

Latitudinal variation and distribution of photoperiod and temperature sensitivity for flowering in the world collection of pearl millet germplasm at ICRISAT genebank

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Abstract

The ICRISAT genebank, Patancheru, India holds 22,211 pearl millet germplasm accessions from 50 countries, including 19,063 landraces. Among these, 15,904 landraces that were geo-referenced are either thermo-sensitive (52.5%), or photoperiod-sensitive (45.6%), or insensitive to both temperature and photoperiod (2%). Latitude ranges of 10–15°N with 39.6% and 15–20°S with 13.1% of total accessions are the important regions for pearl millet germplasm. A study on climate data of the germplasm collection sites revealed that most accessions from latitudes ranging from 10 to 20° on both sides of the equator were highly sensitive to longer photoperiod (>12.5 h) and/or lower temperature (<12°C). Accessions that originated in locations at higher latitudes (>20–35°) on both the hemispheres exhibited low sensitivity to both photoperiod and low temperature, as they were exposed to such climates during their evolution. The accessions that are insensitive to both photoperiod and temperature were few but they originated from locations spread across all latitudes, although the highest numbers were from mid-latitudes (15–20°) in both hemispheres. As germplasm accessions are sensitive to climatic variables such as temperature and photoperiod, recording of location-specific geo-reference data while collecting the germplasm, which can help to elucidate the sensitivity of accessions to temperature and photoperiod, is emphasized. Critical evaluation of photoperiod-sensitive accessions that are late flowering for forage production and the photoperiod-insensitive early-maturing accessions for grain production, multiple cropping and development of parental lines with synchronized flowering for the development of hybrids is suggested.

Keywords: accession; germplasm; latitude; photoperiod; sensitivity; temperature; variation

Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is one of the many important cereal crops grown in a wide range of latitudes (35°S to 35°N of equator). It is important as a grain crop in Africa and Asia and is equally

important as a forage crop in other semi-arid and arid parts of the world (Andrews and Anand Kumar, 1992). Traditionally, pearl millet grains are used in the preparation of conventional foods such as unleavened flat breads (roti or chapati), fermented breads (Kisra, injera, etc.), porridge, dumpling, biscuits, snacks, malt and opaque beer.

It is mainly cultivated in Niger, Nigeria, Burkina Faso, Togo, Ghana, Mali, Senegal, Central African Republic, Cameroon, Sudan, Botswana, Namibia, Zambia,

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Zimbabwe and South Africa in Africa and India, Pakistan and Yemen in Asia (Upadhyaya *et al.*, 2010).

During the process of landraces evolution, days to flowering is one of the most important characters that influenced the cropping pattern in relation to the natural environment and regional agricultural practices (Takei and Sakamoto, 1987). The overall pattern of adaptation and sensitivity of pearl millet to varying latitudes depends on environmental factors such as temperature, day length, rainfall, soils etc. Pearl millet is a facultative short-day species, flowering at all photoperiods, although much earlier with short days. The critical photoperiod and temperature required to trigger flowering is species- and cultivar-specific. Almost all cultivars show some response to temperature and photoperiod according to their specific geographical adaptation (Joshi *et al.*, 2005) and because of this, pearl millet is a potential forage crop for all latitudes.

The world collection of pearl millet germplasm (22,211 accessions) assembled at the ICRISAT genebank, Patancheru, India is from a wide range of latitudes and includes the typical temperature and photoperiod-sensitive and -insensitive accessions. So far, this large collection was not stratified for their response to temperature and photoperiod. Being the single largest collection of pearl millet germplasm, stratification of these accessions for their response to temperature and photoperiod is very important for the well-targeted use of germplasm in crop improvement. The availability of climate data and geographic information system in recent years have opened up avenues in understanding the sensitivity of germplasm accessions to temperature and photoperiod. Therefore, in the present study, pearl millet landrace accessions from different latitudes were stratified based on their flowering response to temperature and photoperiod during contrasting rainy (long days and high temperature) and post-rainy (short days and low temperature) seasons at Patancheru location (near Hyderabad), India and discussed in relation to available information on climatic factors at collection sites.

Materials and methods

The passport information and characterization data of pearl millet germplasm assembled at the ICRISAT genebank, Patancheru, India (22,211 accessions) was used in the present study. The collection includes accessions from diverse environments and almost all pearl millet growing countries across the world. Biological status of the accessions indicated the presence of 19,063 landraces, 2269 breeding materials, 129 improved cultivars and 750 wild accessions belonging to 24 species of genus *Pennisetum* in the collection. Passport information

of the landraces, particularly the location of collecting sites and corresponding geographic coordinates was updated by referring to all related records, collection reports and catalogues. Using Microsoft Encarta[®], an electronic atlas (MS Encarta[®] Interactive World Atlas, 2000), geographic coordinates were retrieved for accessions without coordinates to fill the gaps for landraces having location information. Accuracy of the coordinates was verified by plotting all accessions on the political map of each country. Finally, a set of 15,904 landraces of *P. glaucum* (L.) R. Br., having the geographic coordinates was used in the present study.

Pearl millet accessions were characterized in batches of 500–1000 every year at ICRISAT, Patancheru (17.53°N latitude, 78.27°E longitude and 545 m.a.s.l), in alfisols during the rainy and post-rainy seasons from 1974 through 2010. These two different seasonal conditions are typical to the semi-arid regions (Reddy *et al.*, 2004). During the rainy season, accessions were sown in June and harvested in October/November. On the other hand, during the post-rainy season, accessions were sown in November and harvested in March of the subsequent year. The day length decreases from 13.10 h (in June) to 11.40 h (in November) in the rainy season and increases from 11.10 h (in December) to 12.00 h (in March) in the post-rainy season. The monthly mean minimum temperature varied from 23.6°C (in June) to 16.0°C (in November) and the monthly mean maximum temperature ranged from 34.4°C (in June) to 28.9°C (in November) in the rainy season. During the post-rainy season, monthly mean minimum temperature increased from 12.9°C (in December) to 19.3°C (in March) and the mean maximum temperature increased from 27.9°C (in December) to 35.2°C (in March). The mean annual rainfall at Patancheru location was 908 mm. Each accession was grown in two rows of 4 m length each with a spacing of 75 cm between rows and 10 cm between plants within a row accommodating a total of 80 plants in two rows. Accessions were randomized in all the evaluations. Fertilizers were applied at the rate of 100 kg N and 40 kg P₂O₅/ha. Need-based irrigations were given during the rainy season, while the crop was irrigated at regular intervals during the post-rainy season. The crop was protected from weeds, pests and diseases. Emergence of stigma in 50% plants in a plot (accession) was recorded as days to 50% flowering during both rainy and post-rainy seasons (IBPGR and ICRISAT, 1993).

Photoperiod-sensitive accessions require shortening of photoperiod to the critical level for flowering. On the other hand, temperature-sensitive accessions require higher temperature than the critical temperature. In the present study, photoperiod and temperature responses were defined by the differences in flowering during the

rainy and post-rainy seasons. When the measurements (days to 50% flowering) are high in the relatively cool short-day post-rainy season, the accession was considered as temperature-sensitive and requires higher temperature for flowering. When the measurements are high in the warm long-day rainy season, then the accession was considered as photoperiod-sensitive and requires short days for flowering. When there was no difference in measurements (rainy – post-rainy = 0 d), then the accessions were considered as insensitive to both temperature and photoperiod. Using the data recorded over years, the frequency of photoperiod and temperature-sensitive and -insensitive accessions was estimated. Though this procedure may not give the exact sensitivity of the accessions to temperature and photoperiod, it serves as a preliminary tool to stratify the large number of germplasm accessions based on their sensitivity to temperature and photoperiod. Though the characterization data are preliminary in nature and collected over several years, it still reflects genetic differences among the accessions (Upadhyaya *et al.*, 2007). Frequencies were estimated for temperature and photoperiod-sensitive and -insensitive accessions in the entire collection, in different hemispheres and for each latitudinal range with an interval of 5° on both Northern and Southern hemispheres. Climatic data, such as monthly mean (over the past 30 years) minimum and maximum temperature, rainfall and day length for each collection site, were retrieved from <http://www.worldclim.org/current> in June 2011 (Hijmans *et al.*, 2005). The high-resolution (1 km) interpolated climate surfaces are a useful source of data for studying the spatial relationship between environmental variables and the vegetation existing at that location. Monthly climate variables were extracted from the worldclim (Hijmans *et al.*, 2005) surfaces for each germplasm accession using the spatial analyst extension in ArcGIS® software and analyzed. Accessions were grouped, based on their sensitivity to temperature and photoperiod with an interval of 10 d and corresponding latitudes, annual mean minimum and maximum day length, temperature and rainfall were estimated and related with the sensitivity of pearl millet accessions. Correlation coefficients were estimated between mean latitudes of collection sites and degree of sensitivity of germplasm accessions to temperature and photoperiod (Snedecor and Cochran, 1980). Temperature and photoperiod-sensitive and -insensitive accessions were plotted using ArcGIS.

Results

Large variation was observed in the performance of pearl millet germplasm accessions adapted to different latitudes, when evaluated for flowering during two

contrasting (rainy and post-rainy) seasons at Patancheru, India (rainy – post-rainy = –53 to +87 d). Frequency distribution of temperature and photoperiod-sensitive and -insensitive accessions from different latitude ranges has revealed interesting and useful information. The total collection (15,904 accessions) with geo-reference data includes 52.5% temperature-sensitive, 45.6% photoperiod-sensitive and 2% photoperiod-insensitive accessions (Table 1 and Figs 1 and 2).

Distribution by hemisphere

Analysis of data revealed that 80.5% of total accessions are from the Northern hemisphere and the remaining 19.5% from the Southern hemisphere, indicating the predominance of pearl millet cultivation and the intensity of pearl millet germplasm collection in the Northern hemisphere (Table 1). Of the total 12,808 accessions from the Northern hemisphere, 53.9% are temperature-sensitive, 44.2% are photoperiod-sensitive and 1.9% are photoperiod-insensitive accessions. In the Southern hemisphere, 46.4% are temperature-sensitive, 51.4% are photoperiod-sensitive and 2.3% are photoperiod-insensitive. Irrespective of the latitude group, 77.2% of the total insensitive accessions are from the Northern hemisphere and 22.8% are from the Southern hemisphere. Similarly, 82.8% of temperature-sensitive accessions are from the Northern hemisphere and 17.2% are from the Southern hemisphere; 78.1% of photoperiod-sensitive accessions are from the Northern hemisphere and 21.9% accessions are from the Southern hemisphere, suggesting the predominance of these three groups of accessions in the Northern hemisphere (Table 1).

Distribution by latitude

Pearl millet accessions used in the present study are from a wide range of latitudes ranging from 33.00° in the Southern hemisphere to 34.37° in the Northern hemisphere. Frequency distribution over the entire collection for each latitude range on both sides of the equator indicated that 10–15° on the Northern side and 15–20° on the Southern side of the equator are the important source regions for pearl millet germplasm with 39.6 and 13.1% accessions, respectively (Table 1). The proportion of accessions from latitudes close to the equator (0–5°) and higher latitudes (30–35°) is very low (~1%) (Table 1). Irrespective of magnitude of sensitivity (no. of days), higher latitudes (>20°) resulted in higher proportion of temperature-sensitive accessions in the Northern (>80%) and Southern (>60%) hemispheres. On the other hand, lower latitudes (<20°) resulted in higher proportion of photoperiod-sensitive

Table 1. Frequency (%) distribution of temperature- and photoperiod-sensitive and -insensitive accessions in different latitude ranges

Latitude	Frequency (%) in total collection	Temperature sensitive			Insensitive			Photoperiod sensitive		
		No. of accs. ^a	No. of accs.	Frequency (%) ^a	No. of accs.	Frequency (%) ^a	No. of accs.	Frequency (%) ^a		
Total accessions		15,904	8342	52.5	311	2.0	7251	45.6		
Northern hemisphere		12,808 (80.5)	6908 (82.8)	53.9	240 (77.2)	1.9	5660 (78.1)	44.2		
30–35	2.1	330 (2.6)	322 (4.7)	97.6	2 (0.9)	0.7	6 (0.2)	1.9		
25–30	11.4	1805 (14.1)	1551 (22.5)	86.0	32 (13.4)	1.8	222 (4.0)	12.3		
20–25	7.0	1100 (8.6)	905 (13.2)	82.3	22 (9.2)	2.0	173 (3.1)	15.8		
15–20	12.4	1963 (15.4)	1138 (16.5)	58.0	55 (23.0)	2.9	770 (13.7)	39.3		
10–15	39.6	6291 (49.2)	2646 (38.4)	42.1	116 (48.4)	1.9	3529 (62.4)	56.1		
5–10	7.8	1225 (9.6)	293 (4.3)	24.0	11 (4.6)	0.9	921 (16.3)	75.2		
0–5	0.6	94 (0.8)	53 (0.8)	56.4	2 (0.9)	2.2	39 (0.7)	41.5		
Southern hemisphere		3096 (19.5)	1434 (17.2)	46.4	71 (22.8)	2.3	1591 (21.9)	51.4		
0–5	1.3	195 (6.3)	29 (2.1)	14.9	3 (4.3)	1.6	163 (10.3)	83.6		
5–10	1.5	232 (7.5)	29 (2.1)	12.5	1 (1.5)	0.5	202 (12.7)	87.1		
10–15	1.3	192 (6.3)	75 (5.3)	39.1	10 (14.1)	5.3	107 (6.8)	55.8		
15–20	13.1	2068 (66.8)	917 (64.0)	44.4	52 (73.3)	2.6	1099 (69.1)	53.2		
20–25	2.6	398 (12.9)	375 (26.2)	94.3	4 (5.7)	1.1	19 (1.2)	4.8		
25–30	0.1	8 (0.3)	7 (0.5)	87.5	1 (1.5)	12.5	0 (0.0)	0.0		
30–35	0.1	3 (0.1)	2 (0.2)	66.7	0 (0.0)	0.0	1 (0.1)	33.4		

^aNumbers in parenthesis are frequency (%) of accessions within each latitude range and hemisphere.

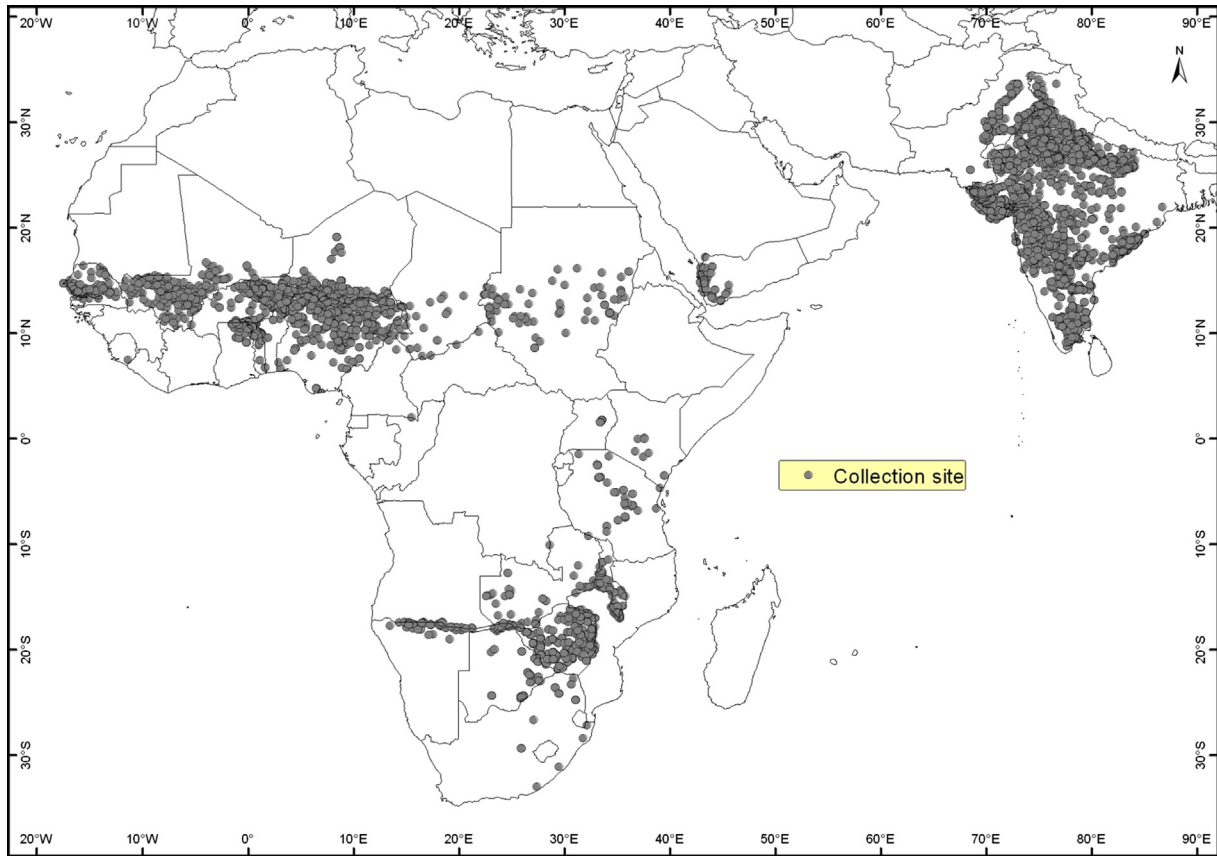


Fig. 1. Geographical distribution of temperature-sensitive pearl millet germplasm accessions (a colour version of this figure can be found online at journals.cambridge.org/pgr).

accessions in the Northern (>39%) and Southern (>50%) hemispheres (Table 1). The frequency of insensitive accessions did not show any pattern and was distributed in almost all latitudes. However, a high proportion (2.7%) of insensitive accessions was found in the mid-latitudes (15–20°) in both hemispheres (Table 2). The latitude range from 10 to 20°, a predominant region for pearl millet adaptation, was characterized by relatively low annual mean (over past 30 years) minimum, maximum and mean temperature at collection sites when compared to that of other latitudes (Table 2). In this region, mean annual rainfall was moderate and ranged from 665.5 to 834.2 mm. Irrespective of hemispheres, 40.8% accessions are from 10 to 15° and 25.3% from 15 to 20° latitudes. A maximum of 97.3% temperature-sensitive accessions are from 30 to 35° latitudes. On the other hand, maximum (77.1%) photoperiod-sensitive accessions are from 5 to 10° latitudes (Table 2).

Distribution by sensitivity

Grouping of accessions based on their sensitivity to temperature and photoperiod with an interval of 10 d on

both sides of the equator revealed that the highly sensitive accessions are from lower latitudes (Table 3). Among the temperature-sensitive accessions, 82.4% showed relatively low sensitivity (1–20 d) and the remaining accessions (17.6%) showed high sensitivity (21–50 d) to temperature (Table 3). Among the photoperiod-sensitive accessions, 53% showed less sensitivity (1–20 d) and 47% accessions showed high sensitivity to photoperiod (21–90 d) (Table 3). In the present study, there was a 1-d delay in flowering per degree latitude in temperature-sensitive accessions and 1.4 d delay per degree latitude in photoperiod-sensitive accessions. The flowering delay was 1.3 d per degree latitude in the entire collection. Sensitivity of accessions increased with the increase in minimum day length, lowest minimum and maximum temperatures and reduction in maximum day length and highest minimum and maximum temperatures at the collection sites. Temperature sensitivity increased with the reduction in mean minimum and maximum temperatures at the collection sites. On the other hand, photoperiod sensitivity increased with the increase in mean minimum and maximum temperatures at the collection sites. Photoperiod sensitivity increased with the increase in annual rainfall at the collection sites

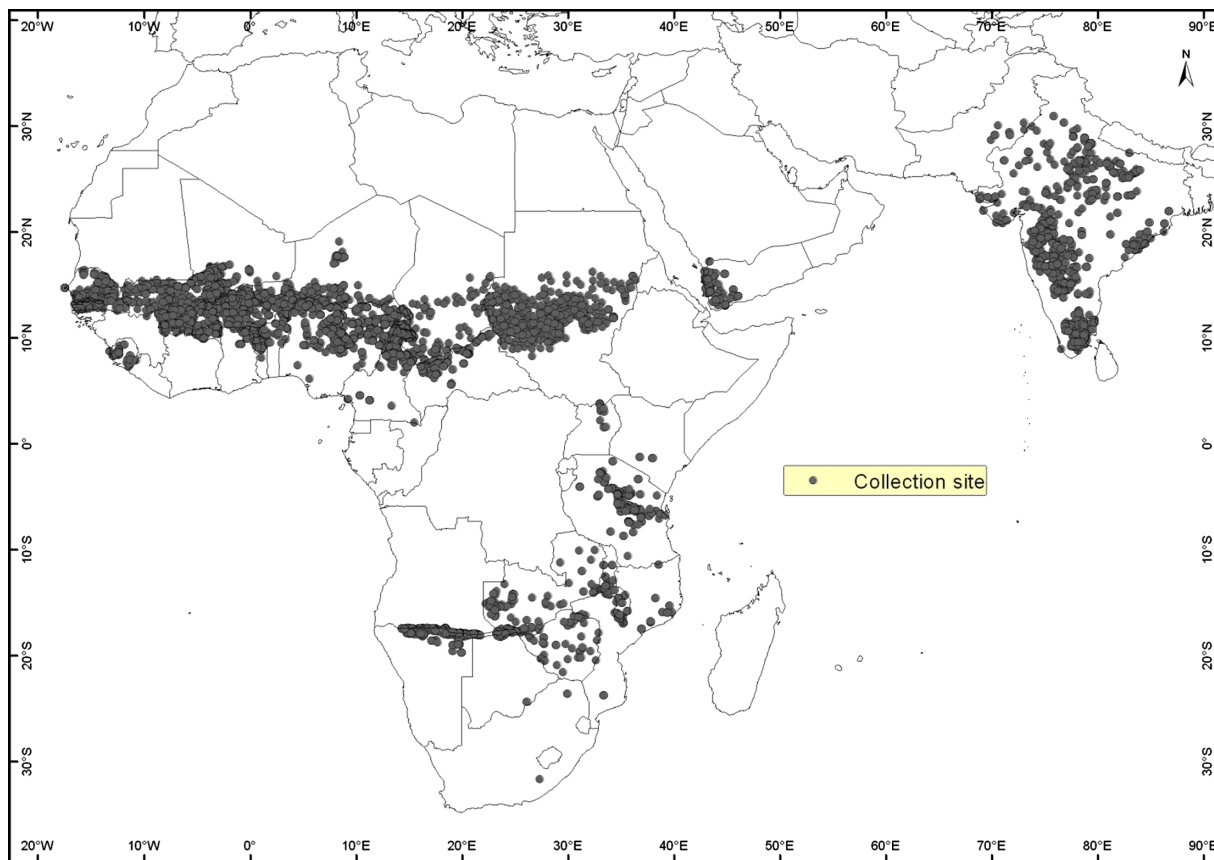


Fig. 2. Geographical distribution of photoperiod-sensitive pearl millet germplasm accessions (a colour version of this figure can be found online at journals.cambridge.org/pgr).

(Table 4). The period of sensitivity to temperature and photoperiod and the latitudes of collection sites have showed highly significant negative correlation (Supplementary Table S1, available online only at <http://journals.cambridge.org>). Accessions from higher latitudes have shown low sensitivity than accessions from lower latitudes (towards the equator), although the percentage of sensitive accessions was high in higher latitudes. The sensitivity is positively correlated between both the hemispheres, indicating similar reaction of accessions from both Northern and Southern latitudes. Climate at the collection sites of the top five temperature-sensitive accessions (IP 16859, IP 21062, IP 8933, IP 9428 and IP 17163) indicated lower day length (minimum = 11.03 h, maximum = 12.77 h and mean = 12.09 h), temperature (minimum = 11.03°C, maximum = 22.28°C, mean = 17.21°C) and rainfall (635 mm) when compared to the sites of the top five photoperiod-sensitive accessions (IP 14855, IP 17279, IP 17280, IP 17278 and IP 17285) (day length: minimum = 12.09 h, maximum = 12.14 h and mean = 12.12 h; minimum temperature = 20.60°C, maximum temperature = 21.64°C, mean = 21.29°C and rainfall = 1136 mm) also indicated the importance of prevailing day length, temperature and rainfall at

collection sites in determining the sensitivity of pearl millet accessions.

Discussion

Pearl millet is a hardy crop and has great potential because of its suitability to extreme limits of agriculture. Evaluation of germplasm for flowering responses to temperature and photoperiod from wide agro-ecological regions will improve the understanding of the photo-thermal basis of natural adaptation. The large variation observed in the world collection of pearl millet germplasm for differential behaviour of accessions in the two contrasting rainy and post-rainy seasons at Patancheru, India can be imputed to the differences in sensitivity of pearl millet accessions for temperature, photoperiod and the minimum time required to flower (Bidingar and Rai, 1989). This behaviour of pearl millet will have influence on the structure and stability of pearl millet gene pools in nature.

The results of the present study revealed that in the pearl millet landrace germplasm conserved at the ICRI-SAT genebank, irrespective of the degree of sensitivity,

Table 2. Annual mean minimum and maximum temperature and rainfall and the frequency of sensitive and insensitive accessions in different latitudes on both hemispheres

Climatic factor	Latitude range (°)						
	0–5	5–10	10–15	15–20	20–25	25–30	30–35
<i>Minimum temperature (°C)</i>							
Lowest	13.4	14.7	10.7	10.4	13.8	13.0	11.2
Highest	25.1	26.4	23.6	23.3	25.6	27.8	25.6
<i>Maximum temperature (°C)</i>							
Lowest	20.0	22.5	22.3	22.9	19.8	18.2	15.5
Highest	24.8	26.1	23.8	23.2	25.3	27.4	25.5
<i>Mean temperature (°C)</i>							
Lowest	21.2	23.5	22.5	20.5	22.0	24.7	24.3
Highest	24.7	25.9	23.9	23.1	25.1	27.0	25.1
Rainfall (mm)	1180.5	944.8	834.2	665.5	734.9	707.8	662.9
Total accessions	289 (1.8)	1457 (9.2)	6483 (40.8)	4031 (25.3)	1498 (9.4)	1813 (11.4)	333 (2.1)
Temperature-sensitive accessions ^a	82 (28.4)	322 (22.1)	2721 (42.0)	2055 (51.0)	1280 (85.4)	1558 (85.9)	324 (97.3)
Insensitive accessions ^a	5 (1.7)	12 (0.8)	124 (1.9)	107 (2.7)	26 (1.7)	33 (1.8)	2 (0.6)
Photoperiod-sensitive accessions ^a	202 (69.9)	1123 (77.1)	2636 (40.7)	1869 (46.4)	192 (12.8)	222 (12.2)	7 (2.1)

^aNumbers in parenthesis are the frequency of accessions in each latitude range.

52.5% (8342) accessions are sensitive to temperature, 45.6% (7251) accessions are sensitive to photoperiod and only 2% (311) accessions are insensitive to both temperature and photoperiod (Table 1). Frequency distribution by latitude range revealed that 10–15°N and 15–20°S are the important source regions for pearl millet germplasm. Though the distribution of insensitive accessions is available at all latitudes, a latitude range of 15–20° on both sides of the equator was found to be a major region for insensitive pearl millet germplasm. The diversity in adaptation of pearl millet could be attributed to the differences in adaptation levels of cultivars/genotypes to the prevailing day length, minimum and maximum temperatures, rainfall and duration of rainfall in each latitude range. The equatorial regions received high rainfall accompanying warm and humid climate (Table 2). The mid-latitude (10–20°) regions received lower rainfall and were characterized by warm and dry climate. The regions in the higher latitudes are cool, dry and receive a fairly good rainfall. Thus, the regions that come under the mid-latitudes are the best suited for the pearl millet as revealed by the maximum number of diverse pearl millet landraces in the region. When a species or crop has wide distribution, there is considerable difference in the latitude between its Northern and Southern limits resulting in different ecotypes, which differ in their response to temperature and day length (Wareing and Phillips, 1981). In the present study, there was 1.0–1.4 d delay in flowering per degree latitude, depending on the sensitivity group. Pearson and Coaldrake (1983) reported the delay in flowering by 4–5 d per degree latitude. Takei and Sakamoto (1987) reported negative correlation of flowering and latitude in foxtail millet.

The results suggest that the prevailing minimum temperature at the collection sites has greater impact on the sensitivity of pearl millet. Sensitivity to low temperature was lowest in accessions from higher latitudes in both hemispheres (Table 4), as these have already been exposed to cool climate of the higher latitudes during their evolution. The temperature sensitivity gradually increased (up to 50 d) in accessions from lower latitudes. The annual mean minimum temperature varied from –5.7 to 26.3°C and the mean maximum temperature varied from 5.2 to 39.5°C in the higher latitudes and accessions that were exposed to these low temperatures for a long period of domestication and cultivation were thus least sensitive to cold spells (Table 4). Ashraf and Hafeez (2004) reported an optimum temperature of 33–34°C for pearl millet and that the growth could be retarded when the temperature is too high or too low. Ong (1983) reported 12°C as base temperature, 30–35°C as optimum temperature and 45°C as

Table 3. Temperature and photoperiod sensitivity (d) and the frequency distribution of pearl millet accessions in different latitudes on the Southern and Northern hemispheres

Sensitivity (d)	No. of accessions	Frequency (%)	Latitude (°) ^a		
			South	North	Mean
<i>Temperature sensitivity</i> ^b					
1–10	3577	42.9	33.0	33.6	33.3
10–20	3294	39.5	28.4	33.6	31.0
20–30	1336	16.0	24.5	34.4	29.2
30–40	120	1.4	24.7	30.2	27.4
40–50	15	0.2	22.6	19.4	21.0
Total	8342				
In sensitive	311				
<i>Photoperiod sensitivity</i> ^b					
1–10	2506	34.6	31.7	30.9	31.3
10–20	1337	18.4	20.2	30.1	25.1
20–30	779	10.7	19.8	28.0	23.5
30–40	671	9.3	24.4	19.7	22.0
40–50	637	8.8	23.8	16.4	20.1
50–60	737	10.2	17.5	16.3	16.9
60–70	448	6.2	16.8	14.9	15.8
70–80	118	1.6	–	4.1–14.4	9.2
80–90	18	0.2	–	7.1–11.9	9.5
Total	7251				

^a South and North of the equator. ^b Extended days to flowering.

lethal temperature for pearl millet. McIntyre *et al.* (1993) reported a 2-d reduction in length of pearl millet growth period for each degree rise in temperature. Probably, because of the large number of collection sites in the present study, the photoperiod and rainfall did not show much variation in the collection sites of these accessions (Table 4). Hellmers and Burton (1972) found substantial effect of temperature on flowering of pearl millet. Erskine *et al.* (1990) reported that phenological flowering response to temperature appears to be under separate genetic control and not closely linked to response to photoperiod in lentil. At higher latitudes, the year is divided into two major seasons defined by the monsoons, and days are longer during the rainy season, during which time pearl millet is cultivated (MS Encarta[®] Interactive World Atlas, 2000). The pearl millet adapted to low temperature, erratic and inconsistent rainfall and longer days at higher latitudes is expected to flower late, but, due to near-optimum minimum (20.8°C) and maximum (30.6°C) temperature and shorter days at Patancheru location than at the collection sites, some accessions might have flowered early in rainy season than in post-rainy season, resulting in high frequency of temperature-sensitive accessions (Hijman *et al.*, 2002).

The photoperiod sensitivity extended up to 70 d in accessions from the Southern hemisphere and up to 90 d in accessions from the Northern hemisphere (Table 3). The accessions that have originated from higher latitudes where the mean day length varied from 10.85 to 13.36 h (~2.5 h longer days) were least

sensitive compared to accessions originating from locations nearer to the equator where the difference in day length varied from a mere 0.16 to 1.24 h. Bidinger and Rai (1989) reported early flowering in pearl millet under 12 h photoperiod and delay in flowering under longer photoperiod (14 h). The accessions originating from sites nearer to the equator where the day length does not vary significantly were most sensitive to longer photoperiods, while the accessions from higher latitudes which were already exposed to longer photoperiods during their evolution were least sensitive. Craufurd *et al.* (1999) reported a strong relationship between photoperiod sensitivity and the latitude of collection site of landraces in Sorghum. Joshi *et al.* (2005) defined photoperiod sensitivity as the delay in flowering due to increasing day length beyond the critical value by virtue of planting dates. Roberts *et al.* (1996) reported that in sorghum, landraces originating from higher latitudes were less photoperiod-sensitive and were inherently earlier than those from lower latitudes. Similar behaviour could also be expected with pearl millet, which is also a short-day plant. Results indicate a stronger association of latitude and the sensitivity of pearl millet to temperature and photoperiod (Erskine *et al.*, 1990). Wareing and Phillips (1981) reported that in many plant species, a day length change as short as 15–20 min will have significant effect on flowering.

The insensitive accessions, which were comparatively few in number, were spread across all latitudes in both

Table 4. Temperature and photoperiod sensitivity (d) and climate at the collection sites of pearl millet accessions conserved at ICRISAT genebank, Patancheru, India

Sensitivity (d)	No. of accns.	Frequency (%)	Day length (h) ^a			Minimum temperature (°C) ^a			Maximum temperature (°C) ^a			Total rainfall (mm) ^a
			Min.	Max	Mean	Low	High	Mean	Low	High	Mean	
<i>Temperature sensitivity^b</i>												
1–10	3577	42.9	10.8	13.5	12.1	2.0	26.4	19.2	18.5	39.7	32.5	679.3
10–20	3294	39.5	10.9	13.4	12.1	–5.7	26.3	19.0	5.2	39.5	32.2	731.5
20–30	1336	16.0	11.0	13.3	12.1	3.4	26.3	18.8	14.7	39.2	32.0	785.9
30–40	120	1.4	11.0	13.2	12.1	7.5	25.2	16.5	22.0	38.5	30.0	733.6
40–50	15	0.2	11.3	12.9	12.1	10.6	22.9	16.6	22.4	36.3	30.8	638.4
Total	8342		10.9	13.3	12.1	5.7	26.0	19.0	21.6	39.4	32.4	733.2
<i>Photoperiod sensitivity^b</i>												
1–10	2506	34.6	10.9	13.4	12.1	5.1	26.4	18.3	18.6	39.7	32.2	660.9
10–20	1337	18.4	11.2	13.1	12.1	6.0	26.3	18.3	22.1	39.7	32.4	596.4
20–30	779	10.7	11.2	13.0	12.1	5.1	26.3	19.8	21.1	39.2	32.8	758.5
30–40	671	9.3	11.3	12.9	12.1	6.8	25.8	19.8	23.5	38.7	33.2	812.3
40–50	637	8.8	11.3	12.9	12.1	12.5	25.9	19.9	24.5	39.0	33.2	930.7
50–60	737	10.2	11.5	12.7	12.1	11.3	25.9	20.1	25.1	38.4	33.3	971.3
60–70	448	6.2	11.5	12.7	12.1	13.2	24.4	20.1	25.3	37.1	33.5	1045.1
70–80	118	1.6	11.9	12.3	12.1	16.1	24.2	20.4	28.4	37.8	33.2	1125.9
80–90	18	0.2	12.0	12.2	12.1	16.3	21.8	20.3	30.2	34.4	33.0	1183.3
Total	7251											

^a Annual mean of all collection sites in the sensitivity class. ^b Extended days to flowering.

hemispheres. These might have developed insensitivity due to their alternate exposure to low and high temperatures as well as short and longer photoperiods (a sort of shuttle breeding) over a long period of time. These are independent of variable climates and might have been dual-season genotypes or genotypes that were very widely grown at both higher and lower latitudes.

More than 50% of accessions from relatively lower latitudes ranging from 0 to 20°, covering countries of Horn of Africa and Western Africa showed high photoperiod sensitivity. On the other hand, most of the accessions from the higher latitudes ranging from 20 to 35° covering mostly the countries of Indian subcontinent and Southern Africa showed low sensitivity. These results are in agreement with those of Roberts and Summerfield (1987), who reported the origin of short-day photoperiod responses in the tropics around the equator and the crops with long-day responses in latitudes greater than 30.00°. In the area, near the equator, day length is constantly around 12 h and relatively shorter than at higher latitudes, facilitating crop growth round the year, with the cropping season not always restricted to the summer season as in the temperate zone. Pearl millet adapted to such near-optimal conditions flowered late in the rainy season with long days than in the post-rainy season, at Patancheru, resulting in high frequency (>50%) of photoperiod-sensitive accessions. The results of the present study are in conformity with those of Ong and Everard (1979) who reported delayed flowering due to long days and that each short day results in 1.4 d reduction for anthesis, leading to early flowering in pearl millet.

Photoperiod and temperature responses have been related to different uses in traditional cropping system. Exploitation of the germplasm for crop improvement suitable for specific locations in a wide range of latitudes is possible only when the knowledge of temperature and photoperiod responses of the parental material is available. The results of the present study emphasize the characterization of pearl millet germplasm during two contrasting seasons to assess the sensitivity of individual accession to photoperiod and temperature. The photoperiod-sensitive, late-maturing forage varieties of pearl millet are reported to be leafier and have a better seasonal distribution for forage production (Burton and Powell, 1968). Highly photoperiod-sensitive and late-maturing pearl millet accessions assembled at ICRISAT genebank are of immense value in developing excellent forage varieties.

The insensitive accessions identified can be used to breed photoperiod- and temperature-insensitive varieties of early maturity for multiple cropping. Photoperiod- and temperature-insensitive parental lines are

of particular interest to breeders, as synchronized flowering of parental lines is essential for successful commercial hybrid seed production programmes. A low degree of photoperiod and temperature sensitivity is also essential for the broad adaptation of pearl millet (Joshi *et al.*, 2005).

Small deviations in the patterns of response to temperature and photoperiod sensitivity in the present study can be attributed to the varying local conditions, elevations, date of sowings, soils, etc in different latitudes. The insensitive pearl millet accessions identified in the present study are very useful in the climate-change scenario. Systematic and critical evaluation of insensitive accessions identified in this study can help in the identification of insensitive parental material and development of pearl millet cultivars suitable for diverse climates. Further evaluation of 311 insensitive accessions is in progress at ICRISAT, Patancheru, India. Based on the present study, collection missions could be launched to collect more germplasm that would be suitable for diverse climates. Further, studies are needed to identify suitable sites for conducting experiments and regeneration of specific germplasm sets, as also to serve as model for identification of germplasm using passport data in the improvement of pearl millet as well as other crops. Therefore, recording of location-specific geo-reference data while collecting the germplasm, which can help to elucidate the sensitivity of accessions to temperature and photoperiod and the evaluation of crops germplasm that are climate-sensitive, for flowering in two contrasting seasons to assess their sensitivity to temperature and photoperiod, is emphasized.

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References

- Andrews DJ and Anand Kumar K (1992) Pearl millet for food and forage. *Advances in Agronomy* 48: 89–139.
- Ashraf M and Hafeez M (2004) Thermotolerance of pearl millet and maize at early growth stages: growth and nutrient relations. *Biologia Plantarum* 48: 81–86.

- Bidinger FR and Rai KN (1989) Photoperiodic response of paternal lines and F1 hybrids in pearl millet. *Indian Journal of Genetics and Plant Breeding* 49: 257–264.
- Burton GW and Powell JB (1968) Pearl millet breeding and cytogenetics. *Advances in Agronomy* 20: 50–69.
- Craufurd PQ, Mahalakshmi V, Bidinger FR, Mukuru SZ, Chanterreau J, Omanga PA, Qi A, Roberts EH, Ellis RH, Summerfield RJ and Hammer GL (1999) Adaptation of sorghum: characterization of genotypic flowering responses to temperature and photoperiod. *Theoretical and Applied Genetics* 99: 900–911.
- Erskine W, Ellis RH, Summerfield RS, Roberts EH and Hussain A (1990) Characterization of responses to temperature and photoperiod for time to flowering in a world lentil collection. *Theoretical and Applied Genetics* 80: 193–199.
- Hellmers H and Burton GW (1972) Photoperiod and temperature manipulation induces early flowering in pearl millet. *Crop Science* 12: 198–200.
- Hijmans RJ, Guarino Luigi and Rojas Edwin (2002) *DIVA-GIS, Version 2. A Geographic Information System for the Analysis of Biodiversity Data. Manual*. Lima: International Potato Center.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG and Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978, doi:10.1002/joc.1276. Available at <http://www.worldclim.org/current> (June 2011).
- IBPGR and ICRISAT, (1993) Descriptors for Pearl Millet [*Pennisetum glaucum* (L.) R. Br.]. Rome/Patancheru: International Board for Plant Genetic Resources/International Crops Research Institute for the Semi-Arid Tropics, p. 43.
- Joshi AK, Pandya JN, Mathukia RK and Dangaria CJ (2005) Initial evaluation for photosensitivity in pearl millet. *Seed Research* 33: 218–220.
- McIntyre BD, Flower DJ and Riba SJ (1993) Temperature and soil water status effects on radiation use and growth of pearl millet in a semi-arid environment. *Agriculture and Forest Meteorology* 66: 211–227.
- MS Encarta[®] Interactive World Atlas (2000) *1995–1999 Microsoft Corporation*. Redmond, WA: One Microsoft Way, pp. 98052–106399.
- Ong CK (1983) Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S&H): II. Reproductive development. *Journal of Experimental Botany* 34: 337–348.
- Ong CK and Everard A (1979) Short day induction of flowering in pearl millet (*Pennisetum typhoides*) and its effect on plant morphology. *Experimental Agriculture* 15: 401–410.
- Pearson CJ and Coaldrake PD (1983) *Pennisetum americanum* as a grain crop in eastern Australia. *Field Crops Research* 7: 265–282.
- Reddy KN, Kameshwara Rao N and Irshad Ahmed (2004) Geographical patterns of diversity in pearl millet germplasm from Yemen. *Genetic Resources and Crop Evolution* 51: 513–517.
- Roberts EH, Qi A, Ellis RH, Summerfield RJ, Lawn RJ and Shanmugasundaram S (1996) Use of field observations to characterize genotypic flowering responses to photoperiod and temperature: a soya bean exemplar. *Theoretical and Applied Genetics* 93: 519–533.
- Roberts EH and Summerfield RJ (1987) Measurement and prediction of flowering in annual crops. In: Atherton JG (ed) *Manipulation of flowering*. Butterworths: London, pp 17–50.
- Snedecor GW and Cochran WG (1980) *Statistical Methods*. 7th edn. Ames, IA: Iowa State University Press.
- Takei E and Sakamoto S (1987) Geographical variation of heading response to day length in foxtail millet (*Setaria italica* P. Beauv.). *Japan Journal of Breeding* 37: 150–158.
- Upadhyaya HD, Reddy KN, Gowda CLL, Irshad Ahmed M and Sube Singh (2007) Agroecological patterns of diversity in pearl millet [*Pennisetum glaucum* (L.) R. Br.] germplasm from India. *Journal of Plant Genetic Resources* 20: 178–185.
- Upadhyaya HD, Reddy KN, Irshad Ahmed M and Gowda CLL (2010) Identification of gaps in pearl millet germplasm from Asia conserved at the ICRISAT genebank. *Plant Genetic Resources: Characterization and Utilization* 8: 267–276.
- Wareing PF and Phillips IDJ (1981) *Growth and Differentiation in Plants*. 3rd edn. Oxford: Pergamon Press, p. 353.