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Geographic patterns of genetic diversity and fertility restoration ability of Asian and African origin pearl millet populations

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ABSTRACT

A set of 45 diverse Asian and African origin/bred populations of pearl millet were investigated multi-locationally for morphological traits including grain yield and assessed for their fertility restoration ability on three cytoplasmic male sterility (CMS) systems in two contrasting seasons. Significant genetic variation was found for all the yield linked traits. Multivariate analysis for grain yield and its component traits grouped these populations into five clusters. Most of the Asian origin populations grouped into single cluster (Cluster III) and separated from the rest of the African origin populations indicating the presence of correspondence between clustering pattern and geographical origin of the populations. Clusters dominated with Asian populations (As-As) had linkages with early flowering, short plant height, more number of tillers, small and thin panicles, small seeded and low grain yield compared to the clusters dominated by African populations (Af-Af) or African origin and Asian bred (Af-As) populations. Genetically related populations having common parentage were found grouped in same clusters. Fertility restoration/maintainer frequency of 45 populations on three diverse CMS systems revealed that overall fertility restoration frequency was highest for A_1 (86%) followed by A_4 (37%) and for A_5 (7%) CMS system. Five populations were identified as potential sources for developing maintainer lines for all three CMS systems and eight populations were identified specifically for A_4 and A_5 CMS systems. A set of 11 and four populations were identified for restorer line development exclusively for A_1 and A_5 CMS system, respectively. Six populations were identified for the development of dual restorers for both A_1 and A_4 CMS system.

1. Introduction

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is an important food and fodder crop in the arid and semi-arid tropics of Asia and Africa. It serves as a staple cereal and most common source of energy and micronutrients for >90 million people living in the arid and semi-arid regions. Pearl millet originated and was domesticated in Sub-Saharan region of West and Central Africa, and later migrated to eastern Africa, semi-arid regions of South Asia, and other parts of the world. ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) conserves the world's largest collection of 22,888 pearl millet germplasm accessions from 51 countries with 6610 accessions from India [1] and 13,185 accessions from Africa [2]. India and Africa together contribute ~98% of the world pearl millet cultivation. Pearl millet cultivation in Africa (~22 Mha) is mainly based on open pollinated varieties (OPVs), landraces and improved populations. Whereas, in India, hybrids occupy about 70% (~5 Mha) of the area under pearl millet; the rest (~2.5 Mha) is under OPVs or landraces [3]. The pearl millet productivity in India increased at the rate of 3% per annum during 1990–2017 [4] due to exploitation of heterosis through hybrid development. In contrast, the productivity has not significantly changed in the African continent in the last three decades from 1988 (691 kg ha^{-1}) to 2018 (718 kg ha^{-1}), though area has increased from 15.8 to 22.1 Mha [5]. Hence, it is necessary to develop new series of high yielding cultivars by involving under-utilized genetic diversity.

Pearl millet breeding in India during 1930 s started with the development of OPVs from locally adapted material through mass selection and progeny evaluation. But, they provided marginal improvement in the yield level. Later, with the establishment of ICRISAT during 1970s resulted into the development of some high yielding OPVs following different population improvement programs utilizing diverse range of Asian and African germplasms. It

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also leads to the development of several trait-based composites [e.g. early composite (EC), medium composite (MC), late composite (LC), smut-resistant composite (SRC), high-tillering composite (HTC), bold-seeded composite (BSC), dwarf composite (DC), high head volume composite (HHVC) and many others] to support the breeding programs. Several high yielding OPVs such as WC-C75, ICMV 221, ICTP 8203, HC 4, Raj 171, JBV 2 and JBV 3, HC 20, RCB 2, CZP 9802 and Pusa 266 were developed from these trait-based composites through recurrent selection [6]. However, many of these composites/OPVs, breeding populations and germplasms were not phenotypically well characterized which limits their utilization in current breeding programs in development of the new range of high yielding cultivars. Initially, during the beginning of hybrid breeding era in pearl millet (1960s), trait based composites and populations were observed for traits and fertility/sterility and were involved in seed parent or restorer parent development programs, but this information was never documented.

Understanding the structure of diversity and identification of distinct materials with desirable traits provides the foundation for effective and sustained pearl millet population breeding, and hybrid development in this cross pollinated crop. Access to well-characterized, adapted germplasm and knowledge about the geographic patterns of genetic variation for various traits in a target region are important prerequisites for successful plant breeding [7]. Previous diversity studies involving diverse germplasms reported wide range of valuable diversity for various agronomic traits, stress tolerance and nutritional traits in African populations [8–12], and in Asian germplasms [1,13,14] and also in ICRISAT bred accessions [15,16]. These studies emphasized that phenotypic characterization is the first step for the assessment, description and classification of germplasm collections to enhance their utilization in pearl millet breeding. The present study systematically characterizes the promising Asian and African germplasms bred/originated in Asia and Africa in the last 40 years and documents their morphological traits to use them in current pearl millet breeding programs.

In addition, these populations were also assessed for their ability to restore fertility or sterility maintenance on A_1, A_4, and A_5 CMS systems. A_1 CMS system is the most commonly used CMS and most of the hybrids cultivated in farm are based on A_1 CMS till date. The A_4 and A_5 CMS systems were found to be a bit more stable than the A_1 CMS system. However, commercial hybrids couldn't be developed using A_4 and A_5 CMS system due to non-availability of suitable restores in these two CMS systems [17]. Hence, the present study aimed to characterize diverse Asian and African origin/bred pearl millet germplasm for agro-morphological traits and to identify promising restorers/maintainer populations for three CMS systems to derive new restorer and maintainer lines to use them as parents in future crop improvement programs.

2. Materials and methods

A set of 45 pearl millet populations maintained by pearl millet breeding program of ICRISAT, Patancheru, Hyderabad, India were investigated. They involved genetic materials of African and Asian origins and were developed either at ICRISAT or in collaboration with partners. These populations are expected to be in Hardy-Weinberg equilibrium (HWE) as they were maintained through different cycles of random mating in isolation at ICRISAT. These 45 populations involved 10 Asian origin-Asian bred (abbreviated as As-As), 7 African origin-African bred (Af-Af), 3 (Asian × African) origin-Asian bred [(As × Af)-As], and 25 African origin-Asian bred (Af-As) populations. Pedigree details of these populations are given in Table S1. This set also involved some of popular OPVs released in Africa such as, GB 8735, SOSAT-C88, Ugandi and ICMV IS 92222 and some of popular OPVs cultivated in Asia (India) such as, ICTP 8203, CZP 86, Raj 171, ICMV 221, ICMV 155, and WRajPop.

Fertility restoration of these 45 populations was assessed on A_1, A_4 and A_5 CMS systems. A-lines of A_1, A_4 and A_5 cytoplasm in three different genetic backgrounds representing different flowering duration such as ICMA 94222 (early flowering habit), ICMA 89111 (medium flowering) and ICMA 91555 (late flowering) were used in order to synchronize the flowering duration of the populations for facilitating the ease of crossing program [18]. A set of 135 top crosses (45 populations × 3 CMS systems) were developed by crossing the male-sterile line with bulked pollen from 20 to 25 random plants of each population during rainy (July–October) season of 2015. Some populations being photo-sensitive, so couldn't be crossed in rainy season of 2015, hence were planted again and crossed in summer (March–June) season of 2016. Soon after pollination, the crossed panicles were covered with parchment paper bag to avoid foreign pollen contamination and labeled properly. The crossed panicles were left covered with parchment paper bags until harvest, at physiological maturity panicles were harvested, sundried and threshed to collect top cross hybrid seeds.

2.1. Experimental layout

2.1.1. Morphological diversity

The experiment was laid out in alpha-lattice design with three replications at two locations in India during rainy season of 2015. The experimental locations were ICRISAT, Patancheru, Telangana (17°30′N, 78°27′E, and 545 m above sea level) and Regional Agricultural Research Station (RARS), Palem, Telangana (16°53′N, 78°23′E, and 545 m above sea level). The main block for each replication had eight sub-blocks with a size of six entries per block. Each population was sown in six rows, 4 m in length with 75 cm inter-row spacing and an intra-row spacing of 15 cm. All the recommended agronomic practices were followed at both the locations to support good crop growth. There were no major incidences of diseases and pests. All the panicles were harvested at physiological maturity and threshed after sun drying for 10–15 days.

Observations on seven phenotypic traits were recorded. Data was recorded on 20 randomly selected plants from each population to appropriately represent the existing diversity present in the populations since populations are heterogeneous and heterozygous in nature. Phenotypic traits such as plant height (cm), number of productive tillers per plant, panicle length (cm) and panicle girth (cm) were recorded on plant basis. Days to 50% flowering, grain yield (kg plot^{-1}) and 1000-grain weight (g) were recorded on plot basis. Grain yield (kg plot^{-1}) was later converted to kg ha^{-1} for analysis.

2.1.2. Fertility restoration

Field evaluation trial of 135 top cross hybrids was conducted at ICRISAT, Patancheru during two contrasting seasons, the rainy (July–October) season of 2016 and summer (March–June) season of 2017. Each hybrid was evaluated in four-row plots of four meter length with about 100–120 plants per plot. One of the tillers of each plant was selfed with parchment paper bag at boot leaf stage. At physiological maturity, bags were opened and observed physically for seed setting to confirm fertile/sterile reaction. Those plant panicles with complete seed set were scored as male-fertile (F) and with no seed set as male sterile (S). Frequency of restoration or maintenance in percentage were calculated using the following formulas:

$$\textit{Restoration frequency}\ (\%) = \frac{\textit{Number of } F_1 \textit{ fertile plants per plot}}{\textit{Total number of } F_1 \textit{ plants per plot}} \times 100$$

$$Maintainer\ frequency(\%) = 100 - restoration\ frequency(\%)$$

2.2. Statistical analysis

2.2.1. Analysis of variance (ANOVA)

Combined ANOVA was carried out using PROC MIXED program [19], considering location, genotypes and replication as fixed and block as random. In order to pool the data across two locations and to make the error variance homogeneous, individual location variances were estimated and modeled to error distribution using residual maximum likelihood (REML) procedure. The analysis procedures used the linear mathematical models with the general notations of b = lattice blocks, r = number of replications and g = number of genotypes. The mathematical model followed for analysis of variance for the alpha-lattice design was:

$$Z_{ijkl} = \mu + e_i + (e/r)_{ij} + (e/r/b)_{ijk} + g_l + (eg)_{il} + \varepsilon_{ijkl}$$

where, μ is the grand mean, e_i is the fixed effect of location i, g_l is the fixed effect of genotype l, $(e/r)_{ij}$ is the fixed effect of replication j nested with in location i, $(e/r/b)_{ijk}$ is the random effect of block k nested with in replication j and location i and is ~ NID(0, $\sigma^2 b$), $(eg)_{il}$ is the fixed effect of the interaction between genotype l in location i; ε_{ijkl} is the random residual effect and is ~ NID(0, $\sigma^2\varepsilon$).

2.2.2. Multivariate analysis

Multivariate analysis suggested by Mahalanobis [20] was used to assess phenotypic diversity in the material. A hierarchical cluster analysis was performed using population means of all the variables for all the 45 populations based on dissimilarity matrix according to Ward's minimum variance method [21] as per the PROC-CLUSTER program in SAS v. 9.4 [19]. This method first computes a matrix based on Euclidean distances among group means and produces a dendrogram depicting successive fusion of individuals, and conclude at the stage in which all the individuals of the same group form a cluster [22].

3. Results and discussion

3.1. Differentiation for morphological traits

Morphological evaluation of the 45 populations revealed wide range of variation for all the traits (Table 1; Fig. 1). Details of mean performance of populations across the locations are provided in Table S2. The wide range of performance *per se* for all the traits under investigation provides an opportunity to select populations for different traits in breeding programs as per requirements/traits performance of different pearl millet growing regions.

Combined ANOVA revealed significant variation for all the traits in the populations evaluated in this study (Table 2). Significant variation due to locations (environments) was observed for all the traits except for days to 50% flowering, indicating that the populations were evaluated under diverse environments. Location × genotype interaction was found non-significant for most of the traits except for plant height and number of productive tillers, indicating that the ranking of populations based on their performance remains same for other traits, like days to 50% flowering, panicle length, panicle girth, 1000-grain weight and grain yield across the locations. Previous reports by Murthy et al. [23], Ouendeba et al. [24], and Ousmane et al. [9] also reported significant variation for location, and genotypic effect for most of the traits, and non-significant variation for interaction effect (location × genotype) while investigating diversity among wide set of germplasms. This non-significant interaction effect might be due to heterogeneous nature of populations which provides them inherent buffering capacity to adapt to different environments [25–27]. On the contrary, other phenotypic diversity studies in pearl millet germplasms [8,10,11,14] reported significant variation for location × genotype interaction.

3.2. Diversity analysis

The multivariate analysis of 45 populations partitioned them into five different clusters (Fig. 2). Of these five clusters, two clusters (designated as Cluster I and II) had majority of the Af-As populations (24 populations, 96%) and third cluster (designated as Cluster III) had majority of Asian populations (6 As-As populations, 60%); fourth cluster (designated as Cluster IV) had only 3 populations of which one was African OPV SOSAT-C88 and other two were (As × Af)-As and Af-As populations. Remaining one cluster (designates as Cluster V) had only one Af-Af population ICMV IS 92222.

Among five clusters, the first cluster (Cluster I) was the largest and composed of 20 populations (44%), out of which 14 were Af-As populations and 3 each of As-As and Af-Af populations. Cluster I had three sub-clusters. Sub-cluster Ia had majority of populations developed from SRC bred at Asia using African germplasms. The SRC was formed at ICRISAT in 1978 using 37 parents with low-susceptible to smut which were derived from an intercross of a wide range of breeding materials selected under disease pressure [28]. Sub-cluster Ib had two Af-As population developed using SRC and New elite Composite (NELC) and two As-As populations

Table 1
Cluster mean values, overall mean and range of yield and its component traits in 45 pearl millet populations.

Cluster/ Sub-cluster*	Number of populations				Total No. of populations	Cluster mean values of phenotypic traits						
	As-As	Af-As	(Af × As)-As	Af-Af		Days to 50% flowering	Plant height (cm)	Number of productive tillers plant^{-1}	Panicle length (cm)	Panicle girth (cm)	1000- grain weight (g)	Grain yield (kg ha^{-1})
Ia	0	8	0	0	8	44	168	2	26.9	2.4	10.1	1489
Ib	2	2	0	0	4	46	176	2	25.7	2.4	10.0	2741
Ic	1	3	1	3	8	44	176	2	25.1	2.2	9.4	2264
I	3	13	1	3	20	44	173	2	25.9	2.3	9.8	2049
IIa	1	5	0	1	7	45	195	2	26.8	2.5	11.0	2461
IIb	0	4	0	1	5	41	165	2	22.9	2.8	12.4	2482
IIc	0	2	0	0	2	39	164	2	20.5	2.9	11.6	1823
II	1	11	0	2	14	42	180	2	24.5	2.7	11.6	2377
III	6	0	1	0	7	40	154	3	21.2	2.2	8.7	1896
IV	0	1	1	1	3	49	189	2	24.7	3.0	9.1	2600
V	0	0	0	1	1	49	231	2	47.5	2.3	9.8	2378

As-As, Asian origin and Asian bred; Af-Af, African origin and African bred; (As × Af)-As, (Asian × African) derived and Asian bred populations, and Af-As, African origin and Asian bred populations.

* a, b, and c indicates sub-clusters of that particular main cluster.

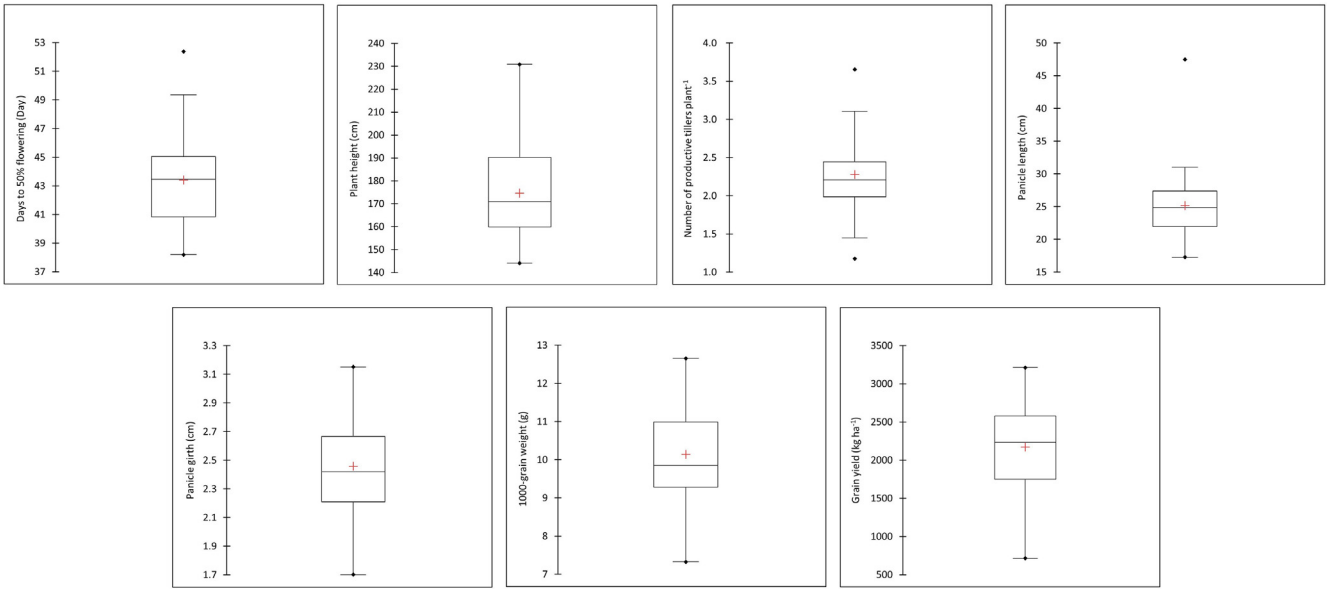

Fig. 1. Box plots showing variation for seven phenotypic traits evaluated for 45 pearl millet populations, combined across locations. (+indicates mean values; — indicates median values; ◆ indicates extreme values).

Table 2
Analysis of variance of pearl millet populations for grain yield and its component traits across two locations (Patancheru and Palem).

Source of variation	Degree of freedom	Days to 50% flowering	Plant height (cm)	Number of productive tillers plant^{-1}	Panicle length (cm)	Panicle girth (cm)	1000-grain weight (g)	Grain yield (kg ha^{-1})
Location	1	0.88	94.29***	82.86***	24.19***	51.10***	12.31***	148.37***
Replication	4	4.44**	6.95***	0.24	2.38	2.36	1.67	9.14
Block (Location × Replication)	30	0.64	0.74	0.78	0.89*	1.46*	0.62	2.28**
Genotype	44	23.10***	44.90***	4.03***	46.60***	20.91***	11.03***	18.37***
Location × Genotype	44	0.97	1.81***	1.42*	1.31	1.21	0.87	1.33

*, **, and ***, significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

developed using Rajasthan (India) material. Grouping of these two As-As populations with the Af-As populations might be due to their closeness for phenotypic traits as observed for high yielding ability (>2 t ha^{-1}), tillering ability (~2), panicle girth (2.4 cm) and 1000-grain weight (10 g) (C Ib) (Table S2). Sub-cluster Ic had intermixing of the three populations each from Af-As and Af-Af category, one population each from As-As (WRajPop bmr) and (As × Af)-As (ICMS 7704). Among the three Af-As populations two were developed from SRC material and other one was from bold seeded early composite (BSEC). Grouping of these two SRC derived populations in sub-cluster Ib instead of sub-cluster Ia might be due to the involvement of diverse composites (like D1C, NEC, IVC, NELC, *togo*, MC, and WC-C75) in addition to SRC, and these populations were characterized by high grain yield (>2 t ha^{-1}) compared to the rest of the SRC derived populations of sub-cluster Ia. Among the rest of the three populations, two were Af-Af populations (NWC C2 and WC C3 bulk), derived from Nigerian World composite [29] and other population (SC1 C4 bulk) was developed using Serere composite from Uganda [30]. The intermixing of the different category of populations in common cluster seems to be due to the close similarity in their mean values for multiple phenotypic traits such as medium flowering duration (44 days), low tillering ability (2), medium plant height (173 cm), 1000-grain weight (9.8 g), panicle girth (2.3 cm), and medium grain yield (2049 kg ha^{-1}) (Table 1).

Cluster II had 14 populations (31%) having three sub-clusters. Sub-cluster IIa had seven populations of which two were developed from West African material and germplasms from Serere composite (Ugandi and ICMP 87237), Sudan (Sudan I and Sudan II), Zimbabwe (ICMP 96601), and one derived from Western Rajasthan (CZP 86). Though, Ugandi and CZP 86 belongs to Af-Af and As-As population category, respectively, and were found grouped with Af-As populations which might be due to their close similarity in the phenotypic traits, as both of them had medium flowering duration (43 days), medium plant height (<200 cm), number of tillers (~2), panicle length, panicle girth and 1000-grain weight as that of the other populations of this cluster. Sub-cluster IIb and IIc had Af-As populations having large seeds developed using Large Grain Population (LaGraP), *togo* population (known for large seeds), and BSEC of African origin (known for large and bold seeds). Hence, all the populations of the Cluster II were predominantly composed of bold seed with high mean 1000-grain weight (11.6 g), with taller plants (180 cm), high panicle girth (2.7 cm) and medium flowering duration (42 days) compared to the rest of the population clusters (Table 1). The popular OPV variety, GB 8735 (Af-Af) grouped with Af-As populations in Cluster II due to its close trait similarities with this cluster (high yielding, bold seeds with high 1000-seed weight, smaller plant height, medium panicle thickness with medium to small panicle). This indicated that African germplasms were used as sources in Asian pearl millet breeding programs for developing germplasm having early maturity with large and bold grains, hence Af-As populations (ICMV 94135, ICMV 94132, ICMV 88908, and ICMP 96132) grouped into a common sub-cluster IIb in the present study. Manga [31] also reported that landrace from African regions such as Benin,

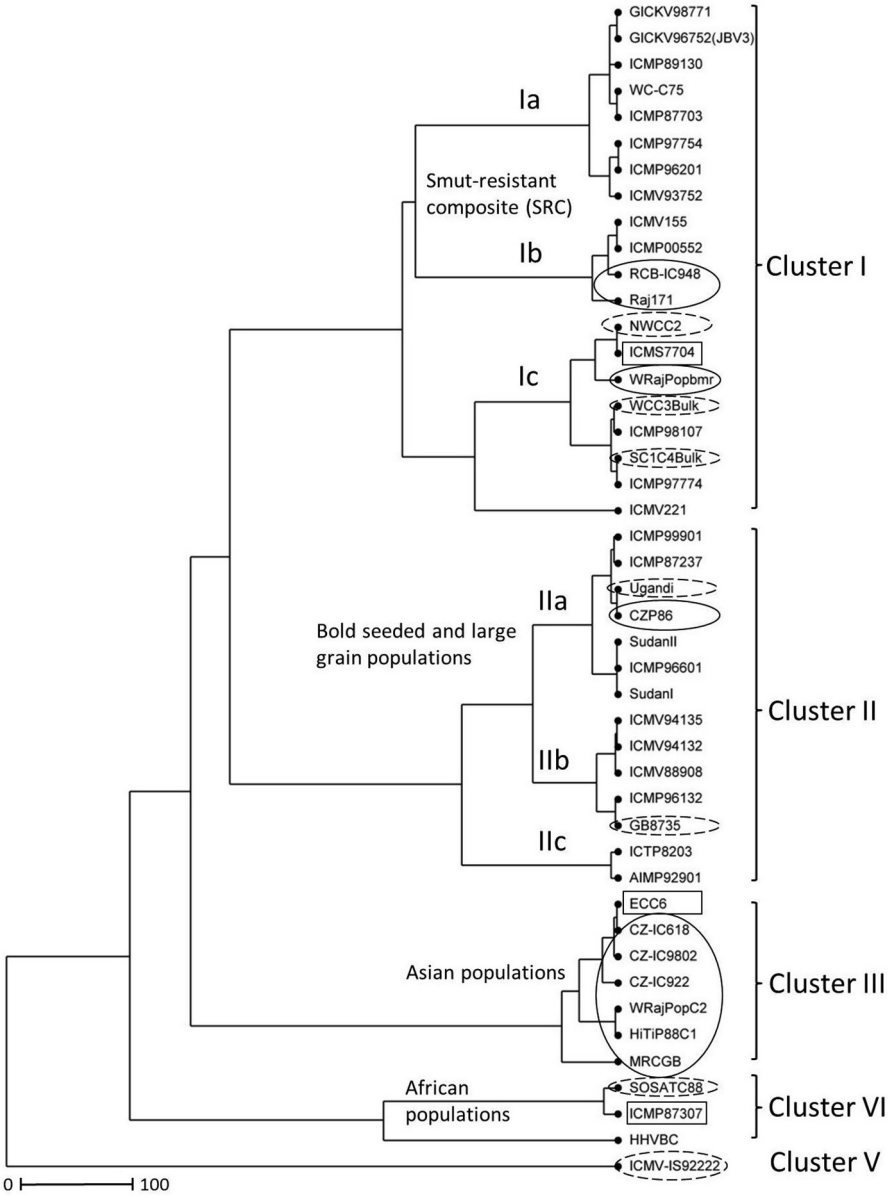

Fig. 2. Clustering pattern of 45 populations based on morphological traits. Full circle, As-As populations; Dotted circle, Af-Af populations; Rectangle, (As × Af)-As and rest are Af-As populations. As-As, Asian origin and Asian bred; Af-Af, African origin and African bred; (As × Af)-As, (Asian × African) derived and Asian bred populations, and Af-As, African origin and Asian bred populations. a, b, and c indicates sub-clusters of that particular main cluster.

Burkina Faso, Ghana and Togo were utilized to breed for bold seeded and early-maturing germplasms in India which led to the release of promising OPVs such as ICTP 8203 and ICMV 221.

Cluster III had 7 populations (16%) which were bred and originated in Asia (As-As). This cluster had populations with mean values of days to flowering (40 days), plant height (154 cm), tiller number (3.2), panicle length (2.11 cm), panicle diameter (2.17 cm), 1000-grain weight (8.74 g) and with mean grain yield (1897 kg ha^{-1}) compared to the rest of the clusters. This indicated that Asian populations were characterized by early flowering, shorter plant height, high tillering, thin panicles and small seed size with low grain yield compared to African populations. Though, the cluster had majority of As-As population (86%), one population EC C6 from (Af × As)-As category grouped in this cluster. This might be due to the pedigree of EC C6 population which involves intercrossing of 41 exotic lines with the large number of Indian entries (151 lines) [32] which might have resulted in similar phenotypic traits and adaptation as that of the As-As populations (Table 2).

Cluster IV had three and Cluster V had only one population bred using African germplasms. Cluster mean of these populations indicated that these were late in flowering, taller, thicker panicles, medium bold seeded and high yielding. Cluster V had only one African population ICMV IS 92222, it had distinct phenotypic characters, like late flowering (49 days), taller plants (231 cm) with large panicle length (47.5 cm) than rest of all the populations of the four clusters.

Population category-wise trait mean values also indicated that As-As populations were early in flowering, shorter plant height, higher number of tillers, smaller and thin panicles, smaller seed size and low grain yielders compared to the rest of the three population categories (Table 3). Af-Af population category showed higher mean values for all the seven traits whereas, Af-As and (Af × As)-As populations were found to be intermediate for trait

Table 3
Population category wise mean values of morphological traits and fertility restoration (%) on three cytoplasmic male sterility systems.

Population category	No. of populations	Days to 50% flowering	Plant height (cm)	Number of productive tillers plant^{-1}	Panicle length (cm)	Panicle girth (cm)	1000-grain weight (g)	Grain yield (kg ha^{-1})	Fertility restoration (%)		
									A_1	A_4	A_5
Af-As	25	43	174.0	2	26	2.6	10.8	2206	83	40	8
As-As	10	42	160.8	3	22	2.1	8.9	2035	91	36	5
Af-Af	7	46	191.9	2	28	2.4	10.0	2339	88	31	5
(Af × As)-As	3	45	183.0	2	25	2.4	9.3	1950	92	33	8

Af-As, African origin and Asian bred populations; As-As, Asian origin and Asian bred; Af-Af, African origin and African bred, and (As × Af)-As, (Asian × African) derived and Asian bred populations.

values between the Af-Af and As-As populations (Table 3). This indicates that African germplasm helped in improving the yielding ability of Asian germplasms through improved panicle and seed traits. Yadav and Rai [6] and Manga [31] stated that Asian cultivars developed using *Iniadi* landraces (derived from the Togo population cultivated in West African region) are known for their unique combination of several useful traits, such as early maturity, high seed yield, large seed size, resistance to multiple pathotypes of downy mildew, tolerance to terminal drought, high quality stover yield, and higher levels of grain Fe and Zn content [33,34] have been widely adopted by farmers in India.

Present study clearly indicated that Asian populations were early in flowering having short plant height, more tillering, smaller and thinner panicles, smaller seeds and low yielding as compared to the African origin and bred populations (Table 1). Thus, it seems that these characters were primarily responsible for divergence

Table 4
Fertility restoration (%) of 45 populations on three diverse A_1, A_4 and A_5 cytoplasmic male sterility systems for individual as well as across the seasons.

S. No.	Entry Name	A_1 cytoplasm restoration (%)			A_4 cytoplasm restoration (%)			A_5 cytoplasm restoration (%)		
		R-2016	S-2017	Mean	R-2016	S-2017	Mean	R-2016	S-2017	Mean
1	ICMP 89130	77	66	71	9	6	7	7	1	4
2	EC C6	94	95	94	7	3	5	5	2	4
3	ICMP 98107	85	82	83	10	18	14	2	0	1
4	ICMP 97774	93	99	96	30	16	23	6	0	3
5	ICMP 99901	92	82	87	46	34	40	8	0	4
6	ICMP 96132	75	79	77	46	33	40	34	5	20
7	ICMP 00552	92	90	91	57	38	48	25	5	15
8	NWC C2	95	89	92	58	50	54	16	0	8
9	ICMP 96601	81	83	82	17	4	10	31	2	16
10	ICMP 87703	98	99	98	69	62	66	12	3	8
11	SC1 C4 Bulk	96	96	96	4	6	5	13	0	7
12	ICMP 97754	90	97	94	29	37	33	22	0	11
13	ICMP 87237	98	96	97	50	40	45	16	4	10
14	WC C3 Bulk	100	96	98	29	23	26	5	0	2
15	AIMP 92901	85	90	87	41	17	29	7	1	4
16	CZ-IC 9802	100	100	100	0	2	1	20	0	10
17	CZP 86	94	98	96	43	32	37	10	0	5
18	GB 8735	77	78	78	24	28	26	14	1	8
19	JBV 3	90	85	88	89	82	85	2	0	1
20	HiTiP 88 C1	91	91	91	82	69	75	20	4	12
21	ICMS 7704	91	95	93	76	51	63	9	0	4
22	ICMV 155	83	86	85	35	18	26	0	2	1
23	ICMV 221	82	83	82	19	2	11	20	5	13
24	ICMV 88908	92	83	88	52	24	38	19	4	11
25	ICMV 93752	97	82	89	45	47	46	5	2	4
26	ICMV 94135	48	51	50	63	57	60	23	9	16
27	ICMV IS 92222	100	95	98	44	51	48	4	1	3
28	Raj 171	91	92	92	57	54	56	2	0	1
29	RCB-IC 948	86	90	88	62	54	58	2	2	2
30	SOSAT-C88	88	75	81	22	2	12	0	1	1
31	Sudan I	94	82	88	58	52	55	15	5	10
32	Sudan II	91	81	86	28	30	29	19	15	17
33	Ugandi	80	66	73	44	54	49	15	0	7
34	WC-C75	75	62	68	51	39	45	4	3	3
35	WRajPop bmr	98	90	94	53	28	41	15	0	7
36	WRajPop C2	98	86	92	47	43	45	2	0	1
37	MRC GB	90	72	81	11	7	9	15	9	12
38	ICTP 8203	40	48	44	69	68	69	10	0	5
39	HHVBC	93	80	86	79	62	71	2	4	3
40	CZ-IC 922	79	75	77	40	14	27	5	1	3
41	CZ-IC 618	100	90	95	22	6	14	2	0	1
42	ICMP 96201	88	82	85	49	46	48	36	16	26
43	ICMP 87307	91	87	89	42	23	32	16	15	16
44	GICKV 98771	92	86	89	62	66	64	17	11	14
45	ICMV 94132	87	75	81	19	4	11	2	0	1
Mean restoration (%)		89	84	86	42	33	37	11	3	7

R-2016, Rainy-2016 season; S-2017, Summer-2017 season.

between the Asian (Indian) and African germplasm. The continuous cultivation of pearl millet in Asia (India) in arid regions and poor agronomical environments might have resulted in the selection for earliness and resulting into the erosion of alleles for productivity [35]. Previous study on diversity of world collection of pearl millet landraces conserved at ICRISAT by Upadhyaya et al. [1] also reported early flowering, short plant height and high tillering among the Asian germplasms and very late flowering, tall plant height, long panicles and large seeds among African populations. Murthy et al. [23] also found that African populations have longer panicle, with high yielding, less tillering and late maturity as compared to Indian landraces while characterizing world collection of pearl millet genetic stocks.

Overall, the clustering pattern showed Af-As and As-As populations delineated into clear-cut separate clusters. However, Af-Af populations were found intermixed with Af-As populations. It was noted that the populations related by their parentage clustered together. For instance, all the nine populations developed using SRC lines were grouped in Cluster I and those developed using Nigerian world composite (WC C75, NWC C2, and WC C3 bulk) also grouped in Cluster I. Those populations developed using BSEC (2 populations), LaGraP (3 populations), and Togo population (originated from landraces cultivated in the Togo region of West Africa known for early flowering, limited tillering, broad panicles and very large seed size with high Fe and Zn content) having bold seeded trait were found grouped together in cluster II. This implies the presence of certain level of congruence in the clustering of populations sharing common genetic material involved in them and their trait values in the present study. Wilson et al. [36] also found some correspondence between the geographical collection sites of pearl millet landraces from Central Burkina Faso and their inclusion in particular clusters.

3.3. Fertility restoration/Sterility maintenance reaction

Across all the 45 pearl millet populations, the fertility restoration ranged from 44% to 100% with a mean of 86% for A_1 CMS system; from 1% to 85% with a mean of 37% for the A_4; and from 0 to 26% with a mean of 7% for A_5 CMS system was observed over the two seasons (Table 4). Among three CMS systems, all the 45 populations restored fertility on A_1 CMS system, of which 18 populations showed >90% of restoration for A_1 CMS across two seasons. However, for A_4 and A_5 CMS system, none of the populations showed >90% of restoration. In case of A_4 CMS system, 8 populations had >60% of restoration and for A_5 CMS system the highest restoration observed was 26% in one population (ICMP 96201). Two populations ICTP 8203 and ICMV 94135 showed higher restoration percentage on A_4 than A_1 cytoplasm. One population GICKV 97652 (JBV 3) showed almost similar level of restoration percentage on both A_1 (88%) and A_4 (85%) cytoplasm. On contrary, CZ-IC 9802 showed 100% restoration on A_1 CMS system, had maintainer reaction on A_4 and showed poor restoration on A_5 (10%) CMS system. The frequency of restorers across all the populations was in the order of $A_1 > A_4 > A_5$.

3.4. Restoration differences in Asian and African populations

Among four different categories of populations, As-As and (As × Af)-As populations showed restoration (>90%), followed by Af-Af (88%) and Af-As (83%) for A_1 cytoplasm. In case of A_4 cytoplasm, Af-As populations had higher restoration (40%) compared to rest of the categories of the population. However, none of the populations of different categories showed satisfactory restoration for A_5 cytoplasm (Table 3; Fig. 3). Rai et al. [18] also reported higher restoration frequency in Asian populations varying form

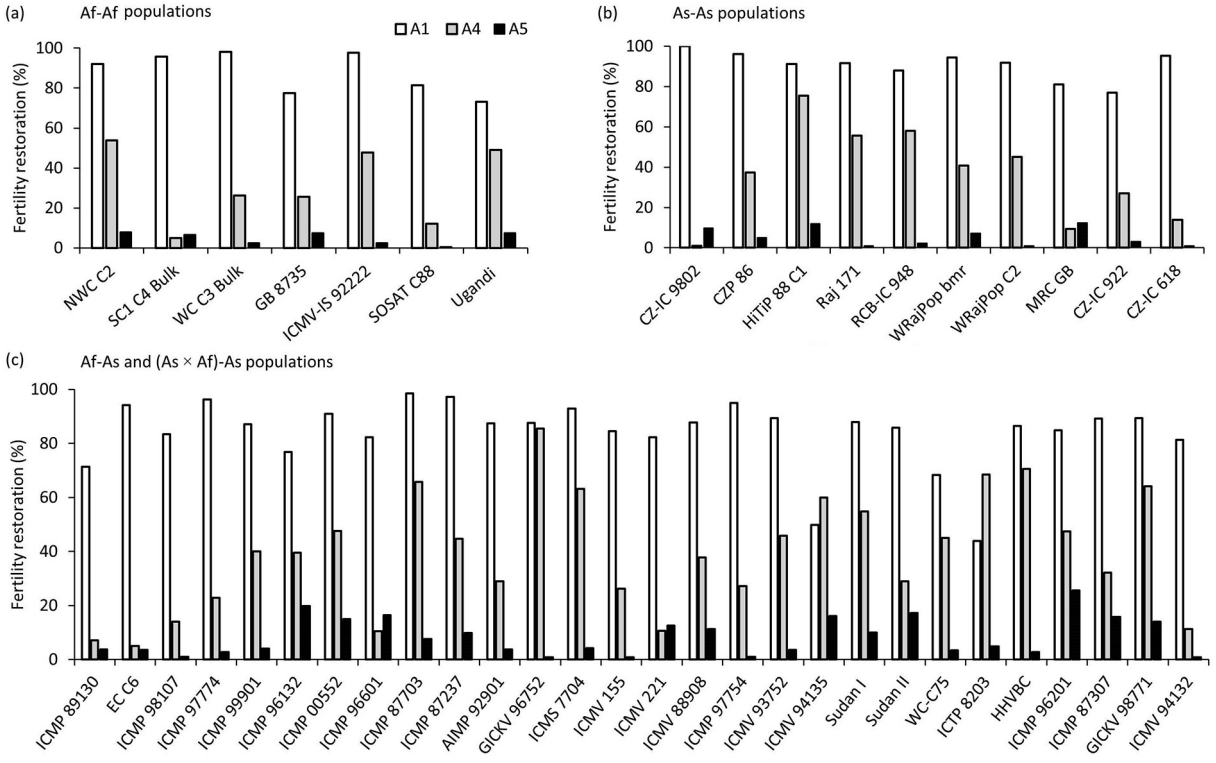

Fig. 3. Fertility restoration frequency of male sterile plants (restorers) in top cross hybrids of A_1, A_4 and A_5 made with pearl millet populations based on their origin and adaptation. As-As, Asian origin and Asian bred; Af-Af, African origin and African bred; (As × Af)-As, (Asian × African) derived and Asian bred populations; Af-As, African origin and Asian bred population.

26%–94% for the A_1 CMS system, from 4% to 72% for the A_4 and from 0 to 13% for the A_5 system as compared to African populations varying form 26% to 84% for A_1 CMS system, from 12% to 73% for the A_4 and from 1% to 12% (except one population with 55%) for A_5 CMS system.

3.5. Seasonal variation in restoration/maintainer frequency

Thirty-six populations showed ≥10% of variation in fertility restoration frequency between two contrasting seasons. Among them, five populations for A_1 CMS, six for A_4, eight for A_5 CMS, six for both A_1 and A_4 CMS, one for both A_1 and A_5 CMS, nine for both A_4 and A_5 and one population (Ugandi) for all the three CMS systems showed seasonal variation (≥10%) in restoration frequency. It indicated that the restoration frequency of the populations was affected by season for all the three CMS systems. However, mean restoration frequency was higher during rainy season than in summer, irrespective of cytoplasmic sources and restorer populations (Table 4). The high fertility restoration/seed set percentage during rainy season as compared to post rainy (summer) has been previously reported by Rai and Hash [37], Rai et al. [18], Lakshmana et al. [38] in pearl millet and Biradar [39] in sorghum. Also, Gupta et al. [40] reported that the enhanced expression of fertility restoration during the rainy season might be due to relatively lower temperature and higher humidity than summer season.

3.6. Restoration/maintenance ability of populations and their utilization in hybrid breeding

Seed and restorer parents in pearl millet breeding programs have been bred for a specific set of traits separately in B- and R-line hybrid parental lines development breeding programs. For instance, maintainer or B-lines are generally bred for short height (<100 cm) and larger seed size while restorer or R-lines are generally bred for taller height (150–180 cm), more tillers, relatively small seed size, and profuse pollen production [17]. Results of the present study indicated that A_1 system provides greatest opportunity for development and diversification of the restorer parents or pollen parents (R-lines) followed by A_4. While, A_5 CMS system with high sterility or maintainer provides higher opportunity for diversification of maintainer lines (B-lines) than other two cytoplasmic male sterile sources A_1 and A_4.

Male sterile A-line or its counterpart maintainers (B-lines) should have high yielding panicle and seed traits, like large and thick panicle, bold seeds to economize the seed production. In case of A_1 CMS system most of the populations showed lesser maintainer frequency (0 to 66%) as compared to A_4 (15% to 99%) and A_5 (74% to 99%) CMS system. However, the A_1 CMS system is most widely used in the pearl millet hybrid breeding program due to its highly stable maintenance or restoration ability across agro-ecologies and seasons across the pearl millet growing regions of the world, and >95% of the hybrids released till date are based on A_1 CMS system. Owing to its highest restoration found in global germplasm, the hybrid breeding programs have preferred A_1 CMS system over other (A_4 and A_5) CMS systems, though A_1 has been found bit lesser stable than A_4 and A_5 CMS system [18]. This necessitates more efforts on the diversification of maintainers for A_1 CMS system to derive new stable maintainer (A-/B- line) breeding lines.

In the present study, five populations were identified for developing maintainers for all the three CMS system (A_1, A_4, and A_5) and eight populations were identified as potential sources for developing maintainers for A_4 and A_5 CMS systems (Table 5). These 13 populations had desirable traits such as high grain yield (>2500 kg ha^{-1}), medium to early flowering (39–49 days), medium to high panicle girth (2.2–3.0 cm) with medium to long panicle length (20–29.5 cm) and bold grains (>10 g of 1000-grain weight) for maintainer line (B-line) development. Though the five populations (ICMV 155, ICMV 221, ICMV 94132, ICMP 96601, and ICMP 98107) have low maintainer frequency for A_1 CMS system (15%–19%) and three populations (RCB–IC 948, Raj 171, and Sudan I) have lower maintainer frequency of 42%–45% for A_4 CMS, yet they can be subjected to recurrent selection for sterility/maintainer reaction to increase the frequency of maintenance to derive new maintainer lines. Previously, Rai et al. [17] demonstrated this increase in the maintainer frequency among Asian and African populations for different CMS systems through recurrent selection. One cycle of selection in favor of sterility/maintainer reaction in Asian population Raj 171 lead to increase in frequency of maintainers from 18% (C0 bulk) to 98% (C1 bulk) for A_1 CMS system and 49% (C0 bulk) to 99% (C1 bulk) for A_4 CMS system. However, all of these 13 populations have higher plant height (>150 cm), hence there is a need to transfer the d_2 gene (dwarfing gene) through the back cross program (using dwarf plant height d_2 donor lines) to develop diverse maintainer lines with lesser plant height [41,42].

Table 5
High grain yield and linked traits in populations for developing maintainers (B-lines) in three different CMS systems.

Population name	Fertility restoration (%)			Phenotypic traits						
	A_1	A_4	A_5	Days to 50% flowering	Plant height (cm)	Number of productive tillers plant^{-1}	Panicle length (cm)	Panicle girth (cm)	1000-grain weight (g)	Grain yield (kg ha^{-1})
For all 3 CMS systems										
ICMV 155	85	26	1	46	178	2	26.0	2.5	10	2983
ICMV 221	82	11	13	39	150	1	20.0	2.7	12	2967
ICMV 94132	81	11	1	40	173	2	25.0	3.0	13	2867
ICMP 96601	82	10	16	44	197	2	27.8	2.6	11	2810
ICMP 98107	83	14	1	43	177	2	26.6	2.6	10	2566
For A_1 and A_4 CMS systems										
Sudan I	88	55	10	45	199	2	26.1	2.4	10	3044
Sudan II	86	29	17	45	201	2	29.4	2.4	11	2870
Raj 171	92	56	1	49	193	2	25.3	2.2	9	2850
ICMP 99901	87	40	4	46	201	2	27.9	2.9	12	2649
ICMP 97774	96	23	3	43	188	2	28.4	2.3	10	2644
ICMV 88908	88	38	11	40	162	2	22.8	2.8	12	2583
ICMP 00552	91	48	15	45	178	2	29.5	2.5	11	2580
RCB-IC 948	88	58	2	42	155	3	21.9	2.2	10	2552

Table 6
High restoring populations for developing restorers (R-lines) in three different CMS systems.

Population name	Fertility restoration (%)			Phenotypic traits						
	A_1	A_4	A_5	Days to 50% flowering	Plant height (cm)	Number of productive tillers plant^{-1}	Panicle length (cm)	Panicle girth (cm)	1000-grain weight (g)	Grain yield (kg ha^{-1})
For A_1 CMS system										
CZ-IC 9802	100	1	10	39	144	4	20.1	1.9	9	1313
WC C3 Bulk	98	26	2	43	166	2	23.5	2.1	8	2109
ICMV IS 92222	98	48	3	49	231	2	47.5	2.3	10	2378
ICMP 87237	97	45	10	46	197	2	26.2	2.6	11	2233
CZP 86	96	37	5	43	178	2	24.3	2.3	10	1739
SC1 C4 Bulk	96	5	7	44	179	2	24.9	2.2	9	2448
CZ-IC 618	95	14	1	41	152	3	24.2	2.2	9	1440
ICMP 97754	95	27	1	42	161	2	28.6	2.4	10	1345
WRajPop bmr	94	41	7	44	157	2	20.4	1.8	8	1573
EC C6	94	5	4	40	154	3	20.8	2.4	10	1635
WRajPop C2	92	45	1	38	148	4	21.6	1.7	8	2336
For A_1 and A_4 CMS system										
HiTiP 88 C1	91	75	12	40	160	3	21.0	2.1	9	2282
GICKV 98771	89	64	14	46	187	2	27.4	2.6	10	2147
JBV 3	88	85	1	44	177	2	27.5	2.4	10	1791
ICMP 87703	98	66	8	44	171	2	25.2	2.3	11	1292
ICMS 7704	93	63	4	47	194	2	28.3	2.2	9	1854
NWC C2	92	54	8	46	200	2	28.6	2.1	9	1949
For A_5 CMS system										
ICMP 96201	85	48	26	45	171	2	31.0	2.3	10	1443
ICMP 96132	77	40	20	41	164	2	22.0	2.8	13	2074
ICMP 87307	89	32	16	49	201	2	26.1	2.7	9	2360
ICMV 94135	50	60	16	40	166	2	23.0	2.8	12	2488

The list of potential populations for developing new restorers for three CMS system are given in Table 6. Eleven populations having high restoration frequency (92%–100%) for A_1 CMS system were identified as source populations for developing restorer parental lines exclusively for A_1 CMS system. In addition, six populations were identified as dual-restorers (for A_1 and A_4 CMS) having a restoration frequency of 88%–98% for A_1 and 54%–85% for A_4 CMS system. The development of dual-restorers which can restore fertility of two different CMS systems (A_1 and A_4 CMS) will be advantageous for the hybrid breeding programs. ICRISAT designates around nine restorer lines each year, and 48 are dual restorer lines (for both A_1 and A_4 CMS) out of the 126 restorers designated since 2006. The dual-restorer populations identified in the present study will be helpful in developing diverse dual-restorer hybrid parental lines. For A_5 CMS system, four populations showing >15% restoration were identified as potential restorer source populations. These populations can be subjected to recurrent selection to increase the frequency of restoration and develop restorer parents for respective CMS system. Rai et al. [17] increased the frequency of restorers through recurrent selection in Raj 171. One cycle of selection in Raj 171 population increased the restoration frequency from 82% (C_0 bulk) to 99% (C_1 bulk) for A_1 cytoplasm and 51% (C_0 bulk) to 96% (C_1 bulk) for A_4 CMS system.

At ICRISAT, four populations such as MRC general bulk, AIMP 92901, JBV 3, and GB 8735 for restorer line development program and HHVBC population in case of B-line development have been extensively utilized till date. Whereas, populations such as ICTP 8203, SOSAT-C88, ICMS 7704, and EC C6 were used in both restorer and maintainer breeding programs. In any crop breeding program it is necessary to maintain the distinct gene pools for maintainer and restorer line development. Hence, in the present study, we identified the distinct populations for their utilization separately in development of maintainer and restorer parents to avoid intermixing of gene pools. Based on the present study, it can be inferred that populations having desirable traits for respective B- or R-line development program provides a great opportunity to derive new diverse restorer and maintainer lines to enhance the genetic diversity.

4. Conclusions

To enhance introgression of new germplasm in current pearl millet breeding programs, the present study showed existence of significant amount of diversity among the Asian and African origin/bred populations for different traits like days to 50% flowering, plant height, panicle traits, 1000-grain weight and grain yield. Most of the As-As populations found clustered together and were found to share common traits, such as early flowering, less plant height, high tillering, small thin panicles, small-seeded, and low yielding as compared to the African origin/bred populations. These diverse populations can be used as base populations to derive new breeding lines with desired traits to broaden the genetic base of current pearl millet breeding programs. Fertility restoration frequency (%) was found highest for A_1 (86%) followed by A_4 (37%) and least for A_5 (7%) CMS system in 45 populations under investigation. Populations were identified as potential sources for maintainer and restorer line development for A_1, A_4 and A_5 CMS systems. These populations can serve as potential sources to diversify the genetic background of the maintainers and restorers in the hybrid pearl millet breeding programs.

CRediT authorship contribution statement

K. Sudarshan Pati: Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft, Writing - review & editing. **Shashi Kumar Gupta:** Conceptualization, Funding acquisition, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data for this article can be found online at https://doi.org/10.1016/j.cj.2021.04.013.

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