

Geographical patterns of diversity for qualitative and quantitative traits in the pigeonpea germplasm collection

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Abstract

We analysed the patterns of variation for 14 qualitative and 12 quantitative traits in 11,402 pigeonpea germplasm accessions from 54 countries, which were grouped into 11 regions. Semi-spreading growth habit, green stem colour, indeterminate flowering pattern and yellow flower colour were predominant among qualitative traits. Primary seed colour had maximum variability and orange colour followed by cream were the two most frequent seed colours in the collection. Variances for all the traits were heterogeneous among regions. The germplasm accessions from Oceania were conspicuous by short growth duration, short height, fewer branches, pods with fewer seeds, smaller seed size and lower seed yields. The accessions from Africa were of longer duration, taller, with multi-seeded pods and larger seeds. The germplasm diversity indicated by Shannon–Weaver diversity index (H') pooled over all traits, was highest for Africa (0.464 ± 0.039) and lowest for Oceania (0.337 ± 0.037). The cluster analysis based on three principal component scores using 12 quantitative traits revealed formation of three clusters: cluster 1 includes accessions from Oceania; cluster 2 from India and adjacent countries; and cluster 3 from Indonesia, Thailand, the Philippines, Europe, Africa, America and the Caribbean countries. Pigeonpea-rich countries such as Myanmar, Uganda, and others like Bahamas, Burundi, Comoros, Haiti and Panama are not adequately represented in the collection, and need priority attention for germplasm exploration.

Keywords: *Cajanus cajan*; diversity; geographical regions; pigeonpea; qualitative traits; quantitative traits

Introduction

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is known to occur in over 60 countries. However, the Food and Agriculture Organization (FAO) database indicates this crop to be cultivated in 19 countries (at least 180 ha area under pigeonpea) only. The largest area under this crop occurs in India (3.2 million ha) followed by Myanmar (480,000 ha), Kenya (150,000 ha), Malawi (120,000 ha)

and Uganda (80,000 ha) (FAO, 2003). The average world productivity of pigeonpea is rather low (700 kg/ha; FAO, 2003) and improving genetic potential of the crop for grain yield is an important objective in most pigeonpea breeding programmes (Singh *et al.*, 1990). The importance of increasing the use of genetic resources to enhance productivity of the crop has been well recognized. The emphasis on assembling the germplasm for present and future utilization has led to build up of large germplasm collections (FAO, 1998). The R. S. Paroda genebank at ICRISAT, Patancheru, India, has assembled 13,632 accessions of pigeonpea

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germplasm including 555 accessions (belonging to 55 species and six genera) of the wild species related to pigeonpea. The germplasm of cultivated pigeonpea (13,077 accessions) represents 62 countries. Of these, 9759 accessions were assembled as donations from 62 institutions worldwide and 3873 accessions of pigeonpea and the related species through 99 collecting missions in 33 countries.

The reports on pigeonpea germplasm characterization are not exhaustive, as only few attempts were made on smaller germplasm sets. For example, 320 accessions were characterized for five traits by Ram Dhari *et al.* (1997), 168 accessions for 20 traits by Satpute *et al.* (1994), 75 accessions for seven traits by Singh *et al.* (2002), 67 accessions for 10 traits by Hazarika *et al.* (1986) and 40 accessions for 11 traits by Khin Myint Kyi *et al.* (2001). In the present study, we characterized 11,402 germplasm accessions for 14 qualitative and 12 quantitative traits, and the variability according to geographical regions is presented.

Materials and methods

Of the total 13,077 cultivated pigeonpea germplasm accessions in the ICRISAT genebank, 11,402 accessions from 54 countries were included in this study. The remaining 1675 accessions were not included due to inadequate characterization data. The experiments were conducted at the ICRISAT research farm at Patancheru (18°N, 78°E, 545 m asl and about 600 km away from the sea) from 1974/75 to 2001/02. Germplasm characterization was carried out except for five seasons: 1976/77, 1983/84 and 1998–2001. The accessions were planted in sets over the years with the onset of rainy seasons (June) and harvested during November to February depending on maturity. Sowings were done on precision fields, soils being the vertisols (Kasireddipally Series, Iso-hyperthermic-type Pellustert). Crop was fertilized with 20 kg of N and 40 kg of P₂O₅ per ha as a basal dose. The crop received adequate cultural practices and plant protection care to control the damage due to pod borer [*Helicoverpa armigera* (Hb.)]. Sowing of the accessions was done according to maturity groups (short duration: days to 50% flowering (DF) less than 101 days; medium: DF from 101 to 130 days; long: DF greater than 130 days) (Sharma *et al.*, 1981) along with appropriate check cultivars for each group. Test accessions and check cultivars were included in proportions of 5:1, 6:1 or 10:1 depending on the number of accessions available for characterization in a year. If the number of accessions was less, checks were repeated more frequently, such as 5:1. Frequency of checks was reduced if the number of accessions was large. The set of check cultivars used was not the same over the years. For example, in a

year if the accessions to be tested were composed of only short- and medium-duration types, checks of corresponding maturity duration were used.

Each accession was sown on three rows of 4 m length on ridges 75 cm apart. Plant to plant spacing was 50 cm, thus having 27 plants per plot. Pigeonpea is often cross-pollinated, due to many insects. However, *Megachile* spp., *Aphis florea* and *Aphis dorsata* are the most important pollinators (Pathak, 1970; Williams, 1977). In order to produce selfed seeds, the plants in the outer two rows were covered with muslin cloth bags on flower initiation. The data on 14 qualitative traits (growth habit, plant pigmentation, flowering pattern, flower colour, streak pattern, streak colour, pod colour, seed colour pattern, primary seed colour, secondary seed colour, seed eye colour, seed eye colour width, seed shape, and seed strophiole) and on two of the 12 quantitative traits (days to flowering and maturity) were recorded on plot basis. For the remaining 10 quantitative traits (plant height, number of primary and secondary branches, number of racemes, seeds per pod, 100-seed weight (g), harvest index (%), shelling percentage, seed protein percentage, and seed yield per plant), three competitive plants were chosen from the middle row to record the data following the 'Descriptors for Pigeonpea' (IBPGR/ICRISAT, 1993).

India is the major pigeonpea-growing country and consists of vast geographical and climatic diversity. Therefore to study the geographical patterns of diversity in the germplasm, the accessions from various states of India were classified into four broad groups based on geographical proximity and similarity of the climate (Brown, 1989; Reddy *et al.*, 2005). These groups are: (i) north-western India (Himachal Pradesh, Punjab, Haryana, New Delhi, Rajasthan and Uttar Pradesh); (ii) north-eastern India (Bihar, West Bengal, Sikkim, Meghalaya, Tripura and Assam); (iii) central India (Daman and Diu, Gujarat, Madhya Pradesh and Maharashtra); and (iv) southern India (Andhra Pradesh, Orissa, Karnataka, Kerala and Tamil Nadu). Based on the above-cited two criteria, the accessions from neighbouring countries were also clubbed with appropriate Indian states. Thus, the accessions from Pakistan and Iran were grouped with those of north-western India, and the region was named Asia 1 (AS 1). Accessions from Bangladesh, Myanmar, Nepal, China and Taiwan were grouped with north-eastern India, and named AS 2. The accessions from central India had their own exclusive group and named AS 3. The accessions from Maldives, Sri Lanka were grouped with southern India and named AS 4. The accessions from India for which precise information on location was not known were named AS 5. The accessions from South-East Asian countries, namely Indonesia, Philippines and Thailand, were named AS 6. Other

Table 1. Number and percentage of pigeonpea accessions from different regions and countries within regions available in the ICRISAT genebank

Country/region	Number of accessions (%)
Africa	976 (8.56)
Cape Verde	6 (0.61)
Central African Republic	2 (0.20)
Ethiopia	14 (1.43)
Ghana	2 (0.20)
Kenya	287 (29.41)
Madagascar	1 (0.10)
Malawi	245 (25.10)
Mozambique	10 (1.02)
Nigeria	54 (5.53)
Rwanda	5 (0.51)
Senegal	3 (0.31)
Sierra Leone	3 (0.31)
South Africa	4 (0.41)
Tanzania	219 (22.44)
Uganda	23 (2.36)
Zaire (Democratic Republic of Congo)	13 (1.33)
Zambia	85 (8.71)
Americas	176 (1.54)
Brazil	17 (9.66)
Colombia	5 (2.84)
Guyana	25 (14.20)
Mexico	2 (1.14)
Peru	5 (2.84)
USA	3 (1.70)
Venezuela	119 (67.61)
Asia 1	2425 (21.27)
India (Himachal Pradesh, Punjab, Haryana, New Delhi, Rajasthan and Uttar Pradesh)	2414 (99.55)
Iran	1 (0.04)
Pakistan	10 (0.41)
Asia 2	1137 (9.97)
Bangladesh	73 (6.42)
China	1 (0.09)
India (Bihar, West Bengal, Sikkim, Meghalaya, Tripura and Assam)	893 (78.54)
Myanmar	55 (4.83)
Nepal	112 (9.85)
Taiwan	3 (0.26)
Asia 3	1223 (10.73)
India (Daman and Diu, Gujarat, Madhya Pradesh and Maharashtra)	1223 (100.00)
Asia 4	4499 (39.46)
India (Andhra Pradesh, Orissa, Karnataka, Kerala and Tamil Nadu)	4424 (98.33)
Maldives	1 (0.02)
Sri Lanka	74 (1.64)
Asia 5	118 (1.03)
India (India state unknown)	364 (100.00)
Asia 6	364 (3.19)
Indonesia	19 (16.10)
Philippines	58 (49.15)
Thailand	41 (34.75)
Caribbean	395 (3.46)
Antigua and Barbuda	2 (0.51)
Barbados	25 (6.33)
Dominican Republic	63 (15.95)
Grenada	15 (3.80)
Guadeloupe	6 (1.52)
Jamaica	61 (15.44)
Montserrat	4 (1.01)
Puerto Rico	74 (18.73)

Table 1. *Continued*

Country/region	Number of accessions (%)
St Kitts and Nevis	6 (1.52)
St Lucia	16 (4.05)
St Vincent and the Grenadines	22 (5.57)
Trinidad and Tobago	101 (25.57)
Europe	29 (0.25)
Belgium	2 (6.90)
Germany	2 (6.90)
Italy	15 (51.72)
UK	10 (34.48)
Oceania	60 (100.00)

groups were Africa (17 countries), America (seven countries), Caribbean (12 countries), Europe (four countries) and Oceania (Australia). Hence a total of 11 regions were formed (Table 1).

Phenotypic proportions for 14 qualitative traits were calculated in each region. Statistical analysis of quantitative traits was performed using the Residual Maximum Likelihood (REML) approach. Data were first analysed separately for each of the years and combined for 22 years to estimate components of variance due to accessions and accession \times year interactions and to obtain predicted means of each of the accessions. Later, the regions (as fixed) and years (as random) were considered using predicted mean of accessions from previous analysis to determine importance of regions and region \times year interactions. The mean, range and variances of all the quantitative traits were calculated for each of the regions. The means of different regions for all traits were compared using the Newman–Keuls procedure (Newman, 1939; Keuls, 1952). The homogeneity of variances of regions was tested using Levene's test (Levene, 1960). The diversity index (H') of Shannon and Weaver (1949) was used as a measure of phenotypic diversity for each trait. The index was estimated for each trait over all accessions and for all traits within a region. By pooling various traits across regions, the additive properties of H' were used to evaluate the diversity of the regions and traits in the germplasm collection.

Principal component analysis (PCA) of 12 quantitative traits was performed. The mean observations of traits for each region were standardized by subtracting from each observation the mean value of the trait and subsequently dividing by its respective standard deviation. This resulted in standardized values for each trait with average 0 and standard deviation of 1 or less. The standardized values were used to perform PCA on Genstat 6.1. Cluster analysis was performed using scores of first three principal components following Ward (1963).

Results and discussion

India, the primary centre of origin of pigeonpea (De, 1974; van der Maesen, 1980) has the largest area under this crop (77.0% of the world). The other countries of importance are: Myanmar (11.5%), Kenya (3.6%), Malawi (3.0%) and Uganda (1.9%). India contributed the largest number of germplasm accessions to the ICRISAT genebank (68.8% of the entire collection) followed by Kenya (2.5%), Malawi (1.9%), Tanzania (1.7%) and Nigeria (1.4%). Owing to the limited area under pigeonpea, some countries are not reported by the FAO; however, we have germplasm accessions from those countries. For example, Nigeria is not listed, however, we have 182 accessions representing Nigeria, and many of them are landraces that were collected from farmers' fields during 1992 and 1993. There are 42 other countries with similar status (Table 2). To estimate the need of securing new germplasm, data of relative representation from different countries was prepared (Table 2). These data revealed that pigeonpea is cultivated in the Bahamas (180 ha), Burundi (2000 ha), Comoros (400 ha), Haiti (6600 ha) and Panama (4600 ha) but these countries are not represented in the world pigeonpea germplasm collection. Myanmar and Uganda are the other countries which grow pigeonpea on a considerable scale but are under-represented in our collection. The relative representation for Uganda is 0.11 accession per 100 ha and for Myanmar 0.02 compared to an average of 0.31 for the whole world (Table 2). This indicates the need for collecting/assembly of germplasm accessions from these countries.

Pigeonpea is an often cross-pollinated crop with an average out-crossing of 13.1% and range of 9.7–24.1% (Githiri *et al.*, 1991). Therefore a lot of heterogeneity (more than one descriptor state occurring in an accession) and heterozygosity existed in the germplasm samples collected from the farmers' fields. These germplasm samples were not separated into homogenous groups, and the variability within samples has been main-

Table 2. List of pigeonpea-growing countries, area and productivity of the crop, and germplasm accessions and their relative representation in the ICRISAT genebank

Country	No. of accessions	Year 2003		Accessions per 100 ha
		Area harvested (ha)	Yield (kg/ha)	
Antigua and Barbuda	2			
Argentina	1			
Australia	61			
Bahamas	0	180	694	
Bangladesh	75	4,050	494	1.85
Barbados	25			
Belgium	2			
Brazil	18			
Burundi	0	2,000	900	
Cape Verde	6			
Central African Republic	2			
China	1			
Colombia	5			
Comoros	0	400	750	
Dominican Republic	63	13,000	1,000	0.48
Ethiopia	14			
Germany	2			
Ghana	2			
Grenada	15	520	1,173	2.88
Guadeloupe	22			
Guyana	28			
Haiti	0	6,600	402	
ICRISAT	1619			
India	9000	3,200,000	700	0.28
Indonesia	21			
Iran	1			
Italy	15			
Jamaica	64	1,100	1,182	5.82
Kenya	332	150,000	367	0.22
Madagascar	1			
Malawi	245	123,000	642	0.20
Maldives	1			
Martinique	1			
Mexico	3			
Montserrat	4			
Mozambique	10			
Myanmar	73	480,000	625	0.02
Nepal	120	25,000	876	0.48
Nigeria	182			
Pakistan	17			
Panama	0	4,600	478	
Peru	5			
Philippines	59			
Puerto Rico	78	740	1,432	10.54
Russia and CIS	2			
Rwanda	5			
St Kitts and Nevis	6			
St Lucia	17			
St Vincent and the Grenadines	22			
Senegal	10			
Sierra Leone	3			
South Africa	25			
Sri Lanka	77			
Taiwan, Province of China	3			
Tanzania	221	66,000	712	0.33
Thailand	41			
Trinidad and Tobago	113	1,000	2,780	11.30

Table 2. *Continued*

Country	No. of accessions	Year 2003		
		Area harvested (ha)	Yield (kg/ha)	Accessions per 100 ha
Uganda	84	78,000	1,000	0.11
UK	10			
Unknown	9			
USA	4			
Venezuela	131	1,950	769	6.72
Zaire (Democratic Republic of Congo)	13			
Zambia	86			
Whole world	13,077	4,158,140		0.31

tained. This resulted in recording of more than one class of individual traits within accessions.

Qualitative traits

Growth habit

The entire germplasm collection was composed of three solitary classes of growth habit (compact, semi-spreading and spreading) and one class of heterogeneity of which semi-spreading was most frequent (84.22%) across the regions followed by compact type (13.28%). The accessions of Oceanian origin had a particularly high proportion (45.00%) of compact growth habit (Table A1). This is because pigeonpea accessions from Oceania are mostly breeding lines with compact plant type, which is preferred in mechanized crop cultivation.

Plant pigmentation

The stem colour was noted as plant pigmentation and recorded in seven classes. Green stem colour was most prominent (84.37%) and the pattern was almost similar across the regions. About 0.73% of the accessions were found having heterogeneity for this trait (Table A1).

Flowering pattern

This trait was noted in three classes (determinate, indeterminate and semi-determinate) (Fig. 1). The indeterminate class was predominant (93.87%), and the pattern was similar across the regions except Oceania where the determinate class was most common (75.00%). Determinate flowering patterns facilitate mechanized cultivation and hence such types were developed and cultivated in Australia.



Fig. 1. Flowering pattern in pigeonpea. Left to right: indeterminate, semi-determinate and determinate.

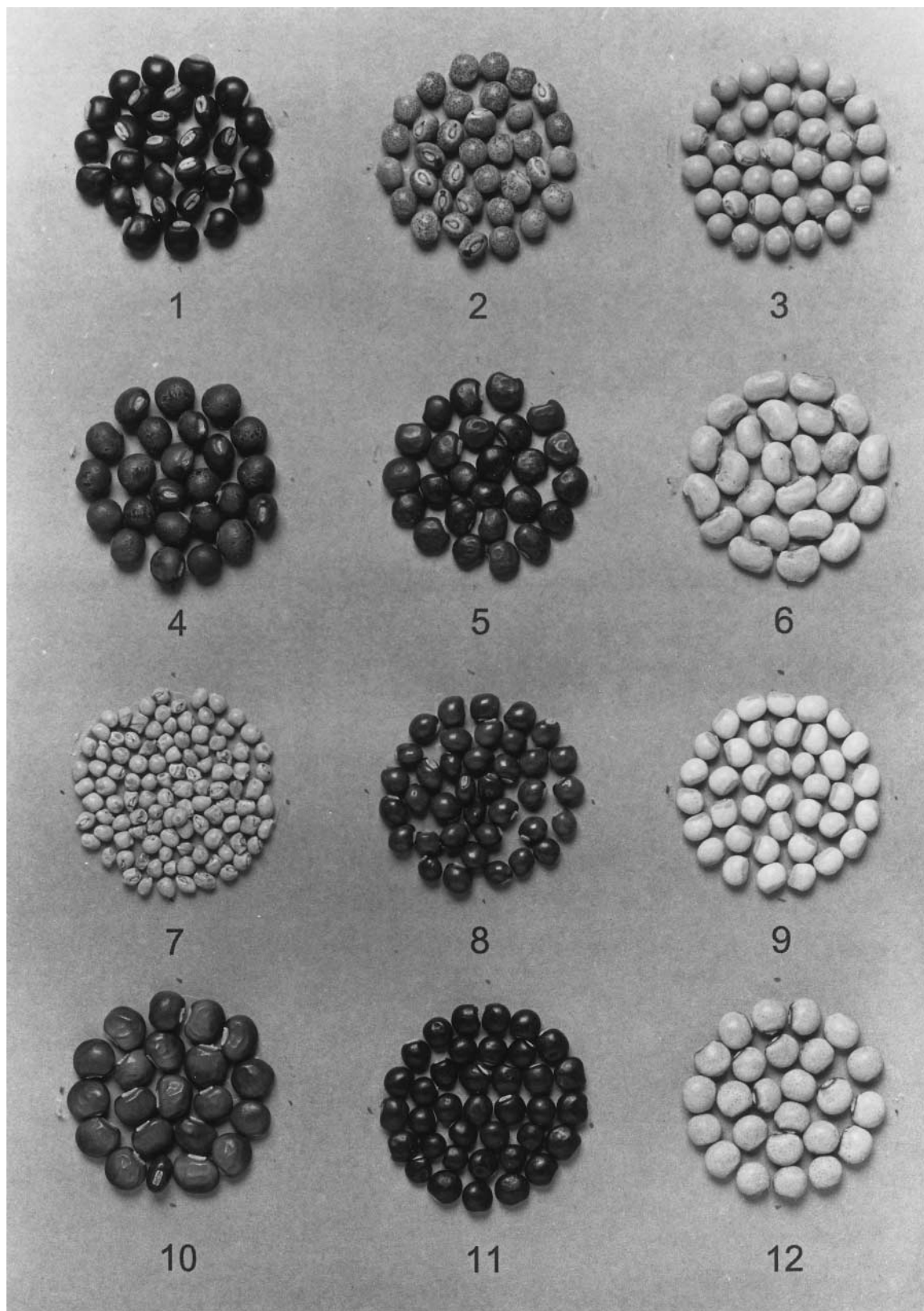


Fig. 2. Variation in pigeonpea germplasm seeds. Strophiole on seed: (1) present, (2) absent. Seed shape: (3) oval, (4) pea, (5) square, (6) elongate. Variation in seed size: (7–12).

Flower colour

In addition to the four base colour patterns, yellow, orange–yellow, light yellow and ivory, heterogeneity for yellow and orange–yellow was observed in the collection. Yellow flower colour was the most frequent (94.54%) class and was the pattern almost similar in all the regions.

Flower streak colour

The colour of streaks on the flower (mainly on the vexillum) was recorded in four classes (none, red, purple, mixed plants of red and none) and the red streaks were most common (89.54%), with almost similar pattern across the regions.

Flower streak pattern

Much diversity was observed for flower streak pattern and was recorded in 15 classes: five classes had solitary pattern and 10 had a combination of two characteristics. Few streaks was the most common class (56.50% of the entire collection). This feature had an almost similar pattern across the regions excepting Africa, America, AS 6, Caribbean and Europe. The germplasm accessions from the latter four regions had an equally high proportion of accessions with three classes of streak pattern: dense, few and plain uniform coverage (Table A1).

Pod colour

This trait was recorded in eight classes, of which green pods having purple streaks was the most dominant class (80.35%). The second most common pod colour was green (14.39%). The pattern was almost similar across the regions.

Seed colour pattern

Seed colour was recorded in 12 classes, five solitary classes and seven classes being the combination of two characteristics. Plain seed colour was the most frequent class (64.58%) followed by speckled (seed coat with fine dots: 13.19%). Region-wise, AS 1–6 regions were dominated by plain colour (65.60–74.44%), accessions from Oceania had almost all plain colour (90.00%) whereas the accessions from Africa, America, Caribbean and Europe had equally high proportions of plain and speckled seed colours (Table A1).

Primary seed colour

There is lot of diversity for primary seed colour in pigeonpea germplasm. This trait was recorded in 53 classes (14 solitary classes and 39 classes having heterogeneity). Orange seed colour was the most common feature (48.62%) followed by cream colour (24.12% of the entire collection). The distribution of this trait across the regions had similar pattern except for

the accessions from Oceania. The germplasm of Oceania origin had predominantly orange seed colour (73.33%). Pigeonpea accessions from Oceania are the results of plant breeding research and selected for high returns including the trader's preferred (orange) seed colour.

Secondary seed colour

This was recorded in 18 classes, 14 being solitary colours and four being the cases of heterogeneity. Absence of secondary colour (i.e. uniformly one colour of the seed coat) was the most predominant feature (71.68%). This trend was observed across all the Asian regions. The occurrence of this trait from four regions, Africa, America, Caribbean and Europe, was between 17.13 and 34.65%, whereas the accessions from Oceania predominantly (91.67%) had no secondary seed colour.

Seed eye colour

Pigeonpea germplasm accessions also exhibit great diversity for seed eye colour. The trait was recorded in 35 classes (14 solitary classes and 21 being the cases of heterogeneity). Brown was the dominant eye colour (82.06% of the entire collection), which was distributed almost evenly across the regions.

Seed eye colour width

The trait was recorded in seven classes, three being solitary classes (large, medium and narrow width) and the remaining four being the cases of heterogeneity within accessions. Narrow eye colour width was the predominant class (81.69% of the entire collection), which had similar distribution across the regions except Africa, America, Caribbean and Europe. In germplasm from America, Caribbean and Europe regions, two classes, narrow eye width and medium width were equally important. In accessions from Oceania, all accessions had narrow eye colour width only.

Seed shape

This trait was recorded in 10 classes, four being solitary classes (elongate, oval-, pea- and square-shaped) (Fig. 2) and the remaining six being heterogeneous (various combinations). The oval seed shape was the predominant class (93.49% of entire collection) and was distributed almost evenly across all the regions.

Seed strophiole

This trait was recorded in only two classes, it was noted as present when conspicuous and absent when not found (Fig. 2). Absence of hilum was the predominant (90.60%) class. The accessions from five Asian regions (AS 1–5) were characterized predominantly by no strophiole trait whereas many accessions from Africa, America, Caribbean, Europe and AS 6 had seeds with strophiole

(17.71–49.64%) (Table A1). Pigeonpea accessions from the later five regions are mostly of long growth duration. Long duration pigeonpea accessions generally exhibit higher expression of strophiole, and so is the observation in the present study. All the accessions from Oceania were characterized without strophiole. This is partly because all accessions were of short growth duration and partly because these were developed/selected for good-looking smooth seeds, hence obviously without strophioles (Table A1).

Quantitative traits

The variance component due to accessions was significant for most of the traits in all the 22 years of germplasm characterization, indicating that over the years significant diversity was added to the germplasm collection. In the combined analysis, all the five components, namely accession, season, region, accession × season, and season × region were significant for all the 12 quantitative traits (data not given). There were significant differences among the means of accessions from 11 regions for all the 12 quantitative traits (Table 3). Accessions from Oceania were earliest to flower (121 days) and maturity (179 days) whereas accessions from Africa took the maximum number of days to flowering (162 days) and maturity (226 days). Accessions from Oceania were shortest by stature (138.03 cm) while those from Africa were tallest (202.93 cm) followed by America (195.39 cm) and AS 1 (194.60 cm). The number of primary branches was highest in accessions from America (14.84) and Europe (14.70) while the accessions from Oceania (9.39) had the lowest number of primary branches. Accessions from Caribbean (17.92) and Oceania (17.09) also had the lowest number of secondary branches. The Oceanian germplasm, besides having lowest number of secondary branches, also had lower number of seeds per pod, 100-seed weight, shelling percentage and seed yield; while the accessions from AS 5 had higher number of secondary branches and racemes, high harvest index, shelling percentage and seed yield (Table 3). Accessions from AS 3 and 5 regions showed conspicuously high harvest index and shelling percentage. Accessions from AS 5 region were the highest yielders (76.87 g per plant) whereas accessions from Oceania gave the lowest yields (33.72 g per plant).

The mean range of quantitative traits in respect to different regions was maximum for AS 4 and minimum for the germplasm accessions from Europe and Oceania (Table 4). The region AS 4 encompasses the area of the primary centre of diversity of pigeonpea and, therefore, the high diversity in the germplasm from that region is not surprising. The accessions from Oceania are mostly

Table 3. Means for quantitative traits in pigeonpea germplasm for different regions

Character	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Days to 50% flowering	162.42 a	129.59 f	136.62 d	134.29 ed	129.17 f	131.57 ef	132.43 ef	145.82 b	140.33 c	141.86 c	120.95 g
Days to 75% maturity	225.60 a	185.07 d	202.70 b	196.15 c	191.23 c	194.00 c	193.79 c	203.17 b	196.28 c	196.48 c	178.89 e
Plant height (cm)	202.93 a	195.39 ba	194.60 ba	184.14 dc	179.37 d	189.86 bc	165.00 e	178.51 d	179.49 d	191.40 bc	138.03 f
Primary branches (no.)	10.69 cb	14.84 a	9.47 c	11.50 b	11.89 b	10.49 cb	12.30 b	11.16 cb	11.28 cb	14.70 a	9.39 c
Secondary branches (no.)	21.86 c	29.80 ba	20.64 dc	25.78 b	27.16 b	22.14 c	31.44 a	27.67 b	17.92 d	31.96 a	17.09 d
Racemes (no.)	79.18 d	109.79 c	182.09 a	166.91 b	175.41 ba	163.94 b	185.22 a	109.43 c	91.16 d	111.68 c	103.65 c
Seeds per pod (no.)	4.29 a	3.77 ed	3.69 ef	3.64 f	3.67 f	3.70 ef	3.66 f	3.93 c	4.13 b	3.82 d	3.48 g
Seed weight (g)	13.09 a	10.47 c	8.45 e	8.64 e	8.64 e	8.83 e	8.47 e	9.82 d	11.99 b	10.19 dc	8.32 e
Harvest index (%)	13.83 g	16.78 f	20.67 cd	21.26 bc	21.96 ba	20.94 bcd	22.45 a	18.72 e	17.21 f	19.82 d	19.97 d
Shelling (%)	55.98 cb	59.05 a	57.94 ba	58.69 a	59.58 a	58.90 a	59.48 a	56.74 bc	56.19 c	59.46 a	51.45 d
Protein content (%)	21.02 cb	21.01 c	22.14 a	21.63 b	21.72 b	21.64 b	21.12 c	21.78 b	21.18 c	20.75 c	22.24 a
Seed yield per plant (g)	39.62 e	48.43 d	67.43 b	65.98 b	67.86 b	63.58 cb	76.87 a	47.39 d	41.13 e	58.99 c	33.72 f

Differences between means of different regions were tested by Newman–Keuls test. Means followed by the same letter are not significantly different at $P = 0.05$.

Table 4. Range and percentage range (in parentheses) of entire collection for quantitative traits in pigeonpea germplasm for different regions

Character	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Days to 50% flowering	98.8–231.2 (76.58)	104.3–180.4 (44.01)	78.6–201.0 (70.79)	90.7–187.0 (55.70)	81.0–170.6 (51.82)	74.8–195.0 (69.52)	105.1–160.8 (32.22)	116.9–226.5 (63.39)	80.6–204.0 (71.37)	118.7–239.2 (69.69)	66.3–147.6 (47.02)
Days to 75% maturity	156.4–296.8 (72.97)	156.3–257.7 (52.70)	126.8–257.5 (67.93)	142.6–245.8 (53.64)	140.3–234.3 (48.86)	127.0–250.3 (64.09)	155.9–228.1 (37.53)	157.5–275.1 (61.12)	149.1–256.8 (55.98)	162.2–301.9 (72.61)	109.5–217.6 (56.19)
Plant height (cm)	87.7–274.0 (81.00)	123.8–227.8 (45.22)	92.1–241.4 (64.91)	107.0–271.9 (71.70)	105.3–235.2 (56.48)	49.2–279.2 (100.00)	113.4–228.1 (49.87)	113.9–228.0 (49.61)	102.2–250.6 (64.52)	150.5–236.8 (37.52)	80.2–228.2 (64.35)
Primary branches (no.)	1.6–36.2 (68.95)	3.9–31.8 (55.65)	0.4–43.1 (85.20)	3.7–28.3 (48.88)	2.8–42.1 (78.52)	5.9–44.2 (100.00)	3.9–25.3 (42.71)	4.0–29.5 (50.84)	3.1–32.3 (58.22)	6.5–23.0 (32.96)	3.8–16.3 (24.98)
Secondary branches (no.)	4.3–54.9 (42.07)	6.9–49.6 (30.35)	1.1–76.4 (55.11)	4.7–76.5 (51.00)	21.8–75.3 (69.01)	7.9–92.9 (71.61)	6.8–118.9 (79.63)	4.1–59.7 (39.48)	0.9–56.8 (39.72)	6.2–45.6 (27.96)	3.9–27.0 (16.38)
Racemes (no.)	20.8–298.9 (61.38)	38.8–286.5 (47.56)	2.8–352.7 (68.25)	15.1–410.0 (75.82)	6.2–433.2 (84.37)	32.8–488.0 (100.00)	46.4–389.7 (65.91)	30.2–225.2 (37.45)	14.7–285.0 (51.90)	7.8–184.5 (33.93)	15.9–266.1 (48.04)
Seeds per pod (no.)	2.6–6.4 (82.88)	3.0–5.2 (48.82)	2.0–5.6 (78.89)	2.4–4.5 (45.48)	2.8–4.6 (39.70)	2.3–5.6 (72.29)	2.8–4.8 (43.53)	2.9–6.6 (78.83)	2.0–6.2 (89.97)	3.3–5.3 (42.95)	2.0–4.3 (50.73)
Seed weight (g)	6.5–23.2 (77.50)	6.2–20.5 (66.32)	5.4–16.9 (53.71)	5.3–17.9 (58.36)	4.0–21.8 (82.65)	3.9–25.4 (100.00)	4.4–17.9 (62.76)	6.5–25.4 (87.51)	5.1–19.7 (67.78)	8.1–19.4 (52.41)	6.2–12.4 (28.52)
Harvest index (%)	0.1–31.1 (66.45)	3.6–30.1 (56.87)	6.8–37.7 (66.22)	4.9–35.7 (66.13)	9.1–37.2 (60.44)	3.3–46.7 (93.19)	12.9–38.5 (55.03)	1.1–32.6 (67.65)	1.5–31.7 (64.86)	2.7–29.6 (57.90)	9.1–33.0 (51.33)
Shelling (%)	15.5–84.6 (96.24)	23.1–75.4 (72.86)	32.2–79.6 (66.17)	22.7–78.0 (77.06)	35.5–82.6 (65.73)	19.2–87.3 (94.86)	45.5–77.1 (44.00)	36.8–71.3 (48.11)	25.6–81.7 (78.15)	41.0–67.5 (36.91)	38.1–65.7 (38.51)
Protein content (%)	16.7–25.1 (61.08)	17.4–24.1 (48.16)	15.9–25.9 (72.20)	17.2–26.7 (68.74)	17.3–25.4 (58.27)	14.9–28.8 (100.00)	17.3–24.7 (53.57)	16.8–25.4 (61.59)	17.6–24.2 (47.73)	19.0–23.4 (31.91)	17.4–24.1 (48.59)
Seed yield per plant (g)	16.8–144.9 (55.71)	13.4–95.8 (28.38)	3.0–145.6 (49.14)	10.8–215.0 (70.34)	9.3–149.5 (48.29)	1.3–273.5 (94.67)	16.2–172.1 (53.72)	3.6–96.1 (31.87)	11.0–163.5 (52.53)	13.4–132.8 (41.12)	6.9–93.1 (29.71)

Table 5. Variances for quantitative traits in pigeonpea germplasm for different regions

Character	Entire	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania	F value ^a	Prob > F
Days to 50% flowering	250.45	646.28	194.42	102.47	155.70	137.40	110.24	70.69	621.46	170.91	1199.47	471.15	224.98	<0.0001
Days to 75% maturity	407.91	893.66	396.22	149.46	305.02	313.23	273.18	139.41	878.75	376.68	1507.06	963.65	208.47	<0.0001
Plant height (cm)	1094.53	1037.48	386.70	1098.27	1049.04	731.48	1154.64	530.04	752.92	705.35	610.21	884.94	33.39	<0.0001
Primary branches (no.)	35.09	16.06	19.85	40.73	36.61	30.08	38.90	21.40	19.15	18.61	13.63	2.89	37.41	<0.0001
Secondary branches (no.)	193.77	81.26	88.87	205.69	192.18	180.45	214.28	155.32	100.42	106.52	91.34	20.51	41.40	<0.0001
Racemes (no.)	3858.21	1737.45	1572.97	2510.66	3194.79	2680.93	3364.76	2765.58	1565.36	3821.78	1208.64	1949.91	23.84	<0.0001
Seeds per pod (no.)	0.15	0.37	0.09	0.07	0.07	0.04	0.08	0.06	0.46	0.28	0.21	0.19	154.90	<0.0001
Seed weight (g)	5.55	9.88	3.43	1.43	1.59	2.41	4.26	1.65	6.66	7.43	4.79	1.36	60.94	<0.0001
Harvest index (%)	22.51	38.50	30.94	7.85	17.33	14.05	17.86	13.18	36.74	27.65	52.17	9.77	60.55	<0.0001
Shelling (%)	39.00	60.34	91.68	18.83	39.23	26.30	39.93	15.92	52.82	97.45	53.91	20.23	59.82	<0.0001
Protein content (%)	2.38	2.43	1.47	1.96	2.52	1.89	2.56	2.03	2.78	1.31	0.74	2.95	15.66	<0.0001
Seed yield per plant (g)	568.09	398.18	234.46	406.72	661.73	461.10	472.29	1020.71	302.86	500.87	578.21	211.89	21.57	<0.0001

^a Variances were tested using Levene's test.

Table 6. Shannon–Weaver diversity index for qualitative and quantitative traits in pigeonpea germplasm for different regions

Character	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania	Mean
Qualitative												
Growth habit	0.159	0.103	0.255	0.192	0.234	0.225	0.164	0.108	0.154	0.200	0.299	0.190 ± 0.018
Plant pigmentation	0.334	0.159	0.247	0.156	0.269	0.193	0.221	0.209	0.131	0.065	0.106	0.190 ± 0.023
Flowering pattern	0.045	0.072	0.053	0.018	0.044	0.160	0.050	0.038	0.202	0.000	0.271	0.087 ± 0.026
Flower colour	0.335	0.179	0.068	0.084	0.065	0.081	0.128	0.222	0.049	0.130	0.086	0.130 ± 0.026
Flower streak colour	0.303	0.191	0.095	0.113	0.111	0.141	0.064	0.288	0.214	0.269	0.106	0.172 ± 0.026
Flower streak pattern	0.795	0.766	0.465	0.464	0.490	0.531	0.436	0.656	0.721	0.682	0.502	0.592 ± 0.040
Pod colour	0.416	0.451	0.246	0.275	0.218	0.225	0.131	0.418	0.609	0.362	0.273	0.329 ± 0.041
Seed colour pattern	0.566	0.590	0.534	0.471	0.475	0.450	0.423	0.488	0.591	0.535	0.169	0.481 ± 0.036
Primary seed colour	0.420	0.755	0.830	0.805	0.736	0.661	0.663	0.858	0.407	0.666	0.427	0.657 ± 0.050
Secondary seed colour	0.284	0.294	0.353	0.456	0.343	0.336	0.402	0.314	0.329	0.376	0.149	0.330 ± 0.023
Seed eye colour	0.231	0.343	0.436	0.443	0.494	0.325	0.558	0.526	0.162	0.065	0.289	0.352 ± 0.047
Seed eye colour width	0.408	0.338	0.175	0.179	0.175	0.215	0.202	0.319	0.294	0.387	0.000	0.245 ± 0.036
Seed shape	0.109	0.144	0.105	0.139	0.173	0.155	0.110	0.223	0.095	0.173	0.123	0.141 ± 0.012
Seed strophiole	0.301	0.203	0.048	0.100	0.061	0.089	0.047	0.215	0.261	0.269	0.000	0.145 ± 0.032
Mean	0.336 ± 0.051	0.328 ± 0.062	0.279 ± 0.060	0.278 ± 0.059	0.278 ± 0.055	0.271 ± 0.046	0.257 ± 0.054	0.349 ± 0.059	0.301 ± 0.056	0.298 ± 0.058	0.200 ± 0.040	0.289 ± 0.048
Quantitative												
Days to 50% flowering	0.639	0.485	0.562	0.602	0.618	0.588	0.608	0.503	0.589	0.320	0.512	0.548 ± 0.027
Days to 75% maturity	0.582	0.533	0.558	0.564	0.628	0.542	0.623	0.542	0.586	0.299	0.444	0.536 ± 0.028
Plant height (cm)	0.621	0.562	0.608	0.585	0.573	0.594	0.536	0.622	0.598	0.475	0.496	0.570 ± 0.015
Primary branches (no.)	0.577	0.617	0.543	0.530	0.579	0.583	0.585	0.562	0.573	0.441	0.518	0.555 ± 0.014
Secondary branches (no.)	0.632	0.587	0.533	0.540	0.567	0.518	0.591	0.607	0.594	0.590	0.628	0.581 ± 0.011

Table 6. *Continued*

Character	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania	Mean
Racemes (no.)	0.596	0.537	0.561	0.612	0.619	0.555	0.604	0.601	0.472	0.521	0.403	0.553 ± 0.020
Seeds per pod (no.)	0.629	0.583	0.589	0.579	0.611	0.583	0.607	0.544	0.607	0.481	0.578	0.581 ± 0.012
Seed weight (g)	0.626	0.585	0.581	0.593	0.581	0.552	0.602	0.497	0.620	0.346	0.533	0.556 ± 0.024
Harvest index (%)	0.631	0.566	0.517	0.575	0.619	0.565	0.513	0.623	0.609	0.554	0.447	0.565 ± 0.017
Shelling (%)	0.621	0.578	0.532	0.569	0.616	0.606	0.599	0.616	0.617	0.528	0.528	0.583 ± 0.011
Protein content (%)	0.601	0.587	0.606	0.622	0.615	0.609	0.621	0.609	0.633	0.500	0.475	0.589 ± 0.016
Seed yield per plant (g)	0.602	0.554	0.548	0.596	0.595	0.567	0.613	0.600	0.512	0.501	0.410	0.554 ± 0.018
Mean	0.613 ± 0.006	0.564 ± 0.010	0.561 ± 0.008	0.580 ± 0.008	0.602 ± 0.006	0.572 ± 0.008	0.592 ± 0.010	0.577 ± 0.013	0.584 ± 0.013	0.463 ± 0.027	0.498 ± 0.019	0.564 ± 0.005
Overall mean	0.464 ± 0.039	0.437 ± 0.041	0.409 ± 0.043	0.418 ± 0.043	0.427 ± 0.044	0.410 ± 0.039	0.412 ± 0.044	0.454 ± 0.039	0.432 ± 0.041	0.374 ± 0.037	0.337 ± 0.037	0.416 ± 0.037

breeding lines and cultivars; characterized by short duration, compact growth habit and greater uniformity that are required for mechanical harvesting. As expected, such materials from Oceania revealed low diversity. Germplasm accessions from Europe are just collection items, never grown there as a crop, which may have been grown in botanical gardens occasionally, and therefore do not show much diversity (Dr L. J. G. van der Maesen, personal communication).

The variances were heterogeneous ($P < 0.0001$) for all the 12 quantitative traits (Table 5). The accessions of the African region had high variance for seeds per pod, 100-seed weight and harvest index. The accessions from America showed high variance for shelling percentage but lowest for plant height. Accessions from the Caribbean had high variances for raceme number, seed number per pod and shelling percentage. The accessions of European origin had highest variances for days to flowering, maturity and harvest index, but lowest variance for protein content. The accessions of Oceania origin showed highest variance for protein content, and lowest variances for primary branches, secondary branches and 100-seed weight. Of the germplasm from different Asian regions, diversity was more apparent in AS 1, 4 and 6 compared to AS 2, 3 and 5 (Table 5).

The Shannon–Weaver diversity index (H') was calculated to compare phenotypic diversity among germplasm accessions in respect to various traits and the regions. The index is used as measure of allelic richness and evenness: a low H' indicates an extremely unbalanced frequency class for an individual trait and lack of genetic diversity. Estimates were made for

each trait and pooled across the traits and regions for both the quantitative and qualitative traits (Table 6). The accessions from AS 6 region had the highest pooled H' for qualitative traits (0.349 ± 0.059) and accessions from Africa for quantitative traits (0.613 ± 0.006). African accessions also had the highest pooled H' (0.464 ± 0.039) over all the traits. The accessions from Oceania had the lowest pooled H' (0.337 ± 0.037) (Table 6). The pooled H' across the regions was highest for primary seed colour (0.657 ± 0.050) followed by flower streak pattern, seed protein content and shelling percentage, whereas it was lowest for flowering pattern (0.087 ± 0.026) (Table 6).

The PCA was used to provide a reduced dimension model that would indicate measured differences among groups. PC 1 is the most important component accounting for 46.96% of the total variation. PC 2 accounted for 30.67% and PC 3 for 14.65% of the total variation. A hierarchical cluster analysis conducted on the first three PC scores (total variation accounted: 92.28%) resulted in three clusters (Fig. 3). Cluster 1 comprised accessions from Oceania (60 accessions), cluster 2 comprised accessions from AS 1–5 [all states of India, India (unknown states) and adjacent countries of Iran, Pakistan, Bangladesh, China, Myanmar, Nepal, Taiwan, Maldives and Sri Lanka: 9648 accessions) and cluster 3 comprised accessions from Africa, America, Caribbean countries, Europe and AS 6 (Indonesia, Philippines and Thailand) containing 1694 accessions. The clustering of pigeonpea germplasm accessions based on their place of origin into three clusters appears to be logical. The first cluster is formed of

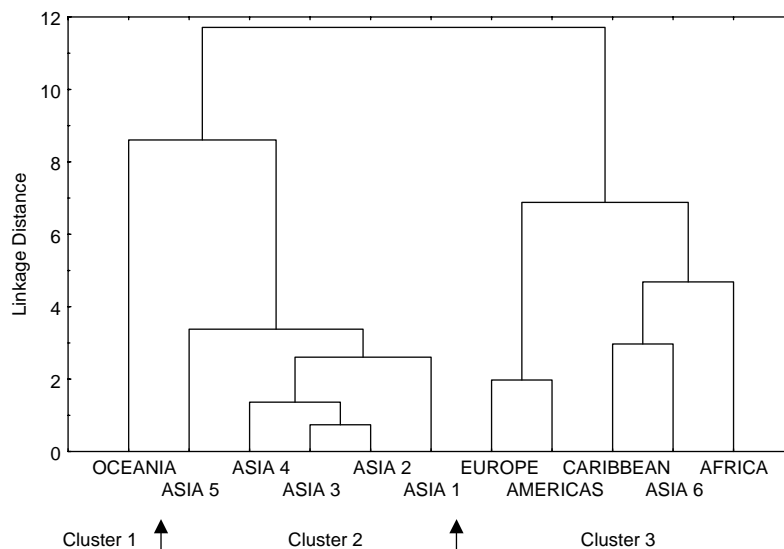


Fig. 3. Dendrogram of 11 regions in the entire pigeonpea germplasm based on the first three principal components.

Table 7. Means and variances for quantitative traits in pigeonpea germplasm for different clusters

Character	Mean ^z			Variance ^y			F value	Prob > F
	Cluster 1	Cluster 2	Cluster 3	Cluster 1	Cluster 2	Cluster 3		
Days to 50% flowering	120.95 c	132.89 b	152.35 a	471.15	121.84	645.70	1215.05	<0.0001
Days to 75% maturity	178.89 c	196.08 b	212.49 a	963.65	261.97	977.90	1370.31	<0.0001
Plant height (cm)	138.03 b	188.11 a	194.78 a	884.94	1094.18	975.26	9.43	<0.0001
Primary branches (no.)	9.39 b	10.60 ba	11.36 a	2.89	38.04	18.89	136.21	<0.0001
Secondary branches (no.)	17.09 b	23.18 a	22.35 a	20.51	210.43	103.27	164.69	<0.0001
Racemes (no.)	103.65 b	171.11 a	87.82 c	1949.91	3085.79	2318.89	28.22	<0.0001
Seeds per pod (no.)	3.48 c	3.68 b	4.16 a	0.19	0.07	0.36	795.74	<0.0001
Seed weight (g)	8.32 b	8.67 b	12.28 a	1.36	2.93	9.54	272.56	<0.0001
Harvest index (%)	19.97 b	21.10 a	15.36 c	9.77	14.84	38.69	289.62	<0.0001
Shelling (%)	51.45 c	58.74 a	56.46 b	20.23	32.18	72.45	188.01	<0.0001
Protein content (%)	22.24 a	21.76 b	21.10 c	2.95	2.36	2.10	5.58	0.003
Seed yield per plant (g)	33.72 c	65.88 a	41.76 b	211.89	505.28	415.27	9.15	<0.0001

^zDifferences between means of different regions were tested by Newman–Keuls test. Means followed by same letter are not significantly different at $P = 0.05$.

^yVariances were tested by Levene's test.

accessions from Oceania where pigeonpea crop is a recent introduction and short duration and short stature types are favoured, and all such lines have fallen into a distinct group of their own. Pigeonpea migrated from

India to Africa about two millennia BC, and from there to America and the Caribbean after 1500 AD (van der Maesen, 1980). Migration of pigeonpea from India towards the East (Indonesia, Philippines, and

Table 8. Shannon–Weaver diversity index for qualitative and quantitative traits in pigeonpea germplasm for different clusters

Character	Cluster 1	Cluster 2	Cluster 3	Mean
Qualitative				
Growth habit	0.299	0.234	0.151	0.228 ± 0.043
Plant pigmentation	0.106	0.216	0.274	0.199 ± 0.049
Flowering pattern	0.271	0.108	0.095	0.158 ± 0.057
Flower colour	0.086	0.081	0.262	0.143 ± 0.060
Flower streak colour	0.106	0.121	0.280	0.169 ± 0.056
Flower streak pattern	0.502	0.509	0.791	0.601 ± 0.095
Pod colour	0.273	0.234	0.486	0.331 ± 0.078
Seed colour pattern	0.169	0.481	0.605	0.418 ± 0.130
Primary seed colour	0.427	0.753	0.530	0.570 ± 0.096
Secondary seed colour	0.149	0.374	0.324	0.282 ± 0.068
Seed eye colour	0.289	0.412	0.262	0.321 ± 0.046
Seed eye colour width	0.000	0.198	0.409	0.202 ± 0.118
Seed shape	0.123	0.145	0.123	0.130 ± 0.007
Seed strophiole	0.000	0.076	0.291	0.122 ± 0.087
Mean	0.200 ± 0.040	0.281 ± 0.053	0.349 ± 0.052	0.277 ± 0.071
Quantitative				
Days to 50% flowering	0.512	0.590	0.607	0.570 ± 0.029
Days to 75% maturity	0.444	0.599	0.606	0.550 ± 0.053
Plant height (cm)	0.496	0.590	0.625	0.570 ± 0.039
Primary branches (no.)	0.518	0.587	0.608	0.571 ± 0.027
Secondary branches (no.)	0.628	0.636	0.606	0.623 ± 0.009
Racemes (no.)	0.403	0.586	0.568	0.519 ± 0.058
Seeds per pod (no.)	0.578	0.634	0.618	0.610 ± 0.017
Seed weight (g)	0.533	0.547	0.610	0.563 ± 0.024
Harvest index (%)	0.447	0.517	0.635	0.533 ± 0.055
Shelling (%)	0.528	0.591	0.605	0.575 ± 0.024
Protein content (%)	0.475	0.608	0.630	0.571 ± 0.049
Seed yield per plant (g)	0.410	0.593	0.613	0.539 ± 0.064
Mean	0.498 ± 0.019	0.590 ± 0.009	0.611 ± 0.005	0.566 ± 0.037
Overall mean	0.337 ± 0.037	0.424 ± 0.042	0.470 ± 0.038	0.410 ± 0.055

Thailand) and perhaps to Europe too happened at a later date and possibly a similar type of material was transferred. Presumably, the pigeonpea types that migrated from India to distant countries excepting Oceania were of similar types, and this has been substantiated by the results of the present study.

Besides the short duration and short stature of the accessions of cluster 1, they had lower means for most of the quantitative traits except for seed protein content which was higher compared to the other two clusters (Table 7). Cluster 2 comprised accessions that are from adjacent geographical regions of India and the neighbouring countries. These accessions were characterized by highest means for raceme number, harvest index, shelling percentage and seed yield. These are also characterized by highest variances for plant height, primary branches, secondary branches, raceme number and seed yield. One of the reasons for good performance of these accessions could be their own native environment in which they were tested. The accessions of cluster 3 were characterized by longer crop duration, taller height, higher number of primary and secondary branches, higher number of seeds per pod and higher 100-seed weight. They also had higher variances for six of the 12 traits (Table 7), indicating greatest diversity among the accessions. The overall average H' of cluster 3 was highest (0.470 ± 0.038) followed by cluster 2 (0.424 ± 0.042). This is expected because the accessions from these two regions represent the greatest geographical diversity (Table 8).

Progress in increasing pigeonpea productivity in the last three decades through the utilization of basic germplasm has been limited. Further progress is possible by broadening the genetic base and increasing productivity of the cultivars developed. The identification of the useful germplasm for breeding programmes is the basic need. This could be achieved by two approaches: (i) identifying regions from where germplasm that has higher mean for desired traits as well as genetic diversity and (ii) by developing and systematically evaluating representative core collections of pigeonpea. In the present study, we have analysed regions that possess high scores of diversity for different traits and individual traits with high diversity indicated by more than one parameter (mean, percentage range of entire collection, variance and Shannon–Weaver diversity index). The germplasm from Africa is the best source for growth duration and plant height; germplasm from America for plant height and primary branches; germplasm from Caribbean for growth duration, primary branches, seeds per pod and 100-seed weight; germplasm from AS 4 for number of primary branches, racemes, higher harvest index, seed yield and seed protein content; and the germplasm from AS 5 for increased number of racemes and higher seed yield. Depending

on the objective of the breeding programmes (such as breeding cultivars for agroforestry, short-season sole cropping, medium- to long-season intercropping), these traits can be selectively deployed for maximization of yield and adaptation to the environment.

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Table A1. Phenotypic proportions of qualitative traits in different regions of pigeonpea germplasm

Character	Entire	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Growth habit												
Compact	13.28	10.04	5.14	18.25	11.92	6.74	14.27	6.18	6.84	10.57	17.24	45.00
Compact; semi-spreading	0.42	0.51	0.57	0.91	0.62	0.25	0.20	0.28				
Semi-spreading	84.22	89.34	94.29	79.64	86.76	84.96	83.54	90.73	93.16	89.18	82.76	55.00
Spreading	2.08	0.10		1.20	0.71	8.05	1.98	2.81		0.26		
Pigmentation												
Dark purple	0.07	0.51		0.04			0.04					
Green	84.37	79.30	90.86	81.79	90.37	75.84	86.48	83.15	86.32	93.30	96.55	93.33
Green; purple	0.56	5.53		0.33	0.09						3.45	
Green; sun red	0.15	0.41		0.12	0.09		0.07		1.71	1.03		
Purple	2.18	9.32	3.43	2.19	0.97	1.89	1.16	1.69	0.85	1.03		
Purple; sun red	0.02	0.10					0.02					
Sun red	12.65	4.82	5.71	15.52	8.48	22.27	12.23	15.17	11.11	4.64		6.67
Flowering pattern												
Determinate	5.26	1.23	0.57	1.57	0.18	0.49	9.89	1.97		11.08		75.00
Indeterminate	93.87	98.16	96.57	97.72	99.38	98.19	89.33	97.75	98.29	86.34	100.00	23.33
Semi-determinate	0.86	0.61	2.86	0.70	0.44	1.31	0.78	0.28	1.71	2.58		1.67
Flower colour												
Ivory	0.69	6.86			0.71		0.04				3.45	
Light yellow	2.32	9.53	3.43	0.58	0.53	1.81	1.60	8.71	11.97	0.52	3.45	5.00
Orange yellow	2.44	5.64	7.43	2.61	2.56	1.07	2.09		3.42	1.55		
Yellow	94.54	77.87	89.14	96.81	96.20	97.13	96.26	91.29	84.62	97.94	93.10	95.00
Yellow; orange yellow	0.01	0.10										
Flower streak colour												
None	10.13	28.79	16.00	5.55	6.97	6.41	9.61	3.37	37.61	12.92	31.03	6.67
None; red	0.07	0.82										
Purple	0.26	1.02		0.04	0.09	0.25	0.11			2.33		
Red	89.54	69.36	84.00	94.41	92.94	93.34	90.28	96.63	62.39	84.75	68.97	93.33
Flower streak pattern												
Dense	9.09	27.15	27.43	5.84	4.94	7.07	6.56	5.62	9.40	23.82	34.48	15.00
Dense; few	0.53	0.72		0.66	0.53	0.25	0.58	0.56				
Dense; medium	0.58	0.41	0.57	0.58	0.79	0.82	0.45	1.40	0.85	0.52	3.45	
Dense; none	0.10	0.61					0.02			0.79		
Dense; plain uniform coverage	0.47	3.18	0.57				0.22			2.88		
Few	56.50	9.43	13.14	66.21	66.99	59.62	63.65	69.38	29.91	8.38	13.79	65.00
Few; medium	0.59	0.41		1.12	0.18	0.82	0.38	1.40	0.85			1.67
Few; cone	0.04	0.31		0.08								
Few; plain uniform coverage	0.36	1.54	1.14	0.21	0.44	0.08	0.18			1.05		1.67
Medium	15.36	6.86	10.86	19.42	17.83	24.75	12.63	17.98	11.11	8.38	13.79	8.33
Medium; none	0.04	0.31					0.02					
Medium; plain uniform coverage	0.06	0.31	1.14	0.04			0.02					
None	10.00	27.56	14.86	5.51	6.97	6.41	9.64	3.37	37.61	12.83	27.59	6.67
None; plain uniform coverage	0.21	1.23	2.86				0.04			1.31		
Plain uniform coverage	6.07	19.98	27.43	0.33	1.32	0.16	5.60	0.28	10.26	40.05	6.90	1.67

Table A1. Continued

Character	Entire	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Pod colour	0.03						0.04			0.26		
Dark purple	0.01									0.26		
Dark purple; green and purple	14.39	31.05	45.98	13.37	12.15	9.48	10.76	5.62	50.43	26.63	17.24	6.67
Green	80.35	61.07	43.68	83.24	81.32	86.81	85.77	92.70	40.17	43.34	68.97	80.00
Green and purple	0.50	0.51	0.57	0.63	0.36	0.25	0.43			2.35		
Green and purple; purple	0.92	3.07	3.45	0.54	0.45	1.65	0.34			3.92		
Green; green and purple	0.26	1.02					0.09			3.66		
Green; purple	3.55	3.28	6.32	2.22	5.72	1.81	2.58	1.69	8.55	19.58	13.79	13.33
Purple												
Seed colour pattern												
Mottled	6.46	2.87	2.30	7.15	5.68	9.03	6.08	8.43	11.97	9.71		
Mottled and speckled	4.60	15.90	1.72	4.99	4.00	1.74	3.06	2.25	2.56	6.56	10.34	
Mottled and speckled; mottled	0.01						0.02					
Mottled and speckled; plain	0.83	1.23		1.46	1.42	0.41	0.49	0.56	0.85	0.26		
Mottled and speckled; speckled	0.05	0.31	0.57	4.24	3.20	0.08	0.02	3.09	1.71	2.10		
Mottled; plain	2.80	0.62	1.72	0.21	0.09	4.89	1.99			0.52		
Mottled; speckled	0.24	0.31	1.72	0.21	0.09	0.29	0.29			27.56	48.28	90.00
Plain	64.58	26.67	42.53	65.60	71.40	68.85	72.40	74.44	65.81	3.94	17.24	3.33
Plain; speckled	7.19	2.36	17.24	9.57	6.39	10.94	6.28	5.90	1.71			
Ringed	0.03						0.04		0.85			
Ringed; mottled and speckled	0.01						0.02					
Speckled	13.19	49.74	32.18	6.78	7.82	4.06	9.28	5.34	14.53	49.34	24.14	6.67
Primary seed colour												
Black	0.07	0.10	1.14	0.08			0.02		1.71			
Brown	0.61	0.21		0.29	0.36	0.08	1.23					
Brown; cream	0.04	0.10	1.14				0.04					
Brown; purple	0.01			0.04								
Cream	24.12	79.90	54.86	10.56	11.37	17.07	19.54	12.36	31.62	75.07	55.17	10.00
Cream; dark brown	0.13	0.41	1.14	0.04	0.18		0.07			0.26	6.90	
Cream; dark grey	0.01											
Cream; grey	0.16	0.10		0.58	0.09	0.17						
Cream; light brown	0.52	1.03	9.71	0.54	0.36	0.08	0.09	0.84	1.71	0.79	6.90	
Cream; orange	2.72	1.74	2.86	3.45	2.66	1.99	3.13	0.84	0.85	0.52	3.45	1.67
Cream; purple	0.18	0.21	1.14	0.08	0.09	0.25	0.11	0.28	2.56	0.26		
Cream; reddish brown	0.01						0.02					
Cream; white	0.04			0.08		0.25						
Dark brown	2.83	4.31	3.43	1.25	2.93	4.81	3.18	0.28	2.56	0.52	10.34	
Dark brown; grey	0.02				0.09		0.02					
Dark brown; light brown	0.13		0.57	0.17	0.18	0.17	0.11		0.85			
Dark brown; orange	0.10	0.10		0.08	0.18	0.08	0.13	0.28				
Dark brown; purple	0.02	0.10										
Dark grey	0.19	0.10		0.46	0.44	0.08	0.04		0.85			
Dark grey; grey	0.04			0.12	0.09							
Dark purple	0.55	0.72	1.71	1.54	0.18	0.08	0.11	0.56	3.42	0.26		
Dark purple; cream	0.02			0.04	0.09							

Table A1. Continued

Character	Entire	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Dark purple; orange	0.03			0.04	0.09		0.02					
Dark purple; purple	0.10	0.21		0.21		0.17	0.02	0.28				
Grey	1.04	0.10		2.95	1.69	0.58	0.27	1.69	0.85			
Grey; light brown	0.10			0.33	0.18		0.02					
Grey; light cream	0.01			0.04								
Grey; light grey	0.03			0.08	0.09		0.02	0.56	0.85			
Grey; orange	0.29	0.10		0.91	0.36	0.17						
Grey; purple	0.04	0.10		0.04	0.18							
Light brown	6.51	3.90	11.43	7.40	13.32	2.90	4.90	7.87	16.24	11.02	6.90	8.33
Light brown; orange	0.62	0.10	1.14	1.12	1.33	0.41	0.38	0.56				1.67
Light brown; purple	0.07	0.31	1.71	0.08								
Light brown; reddish brown	0.12		0.57	0.12	0.36	0.17	0.04					1.67
Light cream	1.42	0.10		1.79	2.31	1.91	1.50	0.28				
Light cream; orange	0.04			0.08	0.09	0.17						
Light cream; purple	0.01				0.09							
Light grey	0.31	0.10	0.57	0.91	0.62	0.08	0.07					
Light grey; orange	0.05			0.17		0.08	0.02					
Orange	48.62	4.51	5.14	54.97	51.69	53.60	57.60	59.27	22.22	8.66	6.90	73.33
Orange; brown	0.09			0.08			0.16	0.28				
Orange; dark grey	0.02			0.08								
Orange; purple	0.24	0.10		0.62	0.18	0.17	0.13		0.85			
Orange; reddish brown	1.60	0.10	0.57	1.33	1.51	3.81	1.61	3.09		0.26		
Purple	2.03	0.92	1.14	2.91	1.87	1.49	1.88	1.40	11.97	1.31	3.45	
Purple; light grey	0.02			0.08								
Purple; reddish brown	0.01			2.83	3.73	6.38	0.02					3.33
Reddish brown	3.17	0.21		0.04			3.04	8.43		0.26		
Reddish brown; dark purple	0.01			1.25	0.98	2.90	0.40	0.56	0.85	0.79		
White	0.88						0.02					
White; brown	0.01				0.09			0.28				
White; light brown	0.01			0.04								
White; orange	0.02											
Secondary seed colour												
Brown	1.33	0.10		0.75	5.60	1.16	0.63	5.90	0.85	0.52		3.33
Brown; none	0.01	0.10										
Cream	1.44	0.10		1.79	3.91	1.91	0.89	3.09		0.26		
Cream; none	0.02			0.04		0.08						
Dark brown	0.04			0.04			0.09					
Dark grey	0.58			1.70	1.24	0.17	0.13	0.56				
Dark purple	0.02						0.02	0.28				
Grey	0.58			0.91	0.27	2.65	0.16	0.28				
Light brown	1.42	2.15	0.57	1.79	1.69	0.17	1.52	1.69	0.85			
Light cream	0.40			0.67	0.27	1.99	0.04					
Light grey	0.11			0.21	0.09	0.08	0.07	0.56				
None	71.68	17.13	34.29	83.37	74.16	81.69	78.18	78.37	65.81	34.65	34.48	91.67
Orange	1.19	0.92		1.70	2.04	1.16	0.89	1.97				

Table A1. Continued

Character	Entire	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Purple	0.04			0.04			0.02	0.56				
Reddish brown	0.26			0.58	0.53	0.25	0.09	0.28		0.26		
White	19.94	79.18	65.14	5.28	9.24	8.45	15.92	6.46	32.48	63.52	58.62	5.00
White; brown	0.22	0.10		0.29	0.36		0.25			0.52		
White; none	0.74	0.21		0.83	0.62	0.25	1.10			0.26	6.90	
Seed eye colour												
Brown	82.06	89.33	83.43	80.04	77.80	73.65	85.42	66.85	66.67	93.18	96.55	81.67
Brown; dark brown	0.11			0.08	0.27	0.25	0.09					
Brown; dark grey	0.43			1.62	0.53	0.17	0.04					
Brown; dark purple	0.44	0.92	1.71	0.67	0.09	0.17	0.34		2.56	0.26		
Brown; grey	0.02				0.18			0.28				
Brown; light brown	0.06			0.21			0.02	0.28				
Brown; none	0.03		0.57			0.08		0.28				
Brown; purple	0.35	0.92	2.86	0.12	0.27	0.08	0.31		2.56	0.26		
Brown; reddish brown	0.31			0.37	0.44	0.50	0.34					
Cream	0.07			0.21	0.09		0.04					
Cream; None	0.01			0.04								
Dark brown	2.02	0.21	2.29	0.79	1.24	4.89	2.41	5.06	0.85	0.52		1.67
Dark brown; light brown	0.01						0.02					
Dark grey	0.33			1.08	0.53	0.08	0.07		0.85			
Dark purple	2.42	1.85	3.43	2.87	2.13	1.66	2.37	1.69	12.82	2.62		
Dark purple; light brown	0.02			0.08								
Dark purple; purple	0.02											
Dark purple; reddish brown	0.01					0.08						
Grey	0.11			0.25	0.18		0.04	0.28	0.85			
Grey; light brown	0.01			0.04								
Greyish brown	0.57			1.41	0.80	0.75	0.16	1.12		0.26		
Greyish brown; brown	0.01			0.04								
Light brown	1.50	1.33	0.57	2.41	1.51	3.56	0.60	2.81				
Light grey	0.02			0.04	0.09							
None	4.08	0.62	1.14	4.49	8.70	6.30	2.82	10.67	3.42	0.52	3.45	11.67
Orange	1.80	0.10	2.29	1.21	1.60	3.48	1.72	6.46	0.85	0.52		
Orange; brown	0.03			0.04			0.02	0.28				
Orange; dark brown	0.02				0.09		0.02					
Purple	1.42	4.31	1.71	0.83	1.87	0.08	1.25	0.28	8.55	1.57		
Purple; light brown	0.01	0.10										
Reddish brown	1.37	0.21		0.75	1.33	3.07	1.59	3.09				1.67
Reddish brown; none	0.01			0.04								
Reddish brown; purple	0.01	0.10										
White	0.35			0.17	0.27	1.16	0.27	0.84		0.26		3.33
White; brown	0.01						0.02					
Seed eye colour width												
Large width	1.80	11.49	1.14	0.71	0.89	1.24	0.89	0.56	2.56	0.26	3.45	
Large width; narrow width	0.01			0.04								
Medium width	13.86	60.00	46.29	5.03	7.02	5.39	10.40	3.93	15.38	34.21	31.03	

Table A1. Continued

Character	Entire	Africa	Americas	Asia 1	Asia 2	Asia 3	Asia 4	Asia 5	Asia 6	Caribbean	Europe	Oceania
Medium width; large width	0.01					0.08						
Medium width; narrow width	0.02								0.85	0.26		
Narrow	81.69	28.00	52.00	90.44	89.79	90.64	86.29	87.92	77.78	65.26	62.07	100.00
No eye colour	2.61	0.51	0.57	3.78	2.31	2.65	2.42	7.58	3.42		3.45	
Seed shape												
Elongate	1.02	0.51	3.43	0.25	0.27	1.24	1.63	0.28	1.71		3.45	5.00
Elongate; oval	0.03	0.10					0.02	0.28				
Elongate; pea	0.01				0.09							
Oval	93.49	94.56	92.57	95.21	93.61	91.88	92.74	94.93	86.32	95.01	89.66	93.33
Oval; pea	0.10				0.09	0.50	0.09					
Oval; square	0.65			1.04	0.80	1.24	0.51	0.28		0.26		
Pea	2.46	4.21	3.43	0.58	2.22	1.74	3.08	0.85	9.40	4.46	6.90	
Square	2.22	0.62	0.57	2.91	2.84	3.40	1.88	3.38	2.56	0.26		1.67
Square; elongate	0.02						0.04					
Square; pea	0.01				0.09							
Seed strophiole												
Absent	90.60	50.36	82.29	97.67	93.87	96.85	94.75	97.75	80.34	71.13	68.97	100.00
Present	9.40	49.64	17.71	2.33	6.13	3.15	5.25	2.25	19.66	28.87	31.03	