Latitudinal patterns of diversity in the world collection of pearl millet landraces at the ICRISAT genebank

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Plant Genetic Resources

DOI: http://dx.doi.org/10.1017/S1479262113000348

Published online: 21 August 2013

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Abstract

The genebank at ICRISAT, Patancheru, India conserves a total of 19,063 pearl millet landraces from latitudes ranging from 33.00^{o} in southern hemisphere to 34.37^{o} in northern hemisphere. Northern hemisphere was found as the major source for pearl millet landraces (80.5%). Lower latitudes (<20^{o}) in both hemispheres resulted in more landraces than higher latitudes. Latitude range of 10^{o}-15^{o} in northern hemisphere and 15^{o}-20^{o} in southern hemisphere are the important source regions for pearl millet with 39.6% and 13.1% landraces, respectively in the world collection. Landraces from lower latitudes on either sides of the equator varied widely for all traits. Landraces from 5^{o}-10^{o}N flowered late and grew tall in both seasons and produced more tillers with thick panicles. Landraces from 10^{o}-15^{o}N, which produced less tillers were found to be a good source for long and thick panicles with larger seeds. Long bristled bird resistant landraces are more in latitudes of 10^{o}-15^{o}S and 20^{o}-25^{o}S. Minimum temperature at the collection sites was found as one of the important factors determining the patterns of pearl millet prevalence across the latitudes. Late maturing, tall and high tillering landraces from lower latitudes are the better sources for fodder production. Early maturing landraces producing long and thick panicles with large seeds from mid-latitudes (15^{o}-20^{o}) in both hemispheres are useful in developing high yielding cultivars. Using the latitudinal patterns of diversity in pearl millet landraces, collection missions may be launched to explore high diversity, under-collected and threatened areas for materials of interest in latitudes of 15^{o}-20$^{o.}$

Keywords: Climate, Collection, Diversity, Landraces, Latitude, Hemisphere

Introduction

Pearl millet [*Pennisetum glaucum* (L.) R.Br.] is one of the important cereal crops grown in a wide range of latitudes (35^{o}S to 35^{o}N of equator). It is important as grain crop in Africa and Asia and as a fodder crop in other arid and semi-arid parts of the world (Andrews and Kumar, 1992). It is mainly cultivated in Niger, Nigeria, Burkina Faso, Togo, Ghana, Mali, Senegal, Central African Republic, Cameroon, Sudan, Botswana, Namibia, Zambia, Zimbabwe and South Africa in Africa and India, Pakistan and Yemen in Asia (Upadhyaya et al., 2010).

Latitude, which is the measurement of distance of a location on earth from the equator, is the primary factor affecting unequal heating of earth's atmosphere. Latitudinal gradient in species diversity was recognized for nearly a century, and some of these polar-equatorial trends have been discussed in detail (Darlington, 1959, Fischer, 1960). Plants experience considerable variation in natural selection across their range for local adaptation, resulting in geographic differentiation of populations (Joshi et al., 2001; Streisfeld and Kohn, 2005; Springer, 2007). Since solar irradiance, temperature and photoperiod changes are known to influence many aspects of plant life (Berry and Raison, 1981), widely distributed plant species may be expected to show phenotypic variability across latitudes. Genetically based latitudinal variation in phenology (Weber and Schmid, 1998), growth (Chapin and Chapin, 1981) and sexual reproduction (Aizen and Woodcock, 1992) has been reported in terrestrial species. The overall pattern of diversity of crops including pearl millet largely depends on selection by nature and man and sensitivity to environmental factors such as daylength, minimum and maximum temperature, rainfall, soils, etc..

The world collection of pearl millet germplasm (22,211 accessions) assembled at the ICRISAT genebank, Patancheru, India is from a wide range of latitudes (0^o-34.37^o on both sides of equator). Being the largest collection of pearl millet germplasm, study of latitudinal patterns of diversity in the collection is very important for its targeted use in crop improvement programmes. The availability of Geographic Information System (GIS) and climate data of collection sites have opened-up avenues in understanding latitudinal patterns of diversity. Therefore, in the present study, pattern of diversity for important morphoagronomic traits in pearl millet landraces from different latitudes was assessed and discussed in relation to the available information on climate in different latitudinal ranges on either side of the equator.

Materials and Methods

The passport information and characterization data of pearl millet germplasm (22,211 accessions) assembled at the ICRISAT genebank, Patancheru, India was used in the present study. The collection consisted 19,063 landraces, 2,269 breeding materials, 129 improved cultivars and 750 wild accessions belonging to 24 species of genus *Pennisetum*. Passport information of the landraces, particularly the location of collecting sites and corresponding geographic coordinates was updated by referring all related records, collection reports and catalogs. Using Microsoft Encarta^{R}, an electronic atlas (MS Encarta^{R} Interactive World Atlas, 2000), geographic coordinates were retrieved for accessions without coordinates to fill the gaps for landraces having location information. Accuracy of coordinates was verified by plotting all landraces on political map of world. Finally, a set of 15,904 landraces having geographic coordinates was used in the present study. The collection includes landraces from latitudes ranging from 0^{o}-34.37^{o} on both sides of equator covering almost all major pearl millet growing countries across the world.

Pearl millet landraces were characterized in batches of 500 to 1000 every year at ICRISAT, Patancheru (17.53^{o}N latitude, 78.27^{o}E longitude and 545 m.a.s.l), in alfisols during the rainy and postrainy seasons from 1974 through 2011. These two different seasonal conditions are typical to the semi-arid regions (Reddy et al., 2004). During rainy season, accessions were sown in June and harvested in October/November. On the other hand, during postrainy season, accessions were sown in November and harvested in March of the subsequent year. At Patancheru, the daylength decreases from 13.10 h (in June) to 11.40 h (in November) in the rainy season and increases from 11.10 h (in December) to 12.00 h (in March) in the postrainy season. The monthly mean minimum temperature varies from 23.6^oC (in June) to 16.0^oC (in November) and the monthly mean maximum temperature ranged from 34.4^oC (in June) to 28.9^oC (in November) in rainy season. During postrainy season, monthly mean minimum temperature increased from 12.9^oC (in December) to 19.3^oC (in March) and the mean maximum temperature increased from 27.9^oC (in December) to 35.2^oC (in March). The mean annual rainfall was 908 mm. Each accession was grown in 2 rows of 4 m length each with a spacing of 75 cm between rows and 10 cm between plants within a row accommodating a total of 80 plants in two rows. Accessions were randomized in all the evaluations. Fertilizers were applied at the rate of 100 kg N and 40 kg P^2O^5 ha^{-1}. Need based irrigations were given during rainy season, while the crop was irrigated at regular intervals during postrainy season. The crop was protected from weeds, pests and diseases. By the end of 2011, almost all landraces were characterized for 20 morpho-agronomic characters following the Descriptors for pearl millet (IBPGR and ICRISAT, 1993). Days to 50% flowering, plant height, panicle length and thickness were recorded during both rainy and postrainy seasons, whereas number of total and productive tillers, panicle exsertion, panicle shape, spikelet density, bristle length, seed yield potential, green fodder yield potential and overall plant aspect was recorded only during the rainy season. For panicle density, bristle length, seed yield potential, green fodder yield potential and overall plant aspect, landraces were visually scored on a 1 to 9 scale, where 1 was most undesirable and 9 was most desirable. Observations on grain characters, such as 1000-seed weight, seed shape and color were recorded after harvesting during the postrainy season. Emergence of stigma in 50% of plants in a plot (accession) was considered as days to 50% flowering (IBPGR and ICRISAT, 1993). Height from base to the tip of panicle was recorded in centimeters as plant height. In each plot, number of total and productive tillers per plant was counted and mean of five plants was recorded. Distance between the ligule of the flag leaf and the base of panicle was recorded as panicle exsertion. Mean panicle length over five plants was recorded in centimeters while the width of the panicle was recorded in millimeters at maximum thickness of panicle. Weight of 1000 seeds drawn from plot harvest was recorded in grams. Green fodder yield potential of accessions was scored on 1-9 scale considering plant height, tillering and leafiness of accessions, while the seed yield potential of accessions was scored on the basis of number of productive tillers, spikelet density, panicle length and thickness and seed size. Overall plant aspect was recorded based on important agronomic traits.

Frequencies were estimated for all qualitative traits under study for northern and southern hemishperes and for each latitudinal range with an interval of $5^{\cdot}00^{o}$ in both Northern and Southern hemispheres. Climatic data such as monthly mean (over past 30 years) minimum and maximum temperature, rainfall and daylength for each collection site, was retrieved from http://www.worldclim.org/current using the spatial analyst extension in ArcGIS® software in June 2011 (Hijmans et al., 2005). The high resolution (1 km) interpolated climate surfaces are a useful source of data for studying the spatial relationship between environmental variables and the vegetation existing at that location. Minimum, maximum and mean of lowest and highest monthly mean minimum and maximum temperature, daylength for entire collection and for northern and southern hemispheres, lower ($<20^{o}$) and higher ($>20^{o}$) latitudes and each latitude range of 5.00^{o} starting from 0.00^{o} to 35.00^{o} on either side of the equator, were estimated.

Agronomic data were analyzed using Residual Maximum Likelihood (REML) procedure in Genstat 14 release (http://www.vsni.co.uk) to partition genotypic variance into between hemispheres, lower (<20^o) and higher (>20^o) latitudes, and latitudinal groups within hemispheres. The respective standard errors were estimated and used to determine the significance of variance components. Mean, range and variances were calculated for 12 quantitative characters, for entire collection, hemispheres, lower and higher latitudes and latitudinal ranges within each hemisphere. The mean values of different traits were compared using the Newman-Keuls procedure (Newman, 1939; Keuls, 1952). Homogeneity of phenotypic variances was tested by Levene's test (Levene, 1960). Shannon and Weaver (1949) diversity index (H`) was used to measure and compare the phenotypic diversity for all 12 traits in entire collection, hemispheres, lower and higher latitudes and all latitudinal ranges within hemispheres. Measured values of individual accessions for a trait were standardized by subtracting the mean value of the trait from each observation and subsequently dividing by its standard deviation. This resulted in standardized values for each trait with an average value of 0 and standardized deviation of 1 or less. The standardized values were used to perform principal component analysis (PCA) on Genstat 14 release. Cluster analysis (Ward, 1963) was performed using scores of first three principal components (PCs) to cluster different latitudinal ranges.

Results

Frequency distribution

Pearl millet landraces used in the present study are from a wide range of latitudes ranging from 33.00^{o} in southern hemisphere (SH) to 34.37^{o} in northern hemisphere (NH). Frequency distribution of landraces indicated 80.5% (12,808) landraces from northern hemisphere and 19.5% (3,096) from southern hemisphere (Table 1). Lower latitudes (<20^{o}) in both hemispheres resulted in more landraces (9,573 in NH and 2,687 in SH) than higher latitudes (3,235 in NH and 409 in SH). Frequency distribution over entire collection for each latitude range on either sides of the equator indicated that 10^{o}-15^{o} on northern side and 15^{o}-20^{o} on southern side of the equator are the important source regions for pearl millet prevalence with 39.6% and 13.1% accessions respectively. The proportion of accessions from latitudes close to the equator (0^{o}-5^{o}) and higher latitudes (30^{o}-35^{o}) is very low (~ 1%) (Table 1).

Diversity for qualitative traits

Panicle shape: Panicle shape recorded on the basis of majority panicles in the plot is useful in classifying the landraces. Nine panicle shapes (cylindrical, conical, spindle, club, candle, dumb-bell, lanceolate, oblanceolate and globose) are recognized in the collection (IBPGR and ICRISAT, 1993) (Table S2). Landraces producing candle shape panicles were more common in the collection, both hemispheres and all latitude ranges except 25^{o}-30^{o} in northern hemisphere and 0^{o}-15^{o} and 20^{o}-25^{o} in southern hemisphere. Latitude ranges 25^{o}-30^{o} in northern hemisphere with 43.4% and 10^{o}-15^{o} in southern hemisphere with 48.9% were found as the important regions for pearl millet producing cylindrical shape panicles. Landraces producing lanceolate shape panicles are predominant in latitude range of 0^{o}-10^{o} and 20^{o}-25^{o} in southern hemisphere.

Seed color: Seed color is an important trait that differentiates landraces. Ten seed colors (ivory, cream, yellow, grey, deep grey, grey brown, brown, purple, purplish black and mixture of grey and white) were found in the collection and 50% of total landraces produced grey color seeds and 32% landraces produced grey brown color seeds (IBPGR and ICRISAT, 1993) (Table S2). All other colors were negligible (<8%) in the collection. Both hemispheres and all latitude ranges were found as predominant source regions for grey to grey brown seeds. Seed colors like ivory and cream are more in latitudes of 0^{o}-15^{o}N and 10^{o}-20^{o}S. Seeds with yellow pericarp are more in in latitudes of 5^{o}-15^{o}N.

Seed shape: Five seed shapes (obovate, oblanceolate, elliptical, hexagonal and globular) were found in the collection (IBPGR and ICRISAT, 1993) (Table S2). A maximum of 25.5% landraces produced globular shape seeds followed by 23.8% elliptical, 18% oblanceolate, 17.3% obovate and 15.5% hexagonal shape seeds. Northern hemisphere was the predominant source for globular, hexagonal and elliptical shape seeds as compared to southern hemisphere, which was found as important source for obovate and oblanceolate shape seeds. Latitudinal ranges of 10^{o}-15^{o}N (39.2%) and 5^{o}-10^{o}N (46.5%) were found as the important source regions for globular shape seeds. In southern hemisphere, latitudes of 0^{o}-15^{o} for obovate seeds, 15^{o}-20^{o} for oblanceolate seeds and 20^{o}-25^{o} for globular seeds were found as important source regions.

***Spikelet density*:** Spikelet density or panicle density is an important yield contributing trait in pearl millet. High scoring (7-9) indicates high panicle density, which is desirable. Only 12.8% landraces in the collection scored high (7-9 score). There were 215 (1.35%) landraces in the collection scoring 8 and five (0.03%) landraces scored 9 for this trait. Northern hemisphere was found as the predominant source for pearl millet landraces with high score for this trait. Among the latitude ranges, 5^o-20^o on both sides of equator was found as important source regions for high scoring landraces for this trait. (Table S2).

Bristle length: High score for bristle length indicates long bristles, which is a desirable trait. Long bristles of panicle will penetrate in to the eye of bird providing self-defense mechanism to scare birds. More than 96% of total landraces produced short bristles (bristles below the level of the apex of the seed). On the other hand, 0.47% (75 landraces) of total collection produced bristles longer than 2 cm above the seed and scored 7-9. All landraces scoring 9 are from southern hemisphere. Within the southern hemisphere, latitudes of 10^o-15^o and 20^o-25^o are the important source regions for long bristle pearl millet (Table S2).

Green fodder yield potential*:* This trait determines the fodder yield potential of landraces. In the entire collection, about 41% landraces had scored 7 whereas 12% scored 8 and 0.7% had scored 9 for green fodder yield potential. More than 50% of landraces from both hemispheres scored more than 6. Within the northern hemisphere, a maximum of 4.0% landraces from 5^o-10^o latitudes scored 9 (Table S2).

Seed yield potential: This is an important trait contributing to the seed yield in pearl millet. A maximum of 43% landraces scored 6, followed by 14% landraces scoring 7, 0.96% landraces scoring 8 and 0.01% landraces scoring 9. All landraces that scored 8 and 9 are from northern hemisphere. All landraces scoring 9 are from latitudes of 10^o-15^oN and 20^o-25^oN (Table S2).

Overall plant aspect: This trait indicates the overall agronomic acceptability of landraces (Table S2). None of the landraces in the collection scored 9. In the entire collection, only 86 landraces scored 8. Only 0.66% landraces from northern hemisphere and 0.03% from southern hemisphere scored 8. However, in northern hemisphere landraces scoring 8 occurred in all latitude ranges.

Diversity for quantitative traits

Range and means

Large variation was observed in the collection for all quantitative traits under study. Landraces from northern hemisphere varied widely for all traits except panicle width as compared to southern hemisphere (Table 1). Landraces from lower latitudes on either sides of the equator varied widely for all traits. Among the latitudinal ranges, 10^{o}-15^{o}N showed high variation for all traits under study except panicle width. Earliest flowering landraces were from 20^{o}-25^{o}N. Very late flowering (>150 days in rainy and >130 days in postrainy), tall (>480 cm in rainy and >420 cm in postrainy), high tillering (35 tillers per plant in rainy and >17 tillers in postrainy), long (>100 cm) and thick panicle (>50 mm) and large seed (>18 g 1000^{-1} seeds) landraces were from 10^{o}-15^{o}N.

Newman-Keuls (Newman, 1939; Keuls, 1952) test of significance for mean values indicated significant differences between landraces from the two hemispheres for all traits except days to 50% flowering in rainy season. (Table 2). Landraces from northern hemisphere flowered early in the postrainy season, grew short, produced more tillers and had highly exserted small thin panicles and large seeds when compared to those from southern hemisphere. Higher and lower latitudes within each hemisphere also differed significantly for all traits. Landraces from higher latitudes in northern hemisphere flowered early in both seasons, grew short in rainy and tall in postrainy season, produced more tillers with small panicles and small seeds. On the other hand, in southern hemisphere, landraces from higher latitudes flowered early in rainy season and late in postrainy season, grew short, produced more tillers with small panicles and small seeds. Significant differences were observed between latitudinal ranges in northern hemisphere for all traits. Landraces from latitudes of 5^{o}-10^{o}N flowered late and grew tall in both seasons and produced more tillers with thick panicles. Landraces from 10^{o}-15^{o}N, which produced less tillers was found as a good source for long and thick panicles with larger seeds. Landraces from higher latitudes (30^{o}-35^{o}N) flowered early and grew to a short height in rainy season (Table 2).

Variances

The homogeneity of variances of the hemispheres and latitudinal ranges within each hemisphere was tested for all the 12 quantitative traits by Levene's test (Levene, 1960) (Table S1). The variances for hemispheres were heterogeneous ($p \leq 0.0001$) for all traits under study except panicle exsertion, and for all traits in lower and higher latitudes on either sides of the equator. Variances were heterogeneous ($p \leq 0.0001$) for all traits except total and productive tillers per plant in all latitudinal ranges in northern hemisphere and for all traits in southern hemisphere.

Phenotypic diversity

The Shannon-Weaver diversity index (H`) (Shannon and Weaver, 1949) was calculated for entire landrace collection, collections from the two hemispheres, lower and higher latitudes in each hemisphere and latitudinal ranges within hemispheres, to compare phenotypic diversity for 12 quantitative traits (Table 3). A low H` indicates extremely unbalanced frequency classes for an individual trait and lack of genetic diversity in the collection or species. In the entire collection, diversity index (H`) ranged from 0.427$\pm$0.020 for total tillers per plant to 0.632$\pm$0.020 for plant height in the postrainy season. Among the hemispheres, mean diversity over all traits was more (H'=0.569$\pm$0.019) in landraces from northern hemisphere as compared to those from southern hemisphere (H'=0.563$\pm$0.027). In northern hemisphere, diversity was high in higher latitudes for all traits under study except flowering in postrainy season, panicle width in rainy season and 1000-seed weight. Within each hemisphere, mean diversity over all traits was high in higher latitudes as compared to lower latitudes. Among the latitudinal ranges, diversity index for overall traits ranged from 0.571$\pm$0.026 in 10^o-15^o to 0.606$\pm$0.009 in 25^o-30^o in northern hemisphere and from 0.276$\pm$0.001 in 30^o-35^o to 0.583$\pm$0.017 in 20^o-25^o in southern hemisphere.

Cluster analysis

Principal Component Analysis (PCA) carried out using standardized data of 12 quantitative traits captured 90% of total variation from the first three principal components (PCs). A hierarchical cluster analysis conducted on the scores of the first three principal components (PCs) resulted in four clusters of latitudinal ranges. Landraces from latitudes of 5^o-15^oN formed cluster 1, those from 0^o-5^oN, 15^o-35^oN and 10^o-15^oS formed cluster 2, those from 0^o-10^oS formed cluster 3 and those from latitudes of 15^o-35^oS formed cluster 4 (Figure S1).

Climate

Daylength

Annual mean daylength over all collection sites was 12.12 h. Annual mean daylength in northern hemisphere (12.13 h) differed significantly from that of southern hemisphere (12.07 h). Significant differences were observed in daylength of higher and lower latitudes in both hemispheres. In northern hemisphere, daylength was high (12.15 h) in higher latitudes than in lower latitudes (12.12 h). It was observed that in both hemispheres as the latitudinal range increased, the minimum, maximum and mean of lowest monthly mean for daylength decreased, whereas, the minimum, maximum and mean of highest monthly mean increased.

Rainfall

Annual mean total rainfall over all collection sites was 737 mm. Collection sites in northern hemisphere received significantly higher (753 mm) rainfall than those in southern hemisphere (673 mm) (Table 4). Lower latitudes in both hemispheres received significantly higher rainfall (772 mm NH and 686 mm in SH) than higher latitudes (697 mm in NH and 580 mm in SH). No clear patterns exist in rainfall of different latitudinal ranges in both hemispheres. Only 0^o-10^o N latitudes received more than 1000 mm rainfall. All latitudinal ranges in southern hemisphere received <1000 mm rainfall with a maximum of 982 mm in 10^o-15^o.

Temperature

Minimum temperature

Annual mean minimum temperature over all collection sites was 19.0^oC (Table 4). Annual mean minimum temperature (20.1^oC) in northern hemisphere was significantly higher than that of southern hemisphere (14.6^{o}C). It was less (19.0^{o}C in NH and 12.9^{o}C in SH) in higher latitudes than in lower latitudes (20.5^{o}C in NH and 14.9^{o}C in SH). No clear pattern exists for different latitudinal ranges in both hemispheres for minimum temperature. However, the minimum lowest monthly mean (-17.6^{o}C) was observed in 30^o-35^{o}N latitude range. Further, there was an abrupt reduction in minimum of lowest and highest monthly mean minimum temperature in 10^o-15^{o}N. The maximum and mean of lowest monthly mean minimum temperature decreased with the increase in latitude in both hemispheres.

Maximum temperature

Annual mean maximum temperature over all collection sites was 32.4^{o}C (Table 4). It was significantly higher (33.3^{o}C) in northern hemisphere than in southern hemisphere (28.9^{o}C). Lower latitudes were significantly warmer (33.6^{o}C in NH and 29.2^{o}C in SH) than higher latitudes (32.4^{o}C in NH and 27.2^{o}C in SH). In different latitudinal ranges of both hemispheres, minimum of lowest and highest monthly mean maximum temperature did not show any pattern. There was an abrupt reduction in minimum of lowest and highest monthly mean of maximum temperature in 10^o-15^o N and 15^o-20^{o}S latitudes. Maximum and mean of highest monthly mean maximum temperature increased with increase in latitudinal range in northern hemisphere and no such pattern was observed in southern hemisphere.

Discussion

Pearl millet is well adapted to areas characterized by drought, low soil fertility and relatively high temperature. It also performs well in soils with high salinity. Because of its tolerance to various stress conditions, it can be grown in areas where other cereal crops, such as maize or wheat, do not perform well. Adaptation of crops to the challenges of climate change will involve exploiting the continually developing technologies, resources and expertise. The world collection of pearl millet landraces used in the present study is from a wide range of latitudes (34.37^{o} N to 33.00^{o}S). Frequency distribution of landraces indicated unequal pearl millet prevalence across the latitudes. The main factors influencing adaptation of pearl millet include selection by nature and man, photoperiod, temperature, soils and rainfall. Results of present study revealed that the higher annual mean daylength (12.13 h), minimum (20.1^{o}C) and maximum (33.3^{o}C) temperature and rainfall (753.6 mm) in northern hemisphere than in southern hemisphere (minimum 12.1^{o}C and maximum 28.9^{o}C temperature and rainfall 672 mm) has led to high prevalence of pearl millet in northern hemisphere resulting in a larger number of landraces. Because of wide variation in climatic factors, landraces from northern hemisphere are highly variable for all traits except panicle thickness and found as good source for early as well as late maturity, short and tall, high tillering landraces. Bidinger and Rai (1989) reported early flowering in pearl millet under 12 h photoperiod and delay in flowering under long photoperiod (14 h). Kipp, (2007) reported the direct effect of heat stress on plant growth and development. Ong (1983) reported 12^{o}C as base temperature, 30-35^{o}C as optimum and 45^{o}C as lethal temperature for pearl millet.

Higher proportion of landraces (9,573 in NH and 2,687 in SH) from lower latitudes than from higher latitudes (3,235 in NH and 409 in SH) indicate high prevalence of pearl millet and intensive collection of germplasm in lower latitudes. These results may be attributed to the near optimum and significantly higher annual minimum (20.5^{o}C in NH and 14.9^{o}C in SH) and maximum (33.6^{o}C in NH and 29.2^{o}C in SH) temperature and rainfall (772 mm in NH and 686 in SH) in lower latitudes (Ong, 1983; Erskine et al., 1990). High range of variation for all traits in landraces from lower latitudes can be attributed to highly variable mean annual rainfall (647-1595 mm) and near optimum minimum and maximum temperature at collection sites in addition to the variation due to natural and human selection over the years (Table 1 and 4). The pearl millet landraces adapted to low annual mean temperature, inconsistent rainfall and longer days at higher latitudes are expected to flower late and grow tall. Due to near optimum minimum (20.8^{o}C) and maximum (30.6^{o}C) temperature and shorter days at Patancheru location (latitude 17.53^o) than at collection sites, landraces from higher latitudes flowered early and grew short (Hijman et al., 2002). Near the equator, daylength is constantly around 12 h and facilitates the crop growth all the year around. Pearl millet is a facultative short day species, flowering at all photoperiods, although much earlier with short days (Ong, 1983). The critical photoperiod and temperature required to trigger flowering is species and cultivar specific. Almost all cultivars show some response to temperature and photoperiod according to their specific geographical adaptation particularly the latitude (Ong 1983; Bidinger and Rai 1989; Joshi et al., 2005). Wareing and Phillips (1981) reported that in many plant species, a daylength change as short as 15-20 minutes will have significant effect on flowering. Pearson and Coaldrake (1983) reported the delay in flowering by 4-5 days per degree latitude. McIntyre et al., (1993) reported a two day reduction in length of pearl millet growth period for each degree rise in temperature. Results of present study are in conformity with those of Ong and Everard (1979) who reported delayed flowering due to long days and that each short day results in 1.4 days reduction to reach anthesis leading to early flowering in pearl millet.

Climate will not be homogeneous over a relatively larger area of hemisphere. Therefore, the assessment of diversity patterns in relation to the crop ecology of more homogeneous and smaller latitudinal ranges reveals patterns of diversity in a better way (Upadhyaya et al., 2007). The prevalence of diverse pearl millet in smaller regions such as different latitudinal ranges in the present study can be attributed to the differences in adaptation levels of cultivars/genotypes to the prevailing daylength, minimum and maximum temperatures, soils, rainfall, duration of rainfall and selection by man and nature in each latitude range. The high prevalence of landraces in 10^o-15^oN and 15^o-20^oS can be imputed to the near optimum minimum of lowest and highest monthly mean minimum and maximum temperature prevailing in the region indicating the minimum temperature at the collection sites as an important factor in determining the adaptation patterns of pearl millet (Table 4). Hellmers and Burton (1972) found substantial effect of temperature on flowering of pearl millet. Deviation in climate from that of 10^o-15^o N and 15^o-20^o S is reflected in reduced prevalence of pearl millet and less number (~ 1%) of landraces. This was evidenced in latitudes close to the equator (0^o-5^o) and in higher latitudes (30^o-35^o). These results indicate a stronger association of latitude and the factors responsible for pattern of diversity (Ong, 1983; Erskine et al., 1990; Upadhayaya et al., 2012). Ashraf and Hafeez (2004) reported an optimum temperature of 33-34^{o}C for pearl millet and the growth retarded when the temperature is too high or too low.

Because of favorable climate for pearl millet, 10^o-15^oN was found as the good source for almost all panicle shapes, seed colors and shapes. Long bristled landraces, which were considered as bird resistant are relatively more in latitudes of 10^o-15^oS and 20-25^oS. When a species or crop has wide distribution, there is considerable difference in the latitude between its northern and southern limits resulting in different ecotypes, which differ in their response to temperature and daylength (Wareing and Phillips, 1981; Santamaria, 2003). Small deviations in the patterns of diversity in the present study can be attributed to the varying local conditions, elevations, date of sowings, soils, etc. in different latitudes. Natural selection pressure for adaptation to different latitudes coupled with farmer's selection for cultivation of a specific type of material in adverse conditions in some areas might have also accounted for the observed patterns of diversity.

Clustering of different latitudinal ranges of both hemispheres was in agreement with natural geographic regions (hemispheres), except the deviation of 10^o-15^oS into cluster 2 along with 0^o-5^oN and 15^o-35^oN. This deviation can be attributed to the near similarity in climate of collection sites, especially annual mean rainfall, which was maximum in 0^o-5^oN in northern hemisphere and 10^o-15^oS in southern hemisphere.

The genetic resource base for developing new climate change-ready crop cultivars has not been adequately explored or shared. Scientists have already embarked on a hunt to identify climate change-ready cultivars of crops in germplasm collection. Studies in different crops have shown that a careful investigation of climatic variables can lead to the identification of germplasm with useful and predictable attributes (Rick, 1973; Klebesadel and Helm, 1986).

Exploitation of the germplasm for developing cultivars suitable for specific locations in a wide range of latitudes is possible only when the information on temperature and photoperiod responses, patterns of geographical adaptation and agronomic performance of the parental material is available. Late maturing tall and high tillering landraces from lower latitudes (<20^{o}) are better sources for fodder production (Burton and Powell, 1968). Early maturing photoperiod insensitive landraces producing long and thick panicles with large seeds from mid-latitudes (15^{o}-20^{o}) in both hemispheres are useful in developing cultivars suitable for diverse latitudes (Upadhyaya et al., 2012). Latitudes of 5^{o}-15^{o}N, which were an important source for landraces with light color seeds, high scoring for spikelet density, fodder yield potential, seed yield potential and overall plant aspect, may be explored. Recording location specific geo-reference data while collecting the germplasm is critical to study agronomic performance of pearl millet landraces.

Using the latitudinal patterns of diversity evidenced in pearl millet landraces under study, cost effective collection missions may be launched to explore areas of high diversity for pearl millet, under-collected and threatened areas for materials of interest. Though, the evaluation data used in the present study are preliminary in nature, and recorded over years, these data reflect the differences in the genetic makeup of the landraces in terms of clear patterns of diversity (Upadhyaya et al., 2007). Further, the present study helps in identifying suitable sites for regeneration and evaluation of trait specific germplasm, introduction of appropriate pearl millet into different regions and emphasizes similar studies on germplasm collections of other crops for enhanced use of germplasm in crop improvement programs.

Acknowledgements

Authors sincerely acknowledge the contribution of all former and present staff of genebank at ICRISAT, Patancheru, India in collection, assembly and conservation of pearl millet genetic resources. The help of D Bapa Rao, G Dasaratha Rao, G Ram Reddy, Shaik Babu and Mohd. Ismail, all Research Technicians, in recording observations, documentation and retrieval of geo-reference and climate data for this study is highly appreciated.

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Caption for Figure S1

Figure S1. Dendogram of different latitudinal ranges based on scores of first three principal components (captured 90% variation) of 12 quantitative traits.