Field Crops Research 171 (2015) 41–53

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Seed set variability under high temperatures during flowering period in pearl millet (*Pennisetum glaucum* L. (R.) Br.)

S.K. Gupta[a,*], K.N. Rai[a], Piara Singh[a], V.L. Ameta[b], Suresh K. Gupta[c], A.K. Jayalekha[d], R.S. Mahala[e], S. Pareek[e], M.L. Swami[c], Y.S. Verma[f]

[a] *International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502324, Telangana, India*
[b] *Devgen Seeds and Crop Technologies Private Ltd., Ahmedabad 382 330, Gujarat, India*
[c] *JK Agri-Genetics Ltd., Hyderabad 500 016, Telangana, India*
[d] *Bayer Bio Science Private Ltd., Hyderabad 500081, Telangana, India*
[e] *Pioneer Overseas Corporation, India Branch, Hyderabad 500082, Telangana, India*
[f] *Metahelix Life Sciences Pvt. Ltd., Ahmedabad 380054, Gujarat, India*

ARTICLE INFO

Article history:
Received 31 August 2014
Received in revised form 6 November 2014
Accepted 8 November 2014

Keywords:
High temperature
Vapor pressure deficit
Variability
Seed set
Flowering period
Inheritance

ABSTRACT

Pearl millet has recently emerged as a significant irrigated summer season cereal crop in north-western India. But its flowering coincides with air temperatures of ≥40 °C, leading to reduced seed set and poor grain yield in most of the available hybrids, although a few hybrids with good seed set and high yield potential are widely cultivated. Under a recent initiative to diversify the genetic base of heat tolerant hybrids, field screening of 221 hybrid parental lines (both B- and R-lines), 53 germplasm accessions and 4 improved populations over four-year period revealed large genetic variability in seed set at daily maximum air-temperature of ≥42 °C during flowering. Two locations data on 46 medium maturing genotypes screened during summer 2009 showed that seed set in pearl millet started declining when maximum air temperatures reached 42 °C and decreased in curvilinear fashion to 20 percent at 46 °C. Similar relationship of seed set with minimum and mean temperature was observed with threshold values of 26.4 °C and 34.2 °C, respectively. Similarly, the relationship of percent seed set with vapor pressure deficit (VPD) showed threshold value of 6.2 kPa for maximum VPD, 1.2 kPa for minimum VPD and 3.7 kPa for mean VPD. Seed set on 2 each of heat tolerant and susceptible genotypes fitted well on the seed set-temperature response curve for the maximum, minimum and mean air temperatures. Based on 3 to 4 year field screening (2009–2012), five hybrid seed parents (ICMB 92777, ICMB 05666, ICMB 00333, ICMB 02333 and ICMB 03555) and a germplasm accession IP 19877 with 61 to 69% seed set as compared to 71% seed set in a heat tolerant commercial hybrid 9444 (used as a control) was identified. Intra-population variability for heat tolerance was observed in four populations, and highly heat tolerant progenies from two of them were identified. Evaluation of six hybrid parents under controlled environment (maximum temperature of 43 °C and minimum temperature of 22 °C) revealed boot-leaf stage of pearl millet plant to be more heat sensitive than panicle-emergence stage, and investigations on 6 A-/B-pairs under controlled environment (max. temperature of 44 °C and min. temperature of 22 °C) revealed female reproductive system of pearl millet to be more heat sensitive than pollen. Comparison of 23 hybrids and their parents for seed set at high air temperature (>42 °C) showed heat tolerance as a dominant trait, implying heat tolerance in one parent would be adequate to produce heat tolerant hybrids in pearl millet. Heat tolerant composite developed using identified lines showed high mean seed set under high air temperatures during flowering.

Abbreviations: CSIRO, Commonwealth Scientific and Industrial Research Organization; ICMB, ICRISAT millet B-line; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; IMD, India Meteorological Department; kPa, kilopascals; NCAR, National Center for Atmospheric Research; R-line, restorer line; RH, relative humidity; S, sensitive; SS, seed set; SSC, seed set class; T, tolerant; VPD, vapor pressure deficit; WANA, western Asia and northern Africa; WCA, western and central Africa.

* Corresponding author. Tel.: +91 9949003066; fax: +91 4030713074.
E-mail addresses: s.gupta@cgiar.org, idguptashashi@rediffmail.com (S.K. Gupta).

http://dx.doi.org/10.1016/j.fcr.2014.11.005
0378-4290/

1. Introduction

Pearl millet (*Pennisetum glaucum* L. (R.) Br.) is an important coarse grain cereal cultivated for grain and fodder on about 30 million hectares worldwide. India is the largest producer of this crop with 9.5 million tons of grain from 9.3 million hectares area (Yadav et al., 2012). It is primarily cultivated in rainy season of dry tropics with an average grain yield of about 800–1000 kg ha^{-1}, but in the past decade it has also occupied large areas (>500,000 ha) in the hot-dry post rainy season (February to June), locally referred as "summer", in the northern and western parts of India (Fig. 1). In this summer crop of about 80–85 days, under well irrigated and well-managed conditions, pearl millet yields about 4–5 t ha^{-1} of grain and 8–10 t ha^{-1} of dry fodder (AICPMIP, 2013). This grain yield advantage and with better grain quality from summer crop has shifted pearl millet cultivation in Gujarat state from rainy season to summer season (Reddy et al., 2013). In these parts of India, maximum air temperatures in the range of 40 °C to 48 °C are prevalent during the months of April–May. Thus, owing to high air temperatures (often >40 °C) coinciding with flowering of pearl millet crop, the summer crop suffers from reproductive sterility leading to drastic reduction in grain yield (Fig. 2.1, 2.2). Very few hybrids with high yield potential have shown good seed set under such high temperature conditions, leaving limited cultivar choice for farmers. With this limited genetic variability, there is always a risk of such hybrids breaking down to downy mildew (*Sclerospora graminicola* (Sacc.) J. Schrot) disease, which is the greatest biotic constraint of pearl millet hybrids in India. Thus, there is need to strengthen breeding of pearl millet for tolerance to heat stress during flowering period to increase genetic diversity of hybrids suitable for summer season cultivation in north–western India. Moreover, pearl millet is being experimented as a summer season crop in western Asia and north African (WANA) region, in central Asian countries and in western and central African countries (WCA) where high temperatures during flowering period is a major constraint (pers. commun. Kristina Toderich, International Center on Biosaline Agriculture—Central Asia and South Caucasus; and C.T. Hash, ICRISAT, Niger). Also, yield stability has gained more importance because of the potential adverse effects of climate changes, and high temperature is especially considered as key stress factor with potentials impact on grain yield. Nelson et al. (2009) reported 8.4% and 7.0% reduction in projected global yields of millets by 2050 using CSIRO (Commonwealth Scientific and Industrial Research Organization, Australia) and NCAR (National Center for Atmospheric Research, USA) models, respectively, under climate change scenario. Hence, higher levels of high temperature tolerance during flowering period in pearl millet will not only have global implications to diversify cropping patterns in ecologies with existing high temperatures but will also ensure stable crop production in future high temperature scenarios. This paper present results on the seed set response at different temperatures and vapor pressure deficits, magnitude of variability for seed set under high temperatures during flowering period in pearl millet, on the identification of heat tolerant sources and examines most heat sensitive stages during the crop development and whether there would be a need to breed heat tolerance in both parental lines to develop heat tolerant hybrids to further enhance the prospects of breeding flowering-period heat tolerant cultivars in pearl millet.

2. Material and methods

2.1. Field screening

Field screening for flowering-period heat tolerance in pearl millet require locations having crop season of about 80 days with good irrigation facilities, and rainfall-free days from boot-leaf stage (40–45 days after sowing) to seed set stage (about 15–20 days after

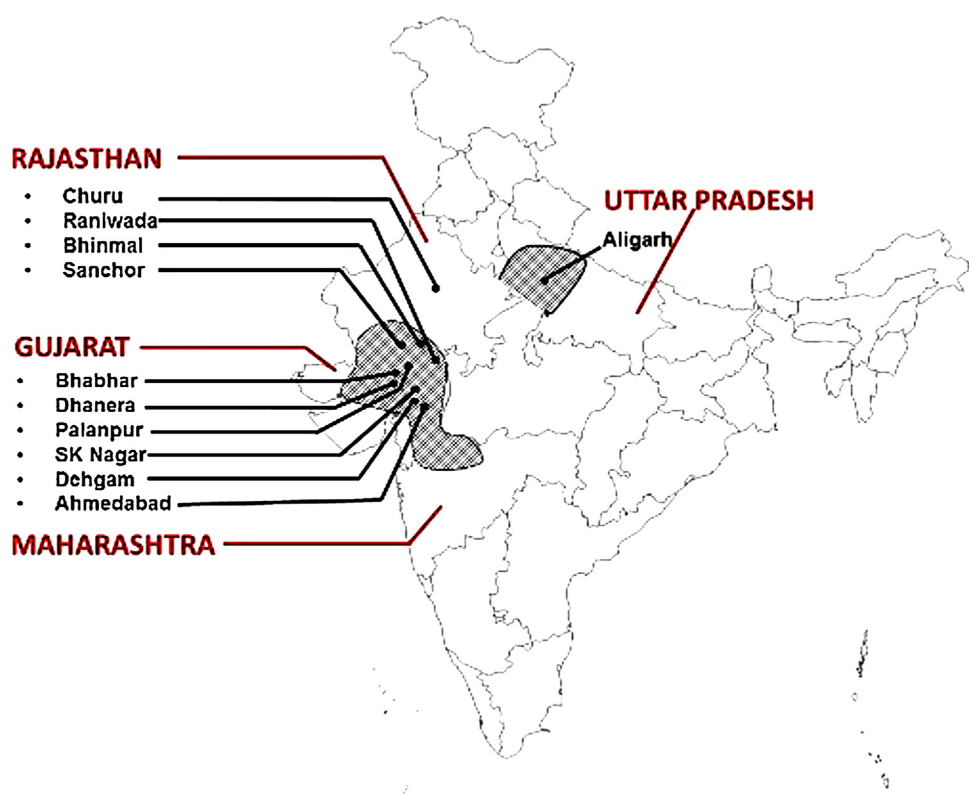


Fig. 1. Summer crop of pearl millet in India (shown as marked area), and testing locations used for screening pearl millet for high heat stress during flowering period in present study.

Fig. 2. (1), (2.2): Pearl millet panicles with reduced seed set due to high temperatures at flowering time.

boot leaf stage) and daily maximum air-temperature of ≥40 °C during this period. Potential test sites with such specifications were selected in north-western India where summer crop of pearl millet is grown from February to June (Fig. 1). The screening nurseries were planted at 4–6 locations in 2009, 2010, 2011, 2012, and 2013 with the assumption that at least 50 percent of these locations would experience weather as required for this screening. Since the weather conditions are unpredictable and variable from year to year, the nursery at each location was planted three times at 10 day interval to ensure that each entry will encounter air temperatures of ≥42 °C during flowering period in at least one of the plantings. The time-course of flowering events in pearl millet plant were consulted from Maiti and Bidinger (1981).

2.1.1. Breeding material, testing locations and planting method

A nursery comprising of 20 hybrid parents (11 designated B-lines and 9 advanced progenies), 2 improved populations viz. Medium maturity composite (MC 94) and ICMV 82132, 53 germplasm accessions and 4 hybrids 9444, Nandi 5, Nandi 32, and Nandi 69 (known to be performing well under high temperatures, hereafter such materials are referred as heat tolerant in this study) was evaluated at four locations in summer 2009. Each hybrid parent, germplasm accession and hybrid was planted in single row of 4 m, while populations were planted in 20 rows with rows spaced 60 cm apart and plants within the rows were spaced at 10–15 cm.

In 2010, a nursery comprising of 70 hybrid parents (49 B-lines which included 2 seed parents found heat tolerant in 2009; and 21 advanced progenies), 23 germplasm accessions found heat tolerant in 2009 and 2 improved populations ICTP 8202 and medium composite (MC-Co Bulk) was evaluated along with 2 heat tolerant check hybrids 9444 and 86M64 at 6 locations. Checks were repeated after every 25 rows in the nursery. Each entry was now planted in a row of 2 m as this much row length was found sufficient to provide required number of plants for screening purpose.

In 2011, a nursery comprising of a total of 83 hybrid parents (47 B-lines and 36 advanced progenies), 1 germplasm accession and two populations ICTP 8202 and MC-Co Bulk was evaluated along with 3 heat tolerant check hybrids 9444, 86M64 and Nandi 52 at 6 locations. This nursery also included 2 B-lines and 1 germplasm accession found heat tolerant based on 2009 and 2010 screening; and also had 5 B-lines and 2 advanced progenies identified heat tolerant during 2010 screening. Also, based on the results of 2009 and 2010 field screening, 7 heat tolerant (*T*) lines and 3 heat susceptible lines (*S*) were selected and 23 hybrids (14 $T \times S/S \times T$ and 9 $T \times T$) were generated to study the relationship between parents and hybrid for flowering-period heat tolerance. This nursery comprising of 23 hybrids along with the 10 parental lines and standard check hybrids 9444 and 86M64 was planted at 3 locations.

In 2012, a nursery comprising a total of 48 hybrid parents (12 B-lines and 36 R-lines), and a germplasm accession was evaluated along with 2 check hybrids 9444 and 86M64 at 5 locations. Also, a heat tolerant composite (HT Composite) developed at ICRISAT, Patancheru in 2011 using nine heat tolerant B-lines (identified from the present study) was planted in 20 rows in each sowing date at 5 locations.

In 2013, 2 known/identified heat tolerant (86M64 and ICMB 05666) and 2 known heat susceptible (ICMB 00222 and ICMB 04555) entries were part of the nursery planted on three dates at each of the 4 locations. Each of these entries was planted in 3 plots in each planting date.

2.1.2. Data recording

Data loggers (U23-001, HOBO Pro v2 Temp/RH) were installed in the experimental fields at an average panicle height (3 to 5 feet above ground) at all the locations in all the years. Data loggers were programmed to record weather variables (air temperature in all the years and relative humidity in 2009 and 2013 only) every half an hour. Normal package of practices was followed to raise good crop and the nursery was irrigated at regular intervals to avoid drought stress. In 2009, five random plants in each entry were tagged with days to flowering (5–7 days after panicle emergence stage when 50% stigmas have appeared) in each planting date. Based on a study conducted at ICRISAT under controlled environmental conditions in 2009 (results reported in this paper), it was found that pearl millet plant is affected by heat stress more at boot leaf stage than at panicle emergence stage, thus 5 random plants were tagged for days to boot leaf stage in each entry in 2010, and onwards. Panicles were bagged after grain formation to protect them from bird damage. At dough stage, seed set in bagged panicles was recorded, following the standard ergot scale (Thakur and King, 1988) where seed set

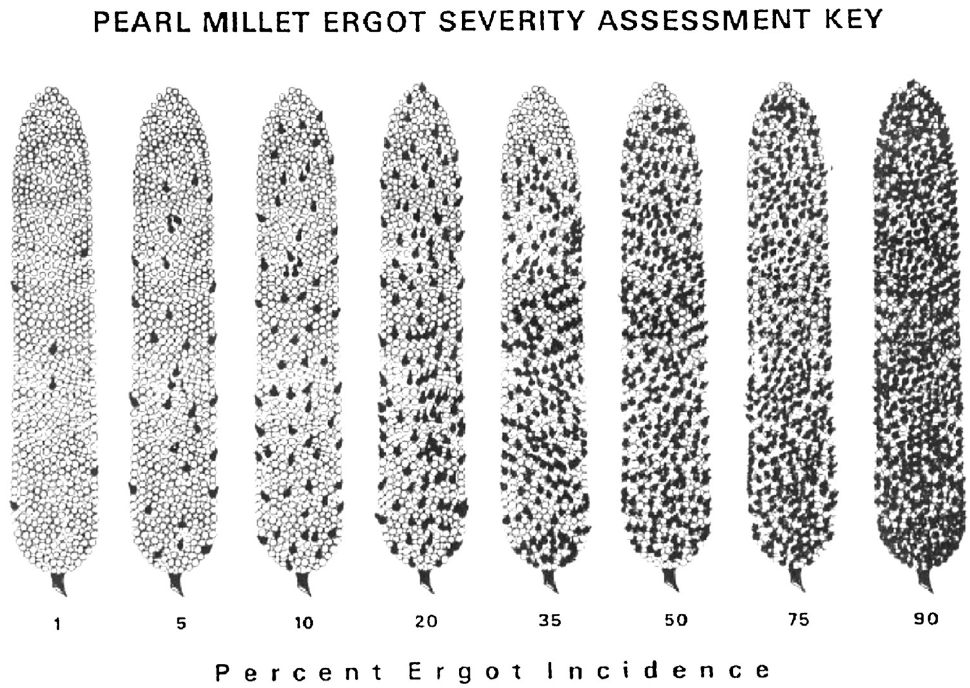


Fig. 3. Ergot severity (%) rating scale (Thakur and King, 1988). At dough stage, seed set was recorded on selected plants, where seed set in percent was considered as equivalent as to the proportion of ergot infected seeds. (for e.g. 90 percent seed set was recorded for panicle least affected by heat stress and having healthy seeds as shown for its equivalent for ergot infected seeds in ergot scale).

was considered as equivalent to the proportion of ergot infected seeds (Fig. 3).

2.2. Controlled environment screening

2.2.1. Heat stress screening for plant-stage

In a study to identify heat stress sensitive plant stage of pearl millet plant, six hybrid parents (four B-lines and 2 R-lines) were screened at 2 reproductive growth stages under controlled environmental conditions in growth chambers (Conviron—Canada, PGW-36) during February–April, 2009. The growth chambers were of 2.45 m length, 1.35 m breadth and 2 m height. Seed parents (B-lines) and restorer parents (R-lines) to be involved in this study were selected based on their dwarf plant height for ease in screening under growth chamber, as plant height of 4 B-lines varied from 100 to 125 cm (Rai et al., 2009) and of 2 R-lines varied from 120 to 140 cm. Also, the 4 B-lines were of similar maturity group (50–55 days from planting to flowering), and had 0–5 days of flowering differences when grown in 2 contrasting seasons (Rai et al., 2009), indicating photo-insensitivity or very low levels of photosensitivity in these lines. To standardize the controlled environmental conditions, weather data for target ecology was procured from India Meteorological Department (IMD), Pune in 2009 for the months during which pearl millet is grown during summer season (for the previous 2 years), which indicated that maximum air temperature in this ecology varies from 40 to 48 °C, minimum air temperature from 20 to 30 °C, RH at maximum temperature from 10 to 25% and RH at minimum temperatures from 40 to 60%. Based on this information, the growth chambers were simulated for a normal day with maximum day temperature of 43 °C, and minimum temperature of 22 °C. The temperature was gradually increased from 22 °C to 43 °C from 6 AM to 2 PM, stayed at 43 °C for 2 h, and then gradually declined from 43 °C to 22 °C from 4 PM to 10 PM. The relative humidity (RH) was set from 30% (at highest air temperature during day) and increased proportionally to 45% (at lowest air temperature during night). Growth chambers had capacity to reach minimum RH of 30% only. Growth chamber was able to maintain exact temperatures as simulated, but minor variations were observed for RH. Temperature, relative humidity (both set and observed), light levels and light intensity (μmol^{-1} m^{-2} s^{-1}) conditions maintained in growth chamber for 24 h period are shown in Fig. 4. Entries were planted in pots of 28 cm height and 30 cm diameter, and potting mix of sterilized soil:sand:FYM::2:2:1 was used. Each entry was planted in 10 pots with 3 to 4 plants each. All the entries were kept in open (February to May is normal summer season of pearl millet crop at ICRISAT, Patancheru) prior to shifting to growth chambers. Plants in pots at appropriate stage were tagged and pots having at least 1–2 such plants of each entry were shifted to growth chambers. Total of eight to ten plants of each entry (in 3–4 pots of each entry) were shifted to growth chamber at (i) initiation of boot leaf stage, and at (ii) initiation of panicle emergence stage (about 7–8 days after initiation of boot leaf stage). All the pots in control and in growth chambers were watered daily to avoid any water stress. All the entries came to boot leaf stage in 40–45 days and to panicle emergence stage in 50–55 days and were shifted to growth chamber accordingly. Plants of different entries had seed setting in the chamber at 20–24 days after boot leaf stage, and 10–15 days after panicle emergence stage. Plants were again shifted from growth chamber to open area soon after their seed set was over which differed by 0–5 days from genotype to genotype. Seed set was recorded as indicated earlier under field screening method. Seed setting was also recorded for plants kept in open (control) encountering maximum temperatures of about 33–36 °C and minimum temperatures of 18–24 °C (as measured on weather logger) from boot-leaf to panicle emergence stage, while RH was 60–73% at 07:17 h and 23–36% at 14:17 h (as available from Meteorological Laboratory, ICRISAT, Patancheru).

2.2.2. Heat stress screening of reproductive organs

In a study on comparative evaluation of reproductive organs susceptible to heat stress, six male sterile lines (A-lines) and their maintainers (B-lines) were selected keeping in view two factors,

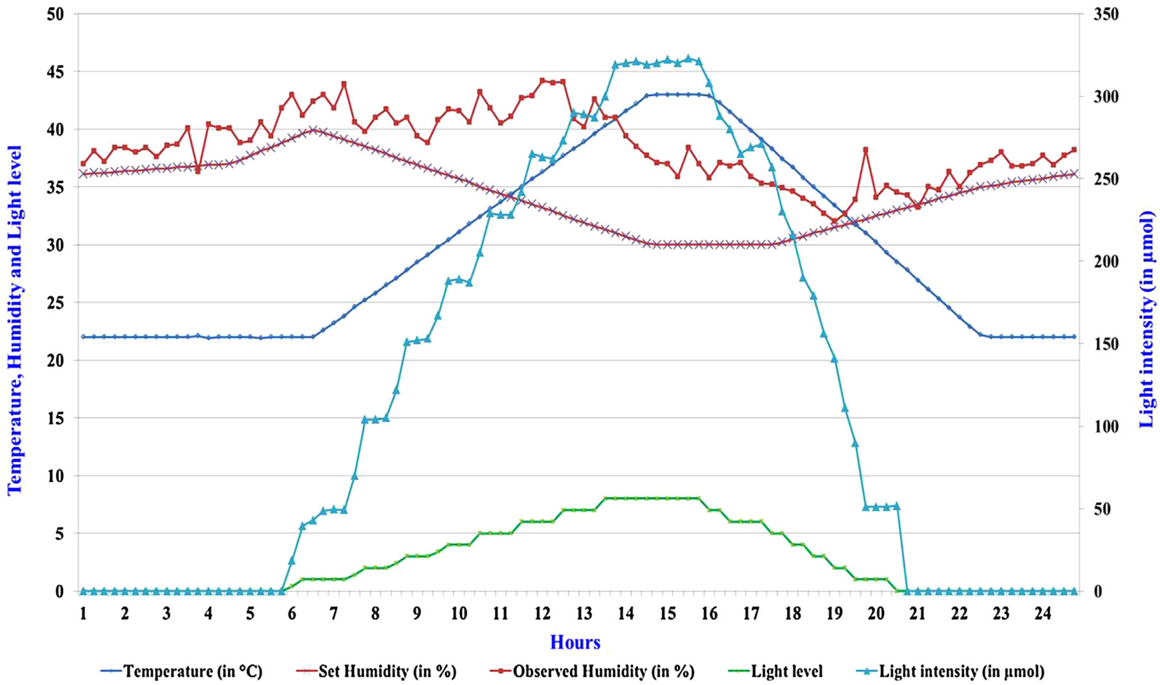


Fig. 4. Temperature, relative humidity and light conditions in growth chamber for 24 h period.

(i) there were no flowering differences between A- and B-line, to enable crossing as required in this study, and (ii) dwarf plant height to enable screening under growth chambers, which varied from 65 cm to 120 cm for these selected B-lines (Rai et al., 2009). These 6 B-lines flower in 42–49 days after planting, and had minor differences (0–6 days) for flowering when planted under different contrasting seasons (Rai et al., 2009), indicating photo-insensitivity or very low levels of photosensitivity in these lines. Eight pots of A- and eight pots of B-line of each A–B-pair were planted in open area with 4–5 plants/pot, during July 2011. Entries were planted in pots of 28 cm height and 30 cm diameter, and potting mix of sterilized soil:sand:FYM::2:2:1 was used. Growth chambers (Conviron—Canada, PGW-36) were used, simulated for a normal day for conditions as earlier mentioned in plant-stage experiment, except that maximum day temperature was now 44 °C (in earlier experiment it was 43 °C) and rest of temperature and RH values were adjusted proportionally. All the entries were grown in open (July is normal planting time of rainy season pearl millet crop at ICRISAT, Patancheru) prior to shifting to growth chambers. Plants were shifted to growth chambers at appropriate stage (after 3 to 4 days after boot-leaf is visible). Pots having at least 1–2 plants of appropriate stage of each entry were shifted to growth chambers, with tagged targeted plants. Four pots of each A- and B-line of each A/B-pair were shifted to growth chamber (under heat treatment, hereafter referred to as A*h* and B*h*), and the remaining four pots were shifted to green house under normal air temperatures, hereafter referred as A*n* and B*n*. Green house had temperature regulation of 32 to 34 °C of maximum day temperatures, and 23–25 °C of minimum night temperatures (as recorded from weather logger installed in green house) during this study period. All the pots in green house and in growth chambers were watered daily to avoid any water stress. All the A-line plants were kept in one growth chamber, and the B-line plants in another chamber to keep control over pollination of A-line plants. The crosses between an A-line and a B-line in each pair were made as shown in Fig. 5. Collection of pollen, followed by crossing on plants under control and under

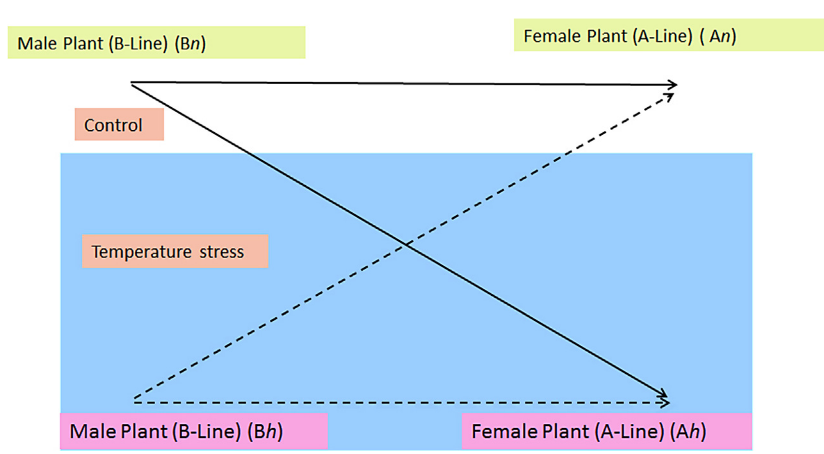


Fig. 5. Diagram depicting the reciprocal crossing strategy employed to determine the reproductive system responsible for temperature stress sensitivity. The dark area represents the controlled temperature environment. Arrows depict the possible combination of crosses. The dashed line represents temperature-stressed male contributions and the solid line represents the control temperature male contribution.

Table 1
Coordinates and temperatures of testing locations during flowering period (2009–2013).

Year	Location	Latitude (°N)	Longitude (°E)	Altitude (m)	Temperature (°C)					
					1st Planting		2nd Planting		3rd Planting	
					Max.	Min.	Max.	Min.	Max.	Min.
2009	Aligarh	27.90	78.08	191	45.2 (5)*	19.8 (12)**	45.0 (6)*	19.8 (15)**	45.5 (11)*	19.8 (11)**
	Bhabar	22.71	88.36	11	48.5 (40)	16.8 (21)	48.0 (28)	16.8 (21)	48.0 (24)	23.4 (20)
2010	Ahmedabad	23.02	72.57	50	49.4 (42)	24.1 (24)	49.4 (35)	24.3 (35)	NA	NA
	Dehgam	23.17	72.82	11	48.7 (25)	9.2 (1)	48.7 (23)	13.0 (2)	48.7 (23)	24.2 (18)
	Palanpur	24.17	72.43	218	47.8 (26)	18.4 (14)	47.8 (26)	18.4 (6)	47.8 (24)	18.4 (7)
	Sanchor	24.75	71.77	63	50.3 (27)	24.1 (25)	50.3 (27)	24.1 (26)	50.3 (23)	24.1 (24)
2011	Aligarh	27.90	78.08	191	46.3 (20)	14.8 (2)	46.3 (24)	14.8 (4)	46.3 (25)	14.8 (4)
	Dehgam	23.17	72.82	11	47.3 (21)	20.9 (16)	47.3 (17)	21.9 (16)	45.0(15)	23.6 (14)
	Sanchor	24.75	71.77	63	46.3 (19)	NA	46.3 (7)	NA	43.3 (7)	NA
2012	Aligarh	27.90	78.08	191	42.3 (1)	17.0 (1)	42.3 (6)	17.0 (2)	44.6 (9)	18.9 (4)
	Dehgam	23.17	72.82	11	45.7 (21)	20.7 (9)	45.1 (12)	20.7 (14)	45.7 (25)	22.0 (23)
	Sanchor	24.75	71.77	63	45.1 (13)	15.3 (4)	45.1 (12)	15.3 (4)	45.3 (13)	17.7 (15)
2013	Ahmedabad	23.02	72.57	50	47.4 (10)	18.2 (0)	48.5 (15)	19.7 (0)	48.5 (23)	19.9 (0)
	Aligarh	27.90	78.08	191	44.2 (13)	17.6 (6)	43.4 (12)	17.6 (0)	44.2 (14)	18.5 (9)
	Dehgam	23.17	72.82	11	47.4 (16)	18.0 (0)	47.9 (17)	18.2 (0)	47.8 (21)	18.3 (0)
	Sanchor	24.75	71.77	63	51.5 (11)	16.3 (6)	51.5 (15)	16.3 (7)	50.0 (23)	16.3 (9)

* In parenthesis are the number of days when max. day temperature exceeded 42 °C at a given location; NA: Not available.
** In parenthesis are the number of days when min. night temperature exceeded 26 °C at a given location.

growth chamber was done in morning hours (8:30 h. to 10:00 h.) to avoid disturbing the plants during rising temperature period. The same cross was attempted twice on two consecutive days (both in and outside the chamber) to ensure that all the stigmas of panicle are crossed and complete pollination is achieved. As an earlier study reported that the fertilized stigmas in pearl millet contract and curls within 3 h of pollination and turns completely brown and withers after 8 h of pollination (Thakur and Williams, 1980), indicating completion of pollination process, so plants with panicles crossed in growth chamber were taken out after 2 days of crossing and kept in green house. Also, it is reported that the grain grows sufficiently to become visible within the floret within 6–7 days after fertilization in pearl millet plant (Maiti and Bidinger, 1981). Further, seed set was recorded as indicated earlier under field screening method, once the entries had seed set visible on panicles. Seed set of crosses An × Bn vs An × Bh were compared to study the effect of heat stress on male reproductive system, specifically pollen here; and An × Bn vs Ah × Bn were compared to study the effect of heat stress on female reproductive system. Seed set of Ah × Bh was also recorded to study the compounding effect of heat stress on pollen and female reproductive systems.

2.3. Data analysis

2.3.1. Identify heat tolerant lines and variability study

In field screening, seed set data from two locations (Bhabhar and Aligarh) in 2009; four locations (Ahmedabad, Dehgam, Palanpur and Sanchor) in 2010; three locations (Aligarh, Dehgam and Sanchor) in 2011; three locations (Aligarh, Dehgam and Sanchor) in 2012; and for 4 locations (Ahmedabad, Aligarh, Dehgam and Sanchor) in 2013 were considered, as these locations experienced maximum air temperatures of ≥42 °C during flowering time. The coordinates of locations finally considered for analysis and their weather variables for the period when experimental material was in flowering are provided in Table 1. All the breeding lines encountered air temperatures of ≥42 °C in one or more of the planting dates across years. The seed set (SS) data of only those plants of a particular entry were considered for analysis where days to flowering (in 2009)/boot leaf stage (in 2010, 2011, 2012 and 2013) coincided with maximum day air temperature of ≥42 °C. The seed set data for all such plants of a particular entry were averaged across three dates of a location to find mean seed set in percentage, and were classified into different seed set classes (SSC) based on percent mean SS over three plantings. The mean seed set of an entry was averaged over all the locations to find over all mean seed set (%). All data were statistically analyzed using SAS PROC ANOVA procedures (SAS Institute, 2003) software. Under controlled environment studies, treatments were compared using standard t-test.

2.3.2. Relationship of seed set with temperature and vapor pressure deficit

In summer 2009, large numbers (77) of diverse pearl millet genotypes (comprising of seed parents, restorer parents, germplasm accessions and hybrids) were screened for heat stress, hence data from this nursery were considered for this analysis. Seed set data of these genotypes screened at Aligarh and Bhabhar for the three planting dates were pooled. First all the relevant data (temperature, relative humidity and percent seed set) for each entry in each plot were averaged over the five plants. To plot the relationship of seed set with temperature or vapor pressure deficit (VPD), the data of only 46 medium maturing entries having similar phenology (flowering in 50–60 days after planting) were used for this analysis. The data of heat tolerant entries (checks and other entries) were excluded from this analysis. Using air temperature and relative humidity data, saturation vapor pressure (e^*), actual vapor pressure (e) and VPD (e^*–e) values in kilopascals (kPa) were calculated using the following relations, $e^*(T) = [6.112 \times \exp\{(17.67 \times T)/(T + 243.5)\}]/10$ and $e(T) = (\%RH/100) \times e^*$ (WMO, 2008). Further, all the selected data were re-arranged in ascending order of mean temperature and moving averages were calculated for each variable taking 20 observations at a time at every one step of the observation. The moving averages of percent seed set were plotted against the moving averages of max., min. and mean temperatures, and max. and min. VPD values associated with max. and min. temperatures, respectively, and with the mean of max. and min. VPD to determine the relationship of seed set with these six climate variables. These relationships were considered as the baseline relationships (or baseline response curves) of the pearl millet crop and compared with the seed set data of heat tolerant and heat susceptible pearl millet entries grown

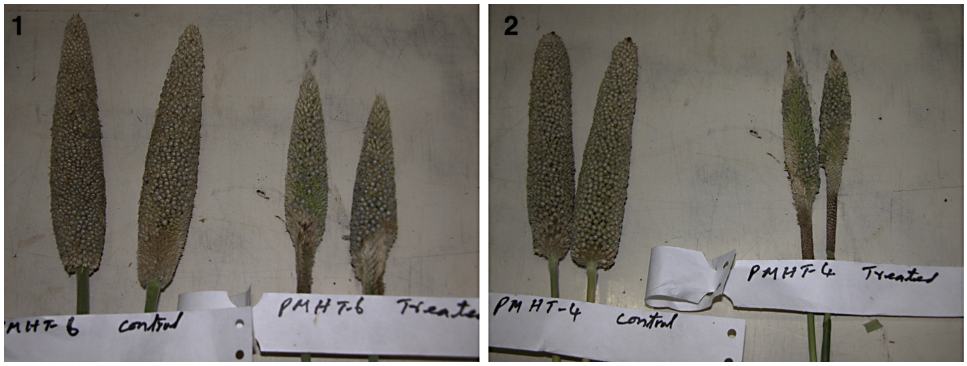


Fig. 6. (1), (6.2): Effect of heat stress on pearl millet panicles; on left hand side are two panicles kept under control, and toward right hand side are two panicles exposed to high heat stress.

during 2013. The 2013 season seed set data of heat tolerant entries and the climate variables were treated in the same way as the 2009 season data for calculating the moving averages of variables, except that 10 data points (as the data points were less) were averaged progressively for each one step of observation.

3. Results and discussion

3.1. Variability for flowering-period heat tolerance

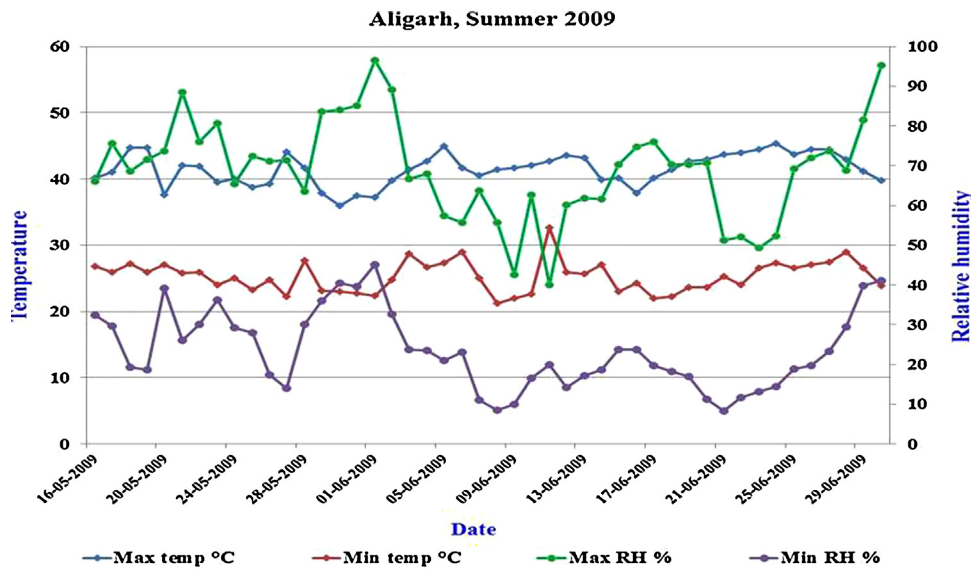
Pearl millet plants exposed to air temperature of ≥42 °C during flowering period showed some morphological changes such as reduced panicle length, reduced panicle exertion, tip sterility in panicle, and reduced seed set in comparison to plants under normal temperatures (33–36 °C) under field as well as in growth chambers (Fig. 6.1 and 6.2).

In summer 2009, relative humidity across locations during flowering period varied from 10 to 30% at maximum air temperatures of 42 to 49 °C during day and from 50 to 80% at minimum air temperatures of 20 to 28 °C at night. Weather variables (max. and min. temperatures; max. and min. RH) for the period when most of the entries came to flowering at Aligarh and Bhabhar during summer 2009 are shown in Fig. 7. Hybrid 9444 had highest overall mean seed set (SS) of 83% followed by Nandi 32 with 81% SS, while the remaining 2 test hybrids had 69 to 73% SS. At Aligarh, 85% lines (17 lines) had >60% SS, while no line had seed set of <20%, whereas at Bhabhar only 10% lines (2 lines) had >60% SS and 40% lines (8 lines) had SS of <20% (Table 2). Thus, more number of lines had lower seed set at Bhabhar than at Aligarh, which could be due to harsher conditions at Bhabhar than at Aligarh, as evident from the weather that prevailed from planting to flowering at these locations. The highest maximum temperature observed at Bhabhar was 48.5 °C with 40 days recording more than 42 °C and had 7 days more than 47 °C, whereas Aligarh had maximum temperature of 45.2 °C with 22 days recording more than 42 °C. Amongst B-lines, ICMB 05666 had highest mean SS of 75% followed by ICMB 92777 with 67% SS and twenty three germplasm accessions had > 60% SS. In summer 2010, maximum of 47% lines were in 21–40 SSC and only 8% lines had >60% SS across the locations. Seven lines (6 B-lines and 1 advanced progeny) had SS of more than 60% with ICMB 03555 having highest mean SS of 67%. These seven lines also included ICMB 92777 and ICMB 05666, with both having 64% SS. In 2011, 12 B-lines had SS of >50%, of which 2 were ICMB 92777 and ICMB 05666 which had high seed set in 2009 and 2010; three were ICMB 03555, -02333, and ICMB-00333 having high seed set in 2010, and rest of 7 were new B-lines ICMB 04999, -05888, -06111, -06555, -07222, -09111, and ICMB 09222. Also, germplasm accession IP 19877 had shown good SS of 60%. In 2012, 16 B-lines had SS of 60–70%, which included all the 12 B-lines which had high seed set in 2011. Amongst 36 designated R-lines, 3 lines viz. ICMR 08444, -09777 and ICMR 09999 had SS of >65%.

Amongst populations, plants in ICMV 82132 had SS range from 75 to 90% (SS mean of 79%) at Aligarh in 2009, followed by MC 94 with SS mean of 76% (Table 3). Both the populations followed same trend for seed set at Bhabhar, as ICMV 82132 had highest mean SS of 54% followed by MC 94 with mean SS of 44%. The populations ICTP 8202 and MC-Co Bulk had wide variation (1–100%) for seed set at all the locations in 2010 and 2011. Based on the high seed set shown by MC 94 in 2009 and ICTP 8202 in 2010, 20 and 16 advance progenies developed from MC 94 and ICTP 8202 populations, respectively, were selected and screened for heat tolerance in 2011. From these lines, 8 and 9 lines derived from MC 94 and ICTP 8202, respectively, had shown SS of >50%.

These results from hybrid parents and populations indicated existence of variability for seed set at maximum air temperatures of ≥42 °C during flowering among the lines and populations as well as within the populations of pearl millet. Though, no such variability studies on heat tolerance traits have been reported so far in pearl millet, studies in other crops like maize (*Zea mays* L.) have indicated that the traits like duration and rate of spikelet production are affected by temperature and there is genotypic variability for heat stress affected traits (Otegui and Melón, 1997; Basetti and Westgate, 1993). Also, genotypic variation has been reported for spikelet sterility at high temperature in rice (*Oryza sativa* L.) (Matsui et al., 2001; Satake and Yoshida, 1978; Prasad et al., 2006).

This multi-locational screening identified breeding materials having high seed set at day-time temperatures of ≥42 °C during flowering period (Table 4); ICMB 92777, ICMB 05666, and a germplasm accession IP 19877 based on 4 year results; ICMB 00333, ICMB 02333 and ICMB 03555 based on 3 year results; and ICMB-04999, -05888, -06111, -06555, -07222, -09111, and ICMB 09222 with 17 advanced progenies derived from MC 94 to ICTP 8202 based on 2 year results. The populations MC 94, ICMV 82132, MC-Co Bulk and ICTP 8202 have shown significant intra-population variability for seed set under high heat stress; hence selections done under high temperature for seed set during flowering time should help derive heat tolerant progenies from them. Also, the plants of heat tolerant composite had SS range from 62 to 79%, with mean SS of >70% across all the locations in 2012 (data not shown), and this composite would thus serve as a useful base population for generating heat tolerant lines. Moreover, some of the seed companies utilized the heat tolerant B-lines identified from this study in their crossing programs and progenies derived from such crosses have shown very high seed set under high temperatures of ≥42 °C during flowering period (pers. commun. VL Ameta, DevGen Seeds).



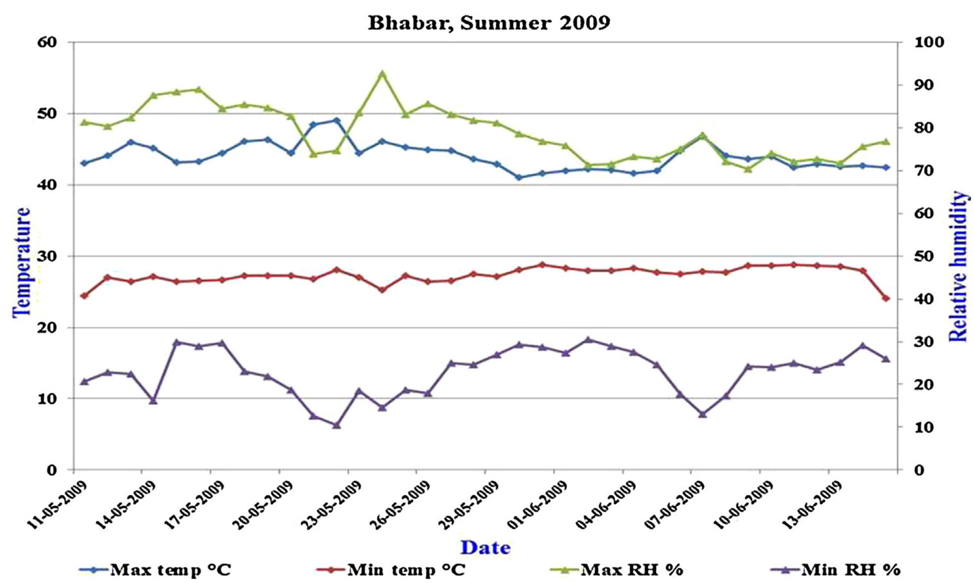


Fig. 7. Temperature and RH conditions at Aligarh and Bhabhar during flowering period in summer of 2009.

Table 2
Frequency distribution of breeding lines and populations in different seed set classes (SSC %) at various locations in summer of 2009, 2010, 2011 and 2012.

Year	Number of hybrid parents	Location	Percent entries in seed set class (SSC %)			
			<20	21–40	41–60	61–80
2009	20	Aligarh	0.0	0.0	15.0	85.0
		Bhabhar	40.0	25.0	25.0	10.0
		Overall	0.0	30.0	50.0	20.0
2010	70	Palanpur	6.9	26.4	54.0	12.6
		Ahmedabad	69.0	21.8	3.4	4.6
		Dehgam	27.6	11.5	25.3	21.8
		Sanchor	41.4	21.8	19.5	16.1
		Overall	16.1	47.1	28.7	8.0
2011	83	Aligarh	23.5	37.6	35.3	3.5
		Dehgam	4.7	24.7	49.4	18.8
		Sanchor	20.0	29.4	28.2	17.6
		Overall	7.1	40.0	45.9	7.1
2012	48	Aligarh	4.0	16.0	24.0	52.0
		Dehgam	4.0	14.0	24.0	56.0
		Sanchor	2.0	22.0	36.0	38.0
		Overall	2.0	16.0	42.0	38.0

Table 3
Percentage of plants in different seed set classes (SSC) observed for populations at different locations in summer of 2009, 2010, and 2011.

Year	Location	Population	Total no of plants	Percent of plants in SSC (%)						
				<20	21–40	41–60	61–80	>81	Mean	Range
2009	Aligarh	MC 94	15	0.0	0.0	20.0	53.3	26.7	76.3	50–90
		ICMV 82132	11	0.0	0.0	0.0	81.8	18.2	78.8	75–90
	Bhabhar	MC 94	44	31.8	18.2	15.9	25.0	9.1	44.1	0–95
		ICMV 82132	23	30.4	13.0	17.4	17.4	21.7	53.7	0–100
2010	Palanpur	ICTP 8202	146	7.5	19.2	33.6	38.4	1.4	53.9	1–90
		MC-Co Bulk	147	8.8	16.3	34.0	39.5	1.4	53.8	0–85
	Ahmedabad	ICTP 8202	200	0.0	7.5	43.5	47.5	1.5	60.7	35–85
		MC-Co Bulk	199	2.0	16.6	23.1	43.7	14.6	63.1	15–95
	Sanchor	ICTP 8202	134	17.9	19.4	38.1	20.1	4.5	50.3	10–90
		MC-Co Bulk	155	44.5	14.8	27.1	13.5	0.0	36.1	0–80
2011	Aligarh	ICTP 8202	192	26.0	24.0	33.9	16.1	0.0	45.2	0–75
		MC-Co Bulk	216	37.0	22.7	32.4	7.4	0.5	37.8	1–90
	Sanchor	ICTP 8202	177	76.3	4.0	14.7	4.5	0.6	25.8	0–100
		MC-Co Bulk	165	6.7	8.5	52.7	27.9	4.2	57.5	0–100

3.2. Relationship of seed set with temperature and vapor pressure deficit

The relationship of seed set with moving average maximum temperature showed that percent seed was not affected until the temperature had reached 42 °C (Fig. 8.1). Beyond 42 °C, seed set had curvilinear decrease and about 20% seed set was observed at 46 °C. Similar relationships of seed set with moving averages of minimum and mean temperature showed threshold values of 26.4 °C and 34.2 °C, respectively, after which seed set started declining. Plot of percent seed set data against moving average values of VPD at max. and min. temperature and mean VPD showed threshold values of 6.2 kPa, 1.2 kPa and 3.7 kPa, respectively, and the decrease in seed set in these cases was linear (Fig. 8.2), indicating that high VPD had negative effect on seed set at higher temperatures in pearl millet. Based on the 2013 seed set data, comparison of seed set vs temperature for the identified heat tolerant genotypes 86M64 and ICMB 05666 showed that they had higher seed set at various values of max., min. and mean temperature than the baseline response curves data (Fig. 9.1) which reflected higher temperature tolerance in these genotypes. While the other two known heat susceptible genotypes (ICMB 00222 and ICMB 04555) had lower values of seed set when compared with the baseline curves for the max., min. and mean temperatures (Fig. 9.2). These seed set results of tolerant and susceptible genotypes fitted well to the temperature response curves developed in this study, indicating that these response curves are well representing pearl millet crop responses to high temperature stress. These response curves were based on field based data, hence it is suggested that these response should be further corroborated by conducting experiments under controlled environmental conditions.

Table 4
Breeding lines found with high mean seed set over all the locations in summer 2009, 2010, 2011 and 2012.

Year of screening	Lines	SS (%)
2009, 2010, 2011, 2012		
B-lines	ICMB 92777	65
	ICMB 05666	69
Germplasm line	IP 19877	69
Check	9444	71
2010, 2011, 2012		
B-lines	ICMB 00333	61
	ICMB 02333	62
	ICMB 03555	63
Check	9444	65
2011, 2012		
B-lines	ICMB 04999	58
	ICMB 05888	66
	ICMB 06111	58
	ICMB 06555	69
	ICMB 07222	64
	ICMB 09111	65
	ICMB 09222	64
R-lines	8-Progenies from MC 94	>60
	9-Progenies from ICTP 8202	>60
Checks (mean of different years)	86M64	64
	Nandi 52	61
	9444	64

3.3. Heat stress sensitive growth stage

Very high seed set (91.2 to 96.2%), as expected, was observed in all the six inbred lines under control conditions (Table 5). Exposure of plants to high temperatures at panicle emergence stage led to significant reduction in seed set that varied from 0.2 to 48% in all except one line. Exposure of plants to high temperatures at the boot leaf stage had further significant reduction in seed set in four lines, which varied from 0.0 to 15.5% in all except one line, indicating boot-leaf stage of pearl millet plant to be more heat sensitive than panicle-emergence stage. The appearance of boot-leaf indicates initiation of reproductive stage in pearl millet plant, and the meiotic processes like microsporogenesis are under progress during this time (Maiti and Bisen, 1978). Only a limited number of reports have been published on the effect of high temperature during the transitional phase (vegetative to reproductive) of development in cereal plants (Damptey and Aspinall, 1976; Mahalakshmi and Bidinger,

Table 5
Percent seed set in hybrid parents at two different reproductive growth stages in controlled environmental conditions and control at ICRISAT, Patancheru.

Sr no.	Hybrid parent	Seed set (%)		
		Growth stage of plant for heat treatment		
		Boot leaf stage (treatment 1)	Panicle emergence stage (treatment 2)	Control (treatment 3)
1	R1*	4.4^{ac**}	45.0^{b}	92.5
2	ICMB 92777	15.5^{ac}	40.0^{b}	96.2
3	ICMB 00999	3.8^{a}	0.2^{b}	91.2
4	841B	39.0^{a}	47.5^{b}	93.7
5	R2*	13.3^{ac}	76.6^{b}	93.7
6	ICMB 95222	0.0^{ac}	12.5^{b}	96.2
	Overall mean	12.4^{ac}	35.0^{b}	93.9

* R-lines procured form private seed company.
** Shows significance of t-test at $p < 0.05$ (a: between treatments 1 and control; b: between treatment 2 and control; c: between treatments 1 and 2).

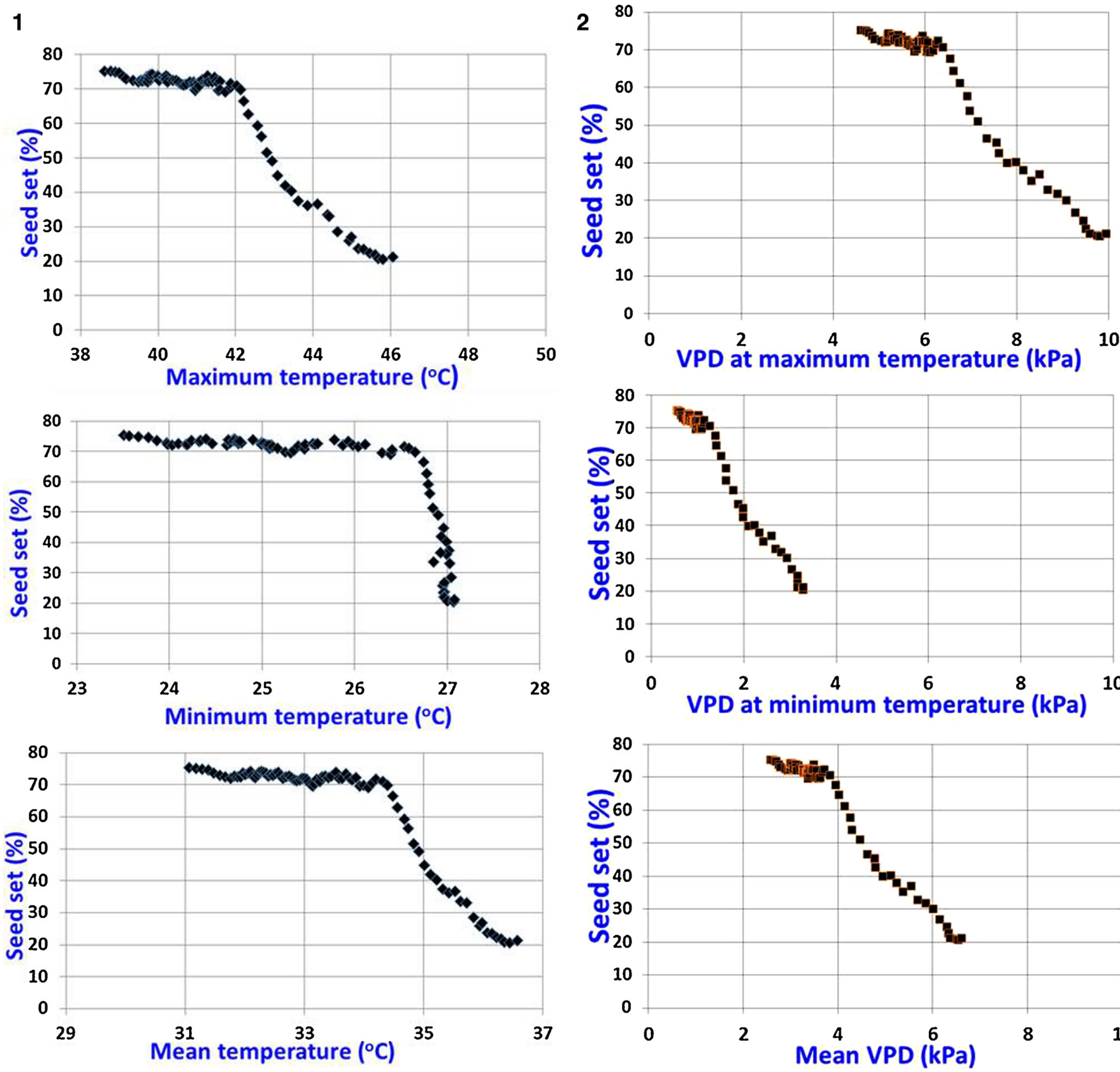


Fig. 8. (1): Response of seed set of 46 pearl millet genotypes to maximum, minimum and mean temperatures during summer 2009 (Aligarh and Bhabhar). All data points are moving averages.
(8 2): Response of seed set of 46 pearl millet genotypes to VPD at maximum and minimum temperatures; and with mean VPD during summer 2009 (Aligarh and Bhabhar). All data points are moving averages.

1985). In rice, flowering (anthesis and fertilization) stage is affected more than the booting (microsporogenesis) stage at high temperature, though both the stages are affected significantly by the high temperature (Satake and Yoshida, 1978; Farrell et al., 2006). In wheat (*Triticum aestivum* L.) temperatures above 30 °C during floret formation causes complete sterility (Owen, 1971; Saini and Aspinall, 1982). Also, Fischer (1985) reported that the number of kernels per unit area in wheat decreases at a rate of 4% for each degree increase in mean temperature during the 30 days preceding anthesis in wheat.

3.4. Heat-stress sensitivity of reproductive organs

Pollination of panicles of plants grown under control conditions (A*n*) with pollen collected from plants grown under control conditions (B*n*) defined as A*n* × B*n* crosses gave very high seed set in all the lines (Table 6). When A*n* plants were crossed with pollen collected from plants grown under high temperatures (B*h*), defined as A*n* × B*h* crosses, there was marginal and non-significant reduction in seed set in five lines with 46.2 to 95% seed set. However, when plants grown under high temperatures (A*h*) were crossed with pollen from B*n* plants, there was significant and drastic reduction in seed set in all the lines with the levels of seed set ranging from 1.6 to 25.0%, implying that it was female reproductive system rather than pollen which was vulnerable to high temperatures during flowering. This finding also support the seed set observed in the field screening experiments, as large differences in seed set among the entries were observed, while each entry had uniform seed set across its plants, in spite of abundant pollen availability from all over the field. Earlier studies on other crops have also indicated that temperature stress can affect male and female organs differently (Herrero, 2003; Hedhly et al., 2008). There are relatively

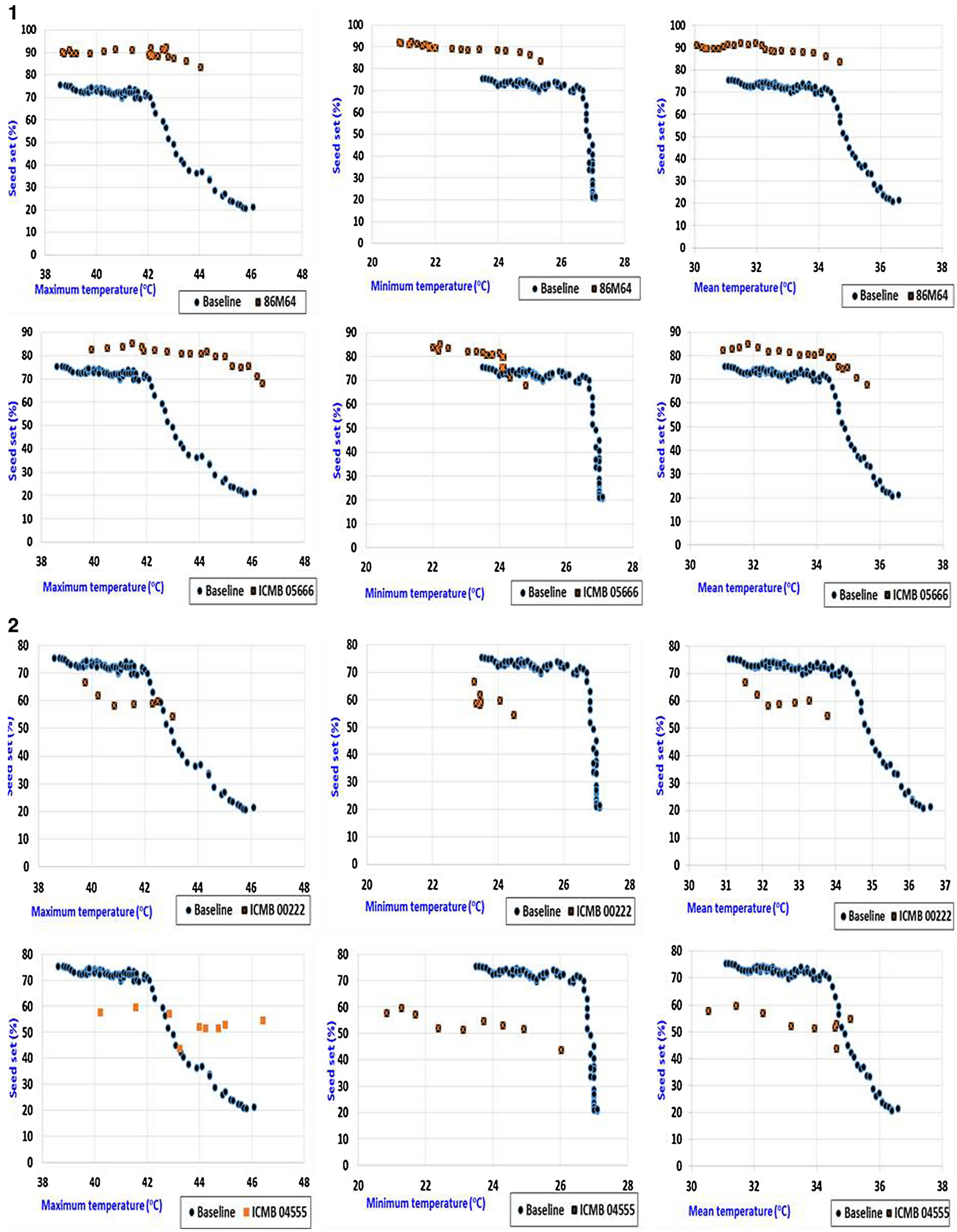


Fig. 9. (1): Response of seed set to max., min. and mean temperature for the 2 identified/known tolerant pearl millet genotypes based on seed set at 4 locations during summer 2013 and compared to the baseline response curves for pearl millet. All data points are moving averages.
(9 2): Response of seed set to max., min. and mean temperature for the 2 identified/ known susceptible pearl millet genotypes based on seed set at 4 locations during summer 2013 and compared to the baseline response curves for pearl millet. All data points are moving averages.

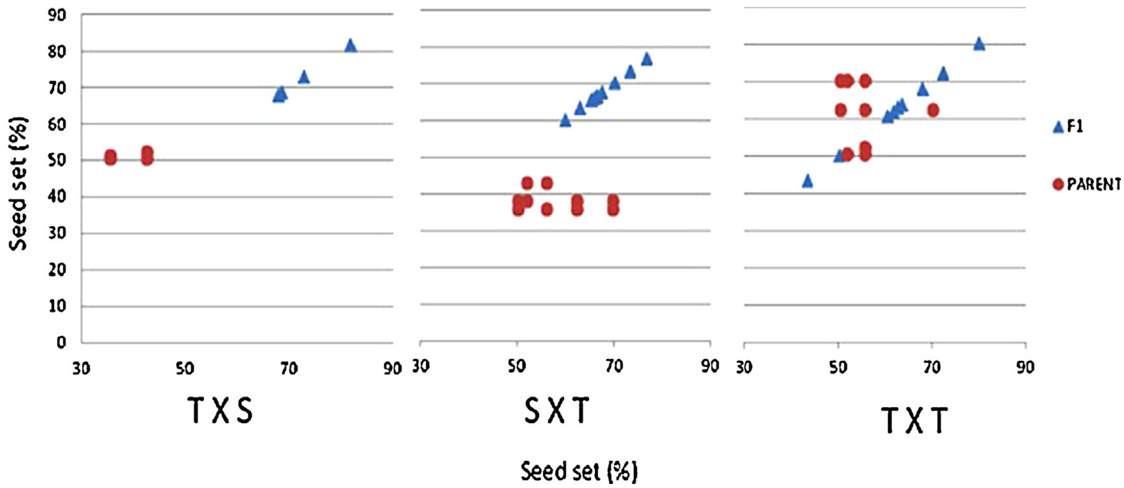


Fig. 10. Reaction of different types of pearl millet crosses to high temperature at flowering time at three locations, summer season 2011; *T*: Tolerant parent, *S*: Susceptible parent; F_1: Hybrid.

Table 6
Mean seed set in crosses to study the effect of heat stress on male and female reproductive organs under controlled environment conditions.

Hybrid parent	Seed set (%)			
	$A^h \times B^h$ (treatment 1)	$A^h \times B^n$ (treatment 2)	$A^n \times B^h$ (treatment 3)	$A^n \times B^n$ (treatment 4)
ICMA/B 91444	0.8^{d*}	1.6^{bc}	95.0	97.0
ICMA/B 92444	1.3^{d}	8.6^{b}	10.2^{a}	89.0
ICMA/B 92777	3.6^{d}	4.5^{bc}	88.3	90.0
ICMA/B 95555	16.0^{d}	3.2^{bc}	57.5	62.5
ICMA/B 97444	15.0^{d}	25.0^{bc}	80.7	84.0
ICMA/B 05666	3.5^{d}	20.0^{bc}	46.2	63.0
Overall mean	6.7^{d}	10.4^{bc}	62.9^{a}	80.9

* Shows significance of *t*-test at $p < 0.05$ (a: between treatments 3 and 4; b: 2 and 4; c: 2 and 3; d: 1 and 3).

fewer studies in which the effects of temperature stress on female reproductive organs have been investigated. For instance, ovary abnormalities were observed under heat stress in wheat (*Triticum aestivum*, variety 'Gabo') (Saini et al., 1983). Also, in Arabidopsis heat stress reduced the total number of ovules and increased ovule abortion (Whittle et al., 2009). Hedhly et al. (2005) reported that the stigmas in peach (*Prunus persica* L.) at 30 °C lost their ability to support pollen germination after 3 days, whereas at 20 °C they were viable for 8 days. Contrary to our finding, Peet et al. (1998) reported in tomato (*Solanum lycopersicum* L.) that heat stress applied to the pollen donor plant before and during pollen release decreased seed number and fruit set more severely than heat stress applied to the developing ovule and to the style after pollen application. More is known of the effects of temperature stress on male reproductive structures (Barnabas et al., 2008; Thakur et al., 2010) due to ease in treating pollen to heat stress than female reproductive systems. As in wheat, heat stress during the period of microsporogenesis was found to induce tapetum degradation (Saini et al., 1984; Sakata et al., 2000), which leads to pollen sterility. Also, pollen dispersal was found to be reduced in rice and tomato under high temperatures which leads to poor anther dehiscence characterized by tight closure of the locules (Matsui and Omasa, 2002; Sato et al., 2002).

3.5. Relationship between parents and hybrids for flowering-period heat tolerance

From breeding point of view it is important to know if breeding of heat tolerant hybrids would require this trait to be bred in both parental lines or heat tolerance in any one of the parents would be adequate to breed heat tolerant hybrids. In the present investigation, different categories of F_1s generated using tolerant (*T*) and susceptible (*S*) parents were evaluated along with parental lines to reveal the relationship between hybrids and their parents. The control hybrids 9444 and 86M64 had SS of about 64 (Fig. 10). All the hybrids and parents with SS of ≥50 were considered as heat tolerant (*T*), and with SS of <50 as heat-susceptible (*S*). All the 14 $T \times S/S \times T$ hybrids were found tolerant with most of F1s having higher seed set than the tolerant parent, indicating that flowering period heat tolerance in pearl millet is a dominant trait. Eight hybrids out of 9 $T \times T$ were found tolerant, while one hybrid was found susceptible. The heat susceptibility of one $T \times T$ hybrid could not be explained. The dominant nature of heat tolerance in pearl millet implies that hybrid developed with one heat tolerant parent should be heat tolerant. From breeding perspective, the improvement of seed parent (B-lines) for heat tolerance will be a good option as this allows using all the available restorer parents for the development of high yielding heat tolerance hybrids. Overall, 87 percent of hybrids (20 out of 23 hybrids) had positive mid-parent heterosis (range of 4.2 to 93.5%) for seed set under high temperature stress at flowering, and only 3 hybrids had negative mid-parent heterosis ranging from −3.9 to −18.4%, indicating the opportunity of developing heat tolerant hybrids in pearl millet.

4. Conclusions

The present investigations on pearl millet revealed that the day-time maximum temperature beyond 42 °C and the associated increase in VPD during flowering time linearly reduced seed set in pearl millet crop; significant variability exists among pearl millet genotypes for seed set at maximum air temperature of ≥42 °C during flowering time and stable sources of flowering-period heat tolerance were identified; provided preliminary inputs on identification of both heat stress sensitive plant-stage and reproductive systems; and the information on the nature of inheritance of flowering period heat tolerance trait was generated. This information will help to develop a focused breeding strategy to deliver more heat tolerant pearl millet hybrids for summer cultivation and for yield-stability under high temperatures in future climate scenarios. The enhanced heat tolerance in pearl millet will also provide alternative cropping options for higher productivity in the hotter environments of the arid and semi-arid regions of the world.

Acknowledgements

The authors acknowledge the funding support provided by ICRISAT-Pearl Millet Hybrid Parents Research Consortium (ICRISAT-PMHPRC) for this study. Preparation of this publication has been undertaken as part of the CGIAR-Research Program on Dryland Cereals.

References

AICPMIP, 2013. Project Coordinator Review, Annual Workshop held at Junagadh, Gujarat, 22–24 March, 2013 , All India Coordinated Pearl Millet Improvement Project, Mandore, Jodhpur, ⟨http://aicpmip.res.in/pcr2013.pdf⟩.

Barnabas, B., Jager, K., Feher, A., 2008. The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ. 31, 11–38.

Basetti, P., Westgate, M.E., 1993. Water deficit affects receptivity of maize silks. Crop Sci. 33, 279–282.

Damptey, H.B., Aspinall, D., 1976. Water deficit and inflorescence development in *Zea mays* L. Ann. Bot. 40, 32–35.

Farrell, T.C., Fox, K.M., Williams, R.L., Fukai, S., 2006. Genotypic variation for cold tolerance during reproductive development in rice: screening with cold air and cold water. Field Crops Res. 98, 178–194.

Fischer, R.A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agri. Sci. 105, 447–461.

Hedhly, A., Hormaza, J.I., Herrero, M., 2005. The effect of temperature on pollen germination, pollen tube growth, and stigmatic receptivity in peach. Plant Biol. 7, 476–483.

Hedhly, A., Hormaza, J.I., Herrero, M., 2008. Global warming and plant sexual reproduction. Trends Plant Sci. 14, 30–36.

Herrero, M., 2003. Male and female synchrony and the regulation of mating in flowering plants. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358, 1019–1024.

Mahalakshmi, V., Bidinger, F.R., 1985. Water stress and time of floral initiation in pearl millet. J. Agric. Sci. 105, 437–445.

Maiti, R.K., Bidinger, F.R., 1981. Growth and Development of Pearl Millet Plant. Res. Bullet No. 6. International Crops research Institute for the Semi-Arid Tropics, Patancheru, AP, India.

Maiti R.K., Bisen, S., 1978. Studies on growth and development of panicles and grains in two contrasting genotypes of pearl millet. In: Physiology of Sexual Reproduction in Flowering Plants: Intern. Sym. Kalyani Publishers, New Delhi, pp. 118–124.

Matsui, T., Omasa, K., Horie, T., 2001. The difference in sterility due to high temperatures during the flowering period among *japonica* rice varieties. Plant Prod. Sci. 4, 90–93.

Matsui, T., Omasa, K., 2002. Rice (*Oryza sativa* L.) cultivars tolerant to high temperature at flowering: anther characteristics. Ann. Bot. 89, 683–687.

Nelson, G.C., Rosegrant, M.W., Koo, J., Robertson, R., Sulser, T., Zhu, T., Ringler, C., Msangi, S., Palazzo, A., Batka, M., Magalhaes, M., Valmonte-Santos, R., Ewing, M., Lee, D., 2009. Climate change impact on agriculture and costs of adaptation. In: Food Policy Report. International Food Policy Research Institute (IFPRI), Washington D.C, 19 pp.

Otegui, M.E., Melón, S., 1997. Kernel set and flower synchrony within the ear of maize: I. Sowing date effects. Crop Sci. 37, 441–447.

Owen, P.C., 1971. Responses of semi-dwarf wheat to temperature representing a tropical dry season II. Extreme temperature. Exp. Agric. 7, 43–47.

Peet, M.M., Sato, S., Gardner, R.G., 1998. Comparing heat stress effects on male-fertile and male-sterile tomatoes. Plant Cell Environ. 21, 225–231.

Prasad, P.V.V., Boote, K.J., Allen, L.H., Sheehy, J.E., Thomas, J.M.G., 2006. Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. Field Crops Res. 95, 398–411.

Rai, K.N., Gupta, S.K., Bhatacharjee, R., Kulkarni, V.N., Singh, A.K., Rao, A.S., 2009. Morphological characteristics of ICRISAT-bred pearl millet hybrid seed parents. J SAT Agri Res. 7, 1–7.

Reddy, A.R., Parthasarathy Rao, P., Yadav, O.P., Singh, I.P., Ardeshna, N.J., Kundu, K.K., Gupta, S.K., Sharma, R., Sawargaonkar, G., Malik, D.P., Shyam Moses, D., Reddy, S.K., 2013. Prospects for *kharif* (Rainy Season) and Summer Pearl Millet in Western India. Working Paper Series No. 36, International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India, 24 pp.

Saini, H.S., Aspinall, D., 1982. Abnormal sporogenesis in wheat (*Triticum aestivum* L.) induced by short periods of high temperature. Ann. Bot. 49, 835–846.

Saini, H.S., Sedgley, M., Aspinall, D., 1983. Effect of heat-stress during floral development on pollen-tube growth and ovary anatomy in wheat (*Triticum aestivum* L.). Aust. J. Plant Physiol. 10, 137–144.

Saini, H.S., Sedgley, M., Aspinall, D., 1984. Developmental anatomy in wheat of male-sterility induced by heat-stress, water deficit or abscisic-acid. Aust. J. Plant Physiol. 11, 243–253.

Sakata, T., Takahashi, H., Nishiyama, I., Higashitani, A., 2000. Effects of high temperature on the development of pollen mother cells and microspores in barley *Hordeum vulgare* L. J. Plant Res. 113, 395–402.

SAS Institute, 2003. The SAS Users Guide, Version 9.1. SAS Inst., Cary, NC.

Satake, T., Yoshida, S., 1978. High temperature induced sterility in *indica* rices at flowering. Jpn. J. Crop Sci. 47, 6–17.

Sato, S., Peet, M.M., Thomas, J.F., 2002. Determining critical pre- and post-anthesis periods and physiological processes in *Lycopersicon esculentum Mill.* exposed to moderately elevated temperatures. J. Exp. Bot. 53, 1187–1195.

Thakur, R.P., King, S.B., 1988. Ergot disease of pearl millet. In: Information Bulletin No. 24. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502324, India, 24 pp.

Thakur, R.P., Williams, R.J., 1980. Pollination effects on pearl millet ergot. Phytopathology 70, 80–84.

Thakur, P., Kumar, S., Malik, J.A., Berger, J.D., Nayyar, H., 2010. Cold stress effects on reproductive development in grain crops: an overview. Environ. Exp. Bot. 67, 429–443.

WMO, 2008. Measurement of humidity, chapter 4. In: Guide to Meteorological Instruments and Methods of Observation (CIMO Guide). World Meteorological Organization, Geneva, Switzerland, pp. 1–30.

Whittle, C.A., Otto, S.P., Johnston, M.O., Krochko, J.E., 2009. Adaptive epigenetic memory of ancestral temperature regime in *Arabidopsis thaliana*. Bot.-Bot. 87, 650–657.

Yadav, O.P., Rai, K.N., Rajpurohit, B.S., Hash, C.T., Mahala, R.S., Gupta, S.K., Shetty H.S., Bishnoi, H.R., Rathore, M.S., Kumar, A., Sehgal, S., Raghvani, K.L., 2012. Twenty-Five Years of Pearl Millet Improvement in India. All India Coordinated Pearl Millet Improvement Project, Jodhpur, India, 122pp.