traits of pearl millet landraces from various countries, evaluated at ICRISAT, India

Country	1[aa]	2	3	4	5	6	7	8
Asia								
India	60.4 fghij	217.5 fghi	3.3 abc	2.5 abcde	6.6 abc	22.5 cdefg	21.8 efghijk	7.4 hijklm
Pakistan	47.3 ij	160.6 i	3.4 abc	2.4 abcde	7.6 ab	21.7 defg	20.2 ghijk	7.6 fghijklm
Yemen	80.5 efg	303.0 bcd	4.4 a	2.8 abcd	7.8 ab	23.2 cdefg	23.9 efghij	8.5 defghijk
East Africa								
Kenya	61.9 fghij	231.4 defgh	2.7 abc	2.4 abcde	4.6 abcde	24.0 cdefg	24.7 defghi	7.3 hijklm
Malawi	64.8 efghij	243.9 cdefg	2.8 abc	2.5 abcde	1.6 abcde	26.0 cdefg	22.4 efghijk	6.7 jklm
Sudan	86.1 ef	250.4 bcdefg	3.2 abc	2.1 abcde	3.4 abcde	23.2 cdefg	22.1 efghijk	8.8 defghij
Tanzania	107.4 cd	303.7 bcd	1.6 bc	1.3 cde	−2.3 cde	31.1 bcdef	25.3 defgh	6.9 ijklm
Uganda	76.1 efgh	214.8 fghi	3.2 abc	2.8 abcd	4.9 abcde	23.5 cdefg	23.4 efghij	7.9 fghijklm
Southern Africa								
Botswana	63.7 efghij	223.1 efghi	2.7 abc	1.7 bcde	1.6 abcde	24.4 cdefg	26.1 defg	8.2 efghijkl
Mozambique	112.1 bc	277.1 bcdef	3.9 ab	2.7 abcd	−2.5 cde	24.7 cdefg	21.0 fghijk	4.6 no
Namibia	72.5 efgh	320.8 b	1.3 c	1.2 de	1.3 abcde	38.3 ab	30.9 abc	9.8 def
South Africa	65.5 efghij	230.6 defgh	2.1 abc	1.6 bcde	2.6 abcde	33.0 bcde	27.2 cde	8.4 efghijk
Zaire	85.3 ef	297.3 bcde	2.2 abc	1.8 abcde	−3.8 de	25.5 cdefg	23.6 efghij	5.9 mn
Zambia	73.9 efgh	243.9 cdefg	2.5 abc	1.8 abcde	1.2 abcde	26.5 cdef	24.7 defghi	6.4 klm
Zimbabwe	70.5 efghi	236.4 cdefgh	1.9 abc	1.6 bcde	3.4 abcde	30.7 bcdef	26.5 def	7.5 ghijklm
West and Central Africa								
Algeria	56.6 ghij	188.0 ghi	4.0 ab	2.8 abc	9.0 ab	19.2 fg	23.2 efghij	8.6 defghijk
Benin	108.0 cd	244.2 cdefg	4.0 ab	2.7 abcd	1.3 abcde	29.7 bcdef	24.9 defghi	12.2 ab
Burkina Faso	105.9 cd	322.5 b	2.0 abc	1.7 bcde	2.2 abcde	30.3 bcdef	23.8 efghij	11.7 bc
C. African R.	129.4 b	314.5 bc	3.4 abc	2.4 abcde	5.2 abcd	20.2 efg	19.2 ijk	9.1 defghi
Cameroon	114.6 bc	292.2 bcdef	3.0 abc	2.4 abcde	4.4 abcde	23.4 cdefg	21.8 efghijk	9.7 defg
Chad	89.8 de	370.7 a	2.8 abc	2.3 abcde	5.4 abcd	24.7 cdefg	22.4 efghijk	8.5 defghijk
Gambia	84.0 ef	272.7 bcdef	1.9 abc	1.8 abcde	0.3 bcde	35.3 bc	23.3 efghij	6.9 ijklm
Ghana	51.3 hij	213.6 fghi	2.6 abc	2.4 abcde	7.9 ab	19.6 fg	29.6 bcd	13.1 ab
Mali	86.1 ef	285.3 bcdef	2.2 abc	1.8 abcde	2.9 abcde	29.5 bcdef	25.6 defgh	9.5 defgh
Niger	74.7 efgh	265.5 bcdefg	1.9 abc	1.6 bcde	−2.2 cde	45.8 a	24.3 defghi	9.2 defghi
Nigeria	80.4 efg	290.7 bcdef	2.2 abc	1.7 bcde	−0.1 bcde	38.9 ab	24.4 defghi	9.2 defghi
Senegal	88.7 de	242.0 cdefg	1.6 bc	1.4 bcde	−0.2 bcde	33.4 bcde	20.9 fghijk	7.4 hijklm
Sierra Leone	146.4 a	160.1 i	3.9 ab	3.3 a	−0.0 bcde	26.1 cdefg	22.2 efghijk	4.3 o
Togo	63.4 efghij	232.3 defgh	3.0 abc	2.3 abcde	6.1 abc	21.5 defg	31.6 ab	13.8 a
Tunisia	43.8 j	166.7 hi	3.9 ab	2.9 ab	10.2 a	13.3 g	35.0 a	10.4 cde

* Mean values were tested using Newman–Keul's test. Mean values with different alphabets are significantly different at 0.05 probability

[aa] 1 = Days to 50 % flowering, 2 = plant height (cm), 3 = total tillers per plant (no), 4 = productive tillers per plant (no), 5 = panicle exsertion (cm), 6 = panicle length (cm), 7 = panicle thickness (mm), 8 = 1000-seed weight (g)

value indicates high diversity. The mean diversity index (H′) over countries varied from $H' = 0.488 \pm 0.0121$ for days to 50 % flowering and total tillers per plant to $H' = 0.575 \pm 0.013$ for 1000 seed weight. Among the countries, the mean diversity index over traits indicated the highest diversity ($H' = 0.593 \pm 0.013$) in the collection from Mali followed by the collection from Sudan ($H' = 0.593 \pm 0.017$). Diversity was low in the collection from Algeria ($H' = 0.379 \pm 0.029$),

Table 4 Country wise Shannon–Weaver diversity index (H′) for quantitative traits of pearl millet landraces from different countries, evaluated at ICRISAT, India

Country	1[a]	2	3	4	5	6	7	8	Mean	SE±
Asia										
India	0.584	0.628	0.449	0.463	0.626	0.626	0.639	0.628	0.580	0.028
Pakistan	0.544	0.550	0.607	0.608	0.474	0.599	0.633	0.594	0.576	0.018
Yemen	0.620	0.610	0.396	0.435	0.603	0.570	0.618	0.576	0.553	0.031
East Africa										
Kenya	0.423	0.515	0.542	0.565	0.472	0.505	0.542	0.507	0.509	0.016
Malawi	0.457	0.578	0.424	0.506	0.611	0.616	0.611	0.603	0.551	0.027
Sudan	0.627	0.627	0.502	0.542	0.596	0.606	0.627	0.620	0.593	0.017
Tanzania	0.549	0.626	0.486	0.397	0.614	0.618	0.619	0.630	0.567	0.030
Uganda	0.235	0.599	0.551	0.618	0.545	0.573	0.580	0.577	0.535	0.044
Southern Africa										
Botswana	0.567	0.597	0.507	0.487	0.554	0.581	0.560	0.613	0.558	0.015
Mozambique	0.460	0.561	0.436	0.573	0.507	0.541	0.452	0.486	0.502	0.018
Namibia	0.616	0.620	0.424	0.483	0.575	0.610	0.584	0.608	0.565	0.026
South Africa	0.412	0.559	0.447	0.470	0.326	0.570	0.593	0.561	0.492	0.033
Zaire	0.487	0.487	0.583	0.539	0.255	0.539	0.132	0.330	0.419	0.057
Zambia	0.423	0.609	0.379	0.455	0.567	0.618	0.604	0.593	0.531	0.034
Zimbabwe	0.630	0.629	0.424	0.430	0.603	0.639	0.590	0.588	0.567	0.031
West and Central Africa										
Algeria	0.413	0.217	0.292	0.413	0.413	0.413	0.413	0.458	0.379	0.029
Benin	0.471	0.602	0.579	0.590	0.564	0.497	0.597	0.607	0.563	0.018
Burkina Faso	0.590	0.608	0.554	0.494	0.619	0.540	0.625	0.625	0.582	0.017
C. African R.	0.536	0.572	0.621	0.565	0.591	0.612	0.614	0.609	0.590	0.011
Cameroon	0.559	0.632	0.551	0.501	0.559	0.580	0.634	0.608	0.578	0.016
Chad	0.596	0.579	0.524	0.505	0.593	0.556	0.600	0.592	0.568	0.013
Gambia	0.292	0.471	0.544	0.509	0.536	0.458	0.504	0.453	0.471	0.028
Ghana	0.246	0.606	0.526	0.503	0.583	0.566	0.588	0.612	0.529	0.042
Mali	0.596	0.636	0.542	0.537	0.608	0.621	0.577	0.630	0.593	0.013
Niger	0.601	0.621	0.297	0.365	0.634	0.616	0.593	0.629	0.545	0.047
Nigeria	0.445	0.618	0.454	0.418	0.538	0.578	0.581	0.627	0.532	0.029
Senegal	0.519	0.582	0.414	0.441	0.613	0.605	0.628	0.641	0.555	0.031
Sierra Leone	0.365	0.517	0.553	0.616	0.532	0.450	0.561	0.582	0.522	0.028
Togo	0.332	0.518	0.571	0.514	0.519	0.599	0.628	0.617	0.537	0.033
Tunisia	0.439	0.439	0.477	0.477	0.540	0.377	0.377	0.439	0.446	0.019
Mean	0.488	0.567	0.488	0.501	0.546	0.563	0.563	0.575	0.536	0.013
SE±	0.021	0.015	0.015	0.012	0.016	0.012	0.019	0.013		

[a] 1 = Days to 50 % flowering, 2 = plant height (cm), 3 = total tillers per plant (no), 4 = productive tillers per plant (no), 5 = panicle exsertion (cm), 6 = panicle length (cm), 7 = panicle thickness (mm), 8 = 1000-seed weight (g)

which was represented by only five landraces. Diversity index for individual traits indicated high diversity for flowering ($H' = 0.630 \pm 0.021$) in the collection from Zimbabwe, for plant height ($H' = 0.636 \pm 0.015$) in the one from Mali, for total tillers ($H' = 0.621 \pm 0.015$) in the one from the Central African Republic, for productive tillers ($H' = 0.618 \pm 0.012$) in the one from Uganda, for panicle exsertion (H′ = 0.634 ± 0.016) in the one from Niger, for panicle length (H′ = 0.639 ± 0.012) in the one from Zimbabwe, for panicle thickness (H′ = 0.639 ± 0.019) in the one from India and for 1000 seed weight (H′ = 0.641 ± 0.013) in the collection from Senegal.

Qualitative traits The Shannon–Weaver diversity index (H′) estimated for qualitative traits revealed high diversity for panicle shape (H′ = 0.640 ± 0.032) and bristle length (H′ = 0.769 ± 0.037) in the collection from Botswana; for panicle density (H′ = 0.740 ± 0.027) in the one from Cameroon; for seed shape (H′ = 0.681 ± 0.026) in the one from Uganda; for seed color (H′ = 0.699 ± 0.027) in the one from Chad; for endosperm texture (H′ = 0.797 ± 0.022) in the one from Senegal; for green fodder yield potential (H′ = 0.765 ± 0.025) in the one from Niger and for seed yield potential (H′ = 0.705 ± 0.025) in the collection from Tanzania (Table 5). Overall mean diversity ranged from H′ = 0.268 ± 0.070 (Pakistan) to H′ = 0.574 ± 0.41 (India) in Asia, from H′ = 0.432 ± 0.041 (Kenya) to H′ = 0.602 ± 0.035 (Tanzania) in East Africa, from H′ = 0.254 ± 0.058 (Zaire) to H′ = 0.578 ± 0.025 (Zambia) in Southern Africa and from H′ = 0.141 ± 0.060 (Tunisia) to H′ = 0.624 ± 0.039 (Senegal) in West and Central Africa. Overall mean diversity for different traits was highest in the collection from Senegal (H′ = 0.624 ± 0.039) and lowest in Tunisia (H′ = 0.141 ± 0.060). Mean diversity for countries was highest for endosperm texture (H′ = 0.670 ± 0.022) and lowest for bristle length (H′ = 0.331 ± 0.037).

Climate

A clear association of latitude and climatic variables at collection sites was observed (Table 6). Irrespective of the hemisphere, long days (>13 h) were observed at collection sites located at higher latitudes in Botswana, India, Malawi, Mali, Mozambique, Namibia, Niger, Pakistan, Senegal, South Africa, Sudan, Zambia, Zimbabwe and Yemen. Day length varied widely in India (9.9–14.4 h), Pakistan (10–14.3 h) and South Africa (9.9–14.2 h). Day length was close to 12 h in countries located close to the equator. Probably, due to the narrow range of latitudes (1.5–3.8°N), the range of variation for day length was the lowest in Uganda (11.9–12.3 h).

Minimum and maximum temperature varied widely in India (−17.6 to 30.2 and −9.2 to 43.1 °C) followed by Pakistan (−1.6 to 29.6 and 12.4 to 43.9 °C) (Table 6). Lowest (<1 °C) minimum and maximum temperature, which contribute largely to the vegetation pattern, was found at collection sites in India, Pakistan, South Africa and Yemen. Highest maximum temperature was high in Pakistan (43.9 °C) and India (43.1 °C). Collection sites close to the equator in Uganda had low variation in minimum (16.2–19.0 °C) and maximum (27.3–34.0 °C) temperature.

Lowest mean annual rainfall was recorded in Yemen (212 mm), Pakistan (274 mm) and Niger (399 mm) (Table 6). Collection sites in all other countries received more than 400 mm rainfall. Highest mean annual rainfall was recorded at collection sites in Sierra Leone (2853 mm) in Northern Hemisphere and in Mozambique (929 mm) in the Southern Hemisphere.

Discussion

The world collection of pearl millet landraces conserved at the ICRISAT genebank is a rich source of variability for several desirable traits. The available variability has not been adequately utilized in pearl millet improvement (Bhattacharjee et al. 2007). Knowledge of the geographical distribution of economically important traits and the diversity is essential for proper understanding and exploitation of genetic resources. In the present study, the frequency distribution of landraces originating in various countries indicated unequal adaptation of pearl millet across the countries, probably due to natural and human selection as well as the photoperiod and temperature response of landraces (Upadhyaya et al. 2012a). Landraces from primary center of diversity for pearl millet covering mostly the West and Central African (WCA) countries harbor a wide range of climatic and environmental conditions as well as diverse farmer preferences and pearl millet utilization habits, were found as highly variable for days to 50 % flowering, plant height, panicle exsertion, length, thickness and shape, seed shape and color (Harlan 1971; Bhattacharjee et al. 2007; Stich et al. 2010). In WCA countries, pearl millet is cultivated throughout three agro-ecological zones (Saidou et al. 2009). The adaptation of pearl

Table 5 Country wise Shannon–Weaver diversity index (H′) for qualitative traits of pearl millet landraces from different countries, evaluated at ICRISAT, India

Country	1[a]	2	3	4	5	6	7	8	Mean	SE±
Asia										
India	0.545	0.607	0.474	0.677	0.382	0.759	0.590	0.558	0.574	0.041
Pakistan	0.141	0.301	0.141	0.405	0.017	0.631	0.145	0.365	0.268	0.070
Yemen	0.195	0.499	0.210	0.244	0.376	0.563	0.246	0.449	0.348	0.051
East Africa										
Kenya	0.371	0.439	0.338	0.506	0.369	0.689	0.369	0.377	0.432	0.041
Malawi	0.444	0.579	0.354	0.411	0.496	0.701	0.428	0.526	0.492	0.039
Sudan	0.513	0.627	0.458	0.564	0.697	0.747	0.537	0.533	0.584	0.035
Tanzania	0.611	0.553	0.506	0.629	0.508	0.775	0.529	0.705	0.602	0.035
Uganda	0.438	0.460	0.549	0.681	0.481	0.614	0.559	0.509	0.536	0.029
Southern Africa										
Botswana	0.640	0.466	0.769	0.642	0.308	0.746	0.522	0.458	0.569	0.056
Mozambique	0.455	0.524	0.634	0.311	0.350	0.613	0.436	0.505	0.478	0.041
Namibia	0.163	0.467	0.104	0.503	0.495	0.555	0.283	0.336	0.363	0.060
South Africa	0.469	0.506	0.221	0.508	0.490	0.766	0.340	0.535	0.479	0.056
Zaire	0.132	0.132	0.001	0.330	0.299	0.539	0.299	0.299	0.254	0.058
Zambia	0.558	0.576	0.631	0.536	0.462	0.704	0.573	0.583	0.578	0.025
Zimbabwe	0.470	0.508	0.479	0.660	0.381	0.740	0.551	0.523	0.539	0.040
West and Central Africa										
Algeria	0.001	0.413	0.217	0.458	0.458	0.458	0.217	0.413	0.329	0.059
Benin	0.404	0.494	0.294	0.325	0.552	0.715	0.407	0.556	0.468	0.049
Burkina Faso	0.441	0.552	0.127	0.399	0.534	0.663	0.523	0.374	0.452	0.057
C. African Rep.	0.511	0.433	0.380	0.469	0.539	0.733	0.551	0.550	0.521	0.037
Cameroon	0.508	0.740	0.370	0.533	0.580	0.751	0.480	0.555	0.565	0.045
Chad	0.353	0.453	0.062	0.457	0.699	0.658	0.453	0.263	0.425	0.073
Gambia	0.252	0.439	0.372	0.581	0.634	0.744	0.349	0.526	0.487	0.058
Ghana	0.540	0.563	0.363	0.326	0.609	0.745	0.464	0.564	0.522	0.048
Mali	0.569	0.639	0.305	0.572	0.495	0.760	0.707	0.595	0.580	0.049
Niger	0.469	0.607	0.407	0.666	0.648	0.732	0.765	0.616	0.614	0.043
Nigeria	0.365	0.539	0.236	0.564	0.491	0.720	0.456	0.398	0.471	0.051
Senegal	0.489	0.721	0.682	0.659	0.569	0.797	0.579	0.498	0.624	0.039
Sierra Leone	0.216	0.515	0.158	0.186	0.331	0.560	0.387	0.324	0.334	0.052
Togo	0.537	0.544	0.083	0.371	0.403	0.713	0.554	0.543	0.469	0.066
Tunisia	0.001	0.001	0.001	0.301	0.196	0.196	0.439	0.001	0.141	0.060
Mean	0.393	0.496	0.331	0.482	0.462	0.670	0.458	0.468	0.470	
SE±	0.032	0.027	0.037	0.026	0.027	0.022	0.025	0.025	0.022	

[a] 1 = Panicle shape, 2 = panicle density, 3 = bristle length, 4 = seed shape, 5 = seed color, 6 = endosperm texture, 7 = green fodder yield potential, 8 = seed yield potential

millet to these different environments has the potential to lead to genetic differentiation (Stich et al. 2010). East and Southern Africa and Asia, which are considered as secondary centres of diversity were good sources of variability for seed weight and tillering respectively suggesting the importance of centers of diversity for trait-specific diversity (Upadhyaya et al. 2014). The *Iniadi*, a prominent landrace mainly distributed in West and Central African countries, particularly in Benin, Burkina Faso, Ghana

Table 6 Range of variation for climatic variables at collection sites of pearl millet landraces from different countries

Country[aa]	1[a]	2	3	4	5	6	7	8	9	10
Asia										
India	8.7	34.4	21.5	9.9	14.4	−17.6	30.2	−9.2	43.1	740.4
Pakistan	25.4	33.6	30.4	10.0	14.3	−1.6	29.6	12.4	43.9	274.1
Yemen	13.0	17.2	14.5	11.1	13.1	−0.8	28.9	16.5	39.6	212.0
East Africa										
Kenya	−7.8	0.1	−2.6	11.6	12.5	7.0	21.6	20.9	31.2	880.1
Malawi	−17.0	−11.5	−15.4	11.1	13.1	7.7	23.5	20.1	36.6	730.2
Sudan	8.3	16.2	12.2	11.2	13.1	3.1	26.5	23.4	42.0	519.4
Tanzania	−10.6	−1.5	−5.4	11.5	12.7	6.1	24.4	16.3	33.5	608.2
Uganda	1.5	3.8	2.0	11.9	12.3	16.2	19.0	27.3	34.0	1258.8
Southern Africa										
Botswana	−24.7	−20.0	−23.1	10.6	13.6	2.9	20.5	21.1	34.9	366.7
Mozambique	−23.8	−11.4	−16.9	10.6	13.5	12.5	23.1	26.4	35.0	928.7
Namibia	−19.8	−17.4	−17.9	10.9	13.2	4.1	19.6	22.4	35.8	462.6
South Africa	−33.0	−22.8	−25.8	9.9	14.2	−1.1	21.0	15.8	32.6	563.4
Zambia	−17.8	−9.3	−15.2	11.0	13.1	4.4	21.5	21.3	36.5	716.3
Zimbabwe	−21.9	−16.1	−19.2	10.8	13.4	3.2	22.3	15.4	37.2	520.0
West and Central Africa										
Benin	6.7	12.2	10.7	11.4	12.8	15.9	27.0	27.0	40.4	1004.8
Burkina Faso	9.9	14.7	12.3	11.3	13.0	14.1	27.4	29.0	41.1	762.2
C. African Rep.	5.6	10.4	7.8	11.5	12.7	10.0	23.2	27.8	39.7	1215.6
Cameroon	2.0	12.7	10.2	11.4	12.8	11.4	26.2	22.7	40.9	889.6
Chad	7.9	15.8	11.1	11.2	13.0	11.4	26.7	28.9	42.4	727.3
Ghana	9.1	11.1	10.5	11.5	12.7	17.5	25.5	28.0	38.6	1003.4
Mali	10.5	16.9	14.0	11.1	13.1	10.9	28.9	28.0	42.1	628.3
Niger	11.9	19.1	14.0	11.0	13.2	7.4	27.7	23.4	41.6	399.1
Nigeria	4.7	13.6	11.2	11.3	12.9	10.4	26.7	23.3	41.4	913.3
Senegal	12.5	16.4	14.1	11.2	13.1	13.3	26.4	26.5	41.6	689.0
Sierra Leone	7.2	9.3	8.4	11.6	12.6	17.4	25.1	27.2	36.2	2852.8
Togo	7.4	11.1	10.4	11.5	12.8	16.4	25.3	27.1	39.2	1085.4

[a] 1 = Lowest latitude (°), 2 = highest latitude (°), 3 = mean latitude (°), 4 = lowest day length (h), 5 = highest day length (h), 6 = lowest minimum temperature (°C), 7 = highest minimum temperature (°C), 8 = lowest maximum temperature (°C), 9 = highest maximum temperature (°C), 10 = mean annual rainfall (mm)

[aa] Climate data at collection sites in Algeria, Gambia, Tunisia and Zaire is not available

and Togo has contributed remarkably to the genetic improvement of pearl millet worldwide and most of the varieties bred at ICRISAT are based on the germplasm of *Iniadi* landrace (Andrews and Anand Kumar 1996). Germplasm screening database for resistance to downy mildew at ICRISAT revealed a high frequency of landraces from Mali (63 %), Niger (58.3 %), Senegal (47.0 %), Chad (43.8 %) and Ghana (39.3 %), as promising sources for downy mildew resistance. This signifies the importance of primary center of diversity for biotic stress resistance (Singh et al. 1997).

Many researchers reported the association of latitude, climate and adaptation pattern of crop species in different countries (Hillebrand 2004; Upadhyaya et al. 2007, 2014). In the collection under study, the latitude of collection sites in different countries varied from 1.5° (Uganda) to 34.4° (India) in the Northern hemisphere and from 7.8° (Kenya) to 33.0° (South Africa) in the Southern hemisphere. The diversity in the adaptation of pearl millet could be attributed to the differences in adaptation levels of landraces to the prevailing day length, minimum and maximum temperature, rainfall and number of rainy days. The countries located between 5° and 15° latitudes that receive high rainfall have a day length around 12 h and an optimum temperature for pearl millet cultivation, which has resulted in a high diversity for the traits under study (Upadhyaya et al. 2014). Ashraf and Hafeez (2004) reported an optimum temperature of 33–34 °C for pearl millet and further mentioned that the growth could be retarded when the temperature is too high or too low. Ong (1983) reported 12 °C as the base temperature, 30–35 °C as the optimum and 45 °C as the lethal temperature for pearl millet. The wide distribution of species in a wide range of latitudes results in different ecotypes, which differ in their response to temperature and photoperiod (Wareing and Phillips 1981). The low latitudinal differences within the countries for latitude and associated climate evidenced in the present study also resulted in less variation for the traits under study.

The high proportion of late flowering landraces in Sierra Leone (146 days) and the Central African Republic (129 days) may be attributed to the high mean annual rainfall (>1200 mm) and increased number of rainy days (Pucher et al. 2015). Haussmann et al. (2006) reported positive correlation between time to flowering in pearl millet and annual rainfall. Therefore, we can assume that the factors controlling the flowering time are the major traits for adaptation of cultivated pearl millet. Sensitivity of landraces to photoperiod and temperature might have also contributed to late flowering in pearl millet from these countries. The collection from Pakistan adapted to low monthly mean minimum temperature, which is considered crucial in adaptation of any crop species, low rainfall at collection sites (274 mm) and longer days (14.3 h) at higher latitudes (>25°) is expected to flower late and grow tall. However, near optimum minimum (22.4 °C) and maximum (31.1 °C) temperature and relatively shorter days at the Patancheru location (17. 53° latitude) where the landraces were evaluated has resulted in a high frequency (18.0 %) of early flowering (33–40 days) landraces. These results are in agreement with those of Ong and Everard (1979), who reported delayed flowering due to long days and that each short day results in a 1.4 days reduction to reach anthesis leading to early flowering in pearl millet.

Due to high rainfall and near optimum temperature and day length in Chad, Burkina Faso, Nigeria and the Central African Republic, a high frequency of landraces from these countries grew tall. Low and unevenly distributed rainfall and sandy soils with low moisture holding capacity at the collection sites, where pearl millet cultivation is common, might have resulted in mild water stress leading to high tillering landraces in India and Yemen. Mahalakshmi et al. (1987) reported reduced plant height and increased tiller number due to water stress during the early stages and during the stem elongation period. Because of favorable conditions, landraces from primary center of diversity, particularly those from Niger and Nigeria with a mean latitude of 11°–14° were found as good source countries for long panicle pearl millet. Botswana, Namibia, and Zimbabwe were the good source countries for thick panicle (41–58 mm) landraces but produced less tillers. West African countries were found to be good sources for large seeded pearl millet. Upadhyaya et al. (2014) reported the occurrence of large seeded pearl millet with long and thick panicles in latitudes ranging between 10° and 15°. The favorable climate in countries with latitude ranging between 5° and 20° has resulted in highly diverse pearl millet, which produced more panicle shapes, seed shapes and seed colors. Panicle compactness, endosperm texture, green fodder yield potential and seed yield potential have been largely influenced by natural and human selection over the years, as well as local temperature, day length, rainfall, soils, elevation patterns, and date of sowing, which have resulted in different patterns of diversity. Farmers' selection for cultivation of a specific type of material in adverse conditions in some areas might have also accounted for the observed distribution of traits (Busso et al. 2000; vom Brocke et al. 2003). Stich et al. (2010) reported that the natural selection is less important than human selection in shaping pearl millet populations (vom Brocke et al. 2003).

A high frequency (>50 %) of landraces, which were evolved through selection by farmers over decades for green fodder were found promising. This has revealed the importance given by traditional farmers to fodder traits. Late maturing tall and high tillering landraces from lower latitudes (<20°) are better sources for fodder production (Burton and Powell 1968). Landraces producing long and thick panicles with large seeds distributed in Ghana, Botswana, Namibia, and Togo are very useful in developing cultivars.

The pearl millet collection under study fits the evolutionary pattern, nearly representing geographical distribution and ecological zones of the crop. Bhattacharjee et al. (2007) reported wide range of variability in the world collection at ICRISAT for all quantitative traits based on their country of origin. In view of climate change resulting in loss of variability, there is a need to analyze the existing collection to know the geographical distribution of trait-specific pearl millet. Results of present study indicated the distribution of the early flowering trait (33–40 days) in Pakistan, Ghana, Togo and India; very late flowering (121–159 days) in Sierra Leone and the Central African Republic; short height trait (80–100 cm) in India, Zambia and Sudan; tall height (401–490 cm) in Chad, Burkina Faso, Nigeria and the Central African Republic; high tillering trait in India and Yemen; high panicle exsertion trait (11–29 cm) in Ghana, Chad, India, Yemen, Pakistan and Burkina Faso; long panicles (75–135 cm) in Nigeria and Niger; thick panicles (41–58 mm) in Namibia, Togo and Zimbabwe and large seeds (16–19 g per 1000 seeds) in Togo, Benin, Ghana and Burkina Faso. Although, the data used in the present study is preliminary in nature and has been recorded over several years, this data reflects the differences in the genetic makeup of the landraces exhibiting a clear pattern of variability (Upadhyaya et al. 2007). Therefore, using the information on geographical distribution of pearl millet traits under study, cost-effective collection missions can be launched to enrich the world collection for desirable traits and also to fill geographical gaps. Upadhyaya et al. (2009, 2010, 2012b) identified several geographical and trait-diversity gaps in the world collection of pearl millet landraces from the various centers of diversity. Exploring these gaps is a priority to increase the variability for quantitative traits in the world collection of pearl millet germplasm. Gaps in countries, which were identified as important sources for diversity of qualitative traits may be explored for additional diversity in the collection. Countries, which were found as good sources for special traits such as disease resistance, cream and ivory color seeds and had high scores for fodder and seed yield potential can be explored for trait-specific germplasm. As the success of gap analysis depends largely on the quality of input data, it is essential to collect all location information particularly, latitude and longitude of collecting site while collecting germplasm to ensure its enhanced utilization in pearl millet improvement.

The present study helps pearl millet germplasm curators across the countries, to identify suitable locations for introduction, collection, regeneration and characterization of trait-specific germplasm. Though the characterization data was recorded in different years, in different fields, it reflects genetic differences between accessions (Upadhyaya et al. 2007). Results of the present study are useful in selecting germplasm for targeted use in crop improvement. The use of geospatial tools to understand the spatial variability in the germplasm collections is the need of the hour. It emphasizes the interdisciplinary nature of crop evolution studies. It also indicates the need for similar studies in other crops for enhanced utilization of large collections conserved in national and international genebanks. ICRISAT pearl millet germplasm passport and characterization databases can be accessed using www.ICRISAT.org or www.genesys-pgr.org. Limited quantity seeds of all in-trust landrace accessions used in this study are available under the Standard Material Transfer Agreement (SMTA) of the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA), for utilization in research globally.

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