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Study of Genetic Architecture for Maturity Traits in Relation to Supra-optimal Temperature Tolerance in Pearl Millet (*Pennisetum glaucum* (L.) R.Br.)

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ABSTRACT

Combining ability for maturity traits was studied in pearl millet. Ten parents selected through a field screening technique for their different response to supra-optimal temperature tolerance were crossed in a diallel manner. Forty-five F_1 hybrids along with their 10 parents were tested for their performance under supra-optimal temperature exposure at seedling stage with an objective to understand the nature of gene action and to identify parents for breeding programme. The experiment was conducted in three different environments created through different dates of sowing from May to July. The Griffings method of diallel analysis was used to obtain the genetic estimates. Variances due to general combining ability and specific combining ability for all the characters studied, viz., Seedling Thermo-tolerance Index (STI), Seed to Seedling Thermo-tolerance Index (SSTI), panicle emergence, effective tillers, plant height, ear length, ear weight, dry fodder yield, grain yield/plant and total biological yield/plant were highly significant in all the three environments (two stress and one normal) and on pooled basis indicating the importance of both additive and non-additive gene actions. The genotype CVJ-2-5-3-1-3 was identified as the best general combiner for STI as well as maturity traits, while, the genotype (77/371×BSECT CP-1) exhibited highest GCA effects for SSTI in both the stress environments. The genotype (77/371×BSECT CP-1) had high GCA effects for STI and SSTI as well as panicle emergence for earliness. Broad sense heritability (h^2_b) was quite high for all the characters studied. However, the estimates of additive genetic variance and narrow sense heritability for STI and SSTI also indicated good chances of effective selection. Preponderance of non-additive (dominance component) was recorded for all the characters suggested the success of hybrid breeding by making use of the expected heterosis. Heat tolerance indices STI and SSTI were not showing any perceptible correlation with either of the maturity traits suggested that pearl millet has great resilience and recovery after stress period during seedling stage.

Key words: Pearl millet (*Pennisetum glaucum*), combining ability, supra-optimal temperature tolerance, diallel analysis, gene action, maturity traits

INTRODUCTION

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is a robust, diploid, cross-pollinated crop with immense genetic diversity. It is a multipurpose cereal grown for grain, stover and green fodder and has a great potential for making bio-ethanol, the area that has not been explored adequately

(Chakauya and Tongoona, 2008). Pearl millet is one of the most important staple crop of millions of people in the semi-arid and arid regions of Asia and sub-Saharan Africa (Arya and Yadav, 2009), where environmental stress such as drought, high temperature and poor soil nutrient availability are endemic (Chakauya and Tongoona, 2008), although pearl millet shows considerable environmental adaptation to these areas. Stand establishment problems of pearl millet are severe constraints to successful production under subsistence farming conditions in the semi-arid tropics (Soman *et al.*, 1987). Transplanting sorghum and pearl millet varieties grown in nurseries has also shown to improve establishment in the field (Mapfumo, 2002; Murungu *et al.*, 2006). Failure to obtain adequate plant populations is often associated with adverse weather conditions occurring at critical times during the germination and seedling establishment process. Kamkar *et al.* (2006) revealed that germination rate of pearl millet increased linearly with temperature from a base of 10 to 12°C to a sharply defined optimum at 33 to 34°C and declined above. The temperature is one of the key climatic factors and has profound effect on the growth and development of the pearl millet. The soil temperatures in farmers' field in India and Africa commonly exceed 45°C and the temperatures as high as 60°C have occasionally been measured (Peacock and Ntshole, 1976; Soman *et al.*, 1981; Singh, 1993; Yadav *et al.*, 2006). The supra-optimal temperatures are known to be the most important cause of poor crop stands in farmers' field (Ong, 1983; Rai and Kumar, 1994). The rate of temperature change and the duration contribute to the intensity of heat stress. The most profound effect of high temperature has been well documented on early growth stages of pearl millet. To avoid future yield losses from higher than ceiling temperature due to climate change, crop improvement for heat tolerance is inevitable (Gholipour and Solotani, 2009). High temperature or heat being solely a climatic factor cannot be controlled by any artificial means which claims the modification in the response of plants to high temperature tolerant pearl millet varieties.

Information about genetic mechanisms and combining ability for supra-optimal temperature tolerance would be helpful in the development of a successful breeding programme. The purpose of this study was to investigate the nature and magnitude of different types of gene actions in controlling the inheritance of maturity traits including the ultimate end product fodder and grain yield in pearl millet from crosses of parental inbreds differing in their responses to supra-optimal temperature exposure at seedling stage and to suggest breeding strategies for the improvement thereof. The study also aimed at classification of the parental genotypes and their hybrids relative to the combining ability effects. Such classification would help identify good general combiners to be used as donor parents for the improvement of the traits and specific cross-combinations for the utilization of heterosis effect through the development of hybrid and/or isolation of superior segregates in advance generations of segregation.

MATERIALS AND METHODS

Ten genotypes of pearl millet selected on the basis of different response to supra-optimal temperature tolerance (Peacock *et al.*, 1993) screened earlier. Of these 10 genotypes, 7 tolerant genotypes, viz 'H77/833-2', 'G73-107', 'CVJ-2-5-3-1-3', '77/371×BSECT CP-1', '96AC-93', 'Togo-II' and '99HS-18' and three susceptible genotypes ('H77/29-2', '77/245' and '1305') were used as parents (Table 1) and crossed in a half-diallel mating system (excluding reciprocals). These ten parents alongwith 45 F₁ hybrids produced were tested for performance for heat tolerance at seedling stage as well as effect of supra optimal temperature exposure at seedling stage on maturity traits including fodder and grain yield in randomized block design with three replications and in three environments (two stress and one normal) created through dates of sowing 21st May (E₁),

Table 1: List of selected parents and their response to supra-optimal temperature at seedling stage

| Genotypes/parents | STI | SSTI | Response to supra-optimal temperature |
|-------------------|-------|-------|---------------------------------------|
| H77/833-2 | 96.94 | 78.97 | Tolerant |
| H77/29-2 | 49.19 | 35.19 | Susceptible |
| G73-107 | 89.56 | 83.10 | Tolerant |
| 77/245 | 48.49 | 38.58 | Susceptible |
| CVJ-2-5-3-1-3 | 95.78 | 75.79 | Tolerant |
| 1305 | 44.58 | 33.18 | Susceptible |
| 77/371×BSECT CP-1 | 92.36 | 87.12 | Tolerant |
| 96AC-93 | 91.16 | 83.80 | Tolerant |
| Togo-II | 90.71 | 72.33 | Tolerant |
| 99HS-18 | 94.27 | 79.56 | Tolerant |

13th June (E_2) and 17th July, 2005 (E_3) so as to conduct the experiment under different range of temperatures. Each genotype was grown in 3 rows each of 3 m length spaced 30 cm apart. Fifteen seeds were dibbled in each row at a distance of 10 cm each. The field was given medium irrigation and precisely leveled before sowing. The seeds were sown in the absence of a mechanized planter. Initially emphasis of observation centred on germination, survival and mortality of the seedlings and later on maturity traits. The seedlings were inspected every day in the morning. The seedlings which had died due to heat desiccation were spotted in each genotype on everyday basis. Such seedlings were marked by fixing a small wooden stick along their side as a check against the loss of dead seedlings. Process was continued up to a date till the surviving seedlings were established and there was no more mortality.

The experiment was conducted at the research area of Department of Plant Breeding of the University, Hisar (Lat: 29°10'N, Long: 75°46'E and 215.2 m above mean sea level), located in subtropical region in Haryana, India. Standard agronomic package of practices were taken to raise a healthy crop. The soil surface temperature was measured by a soil thermometer at soil surface, temperature at 5 and 100 cm (1 m) above the soil surface were recorded between 2:00 pm and 2:30 pm daily. A condition of no-drought was maintained in order to determine the exclusive effect of temperature at seedling stage. This was maintained by measuring the moisture status of the soil by gravimetric method on alternate days. Data were recorded on following traits, viz., Seedling Thermo-tolerance Index (STI), Seed to Seedling Thermo-tolerance Index (SSTI), panicle emergence (days), effective tillers/plant, plant height (cm), Ear length (cm), ear weight g plant⁻¹, dry fodder yield g plant⁻¹, grain yield g plant⁻¹ and total biological yield g plant⁻¹. The data were recorded on 10 random plants per replication. Seedling Thermo-tolerance Index (STI) was calculated as the ratio of number of seedling survived to the number of seedling emergence, expressed in percentage. Seed to Seedling Thermo-tolerance Index (SSTI) was calculated as the ratio of seedling survival to the number of seedling expected to emerge, expressed in percentage (Singh, 1993; Yadav *et al.*, 2006, 2011). The SSTI is an extension of STI by taking expected germination into account. It was necessary to correct the effect of under Soil Mortality (USM). The germination under monsoon environment of the same lot of spare seed was taken as expected germination in this experiment. Analysis of variance for Randomized Block Design (RBD), diallel analysis of Griffing's Method 2, Model 1, variances due to GCA and SCA and correlations among the various characters were calculated in relation to thermo-tolerance indices (Sharma, 1998).

RESULTS AND DISCUSSION

The excessive heat (soil temperature up to 63.0°C in E_3) about 18°C higher than the normal atmospheric temperature (Fig. 1a and b) was responsible for mortality of seedlings. Many seedlings

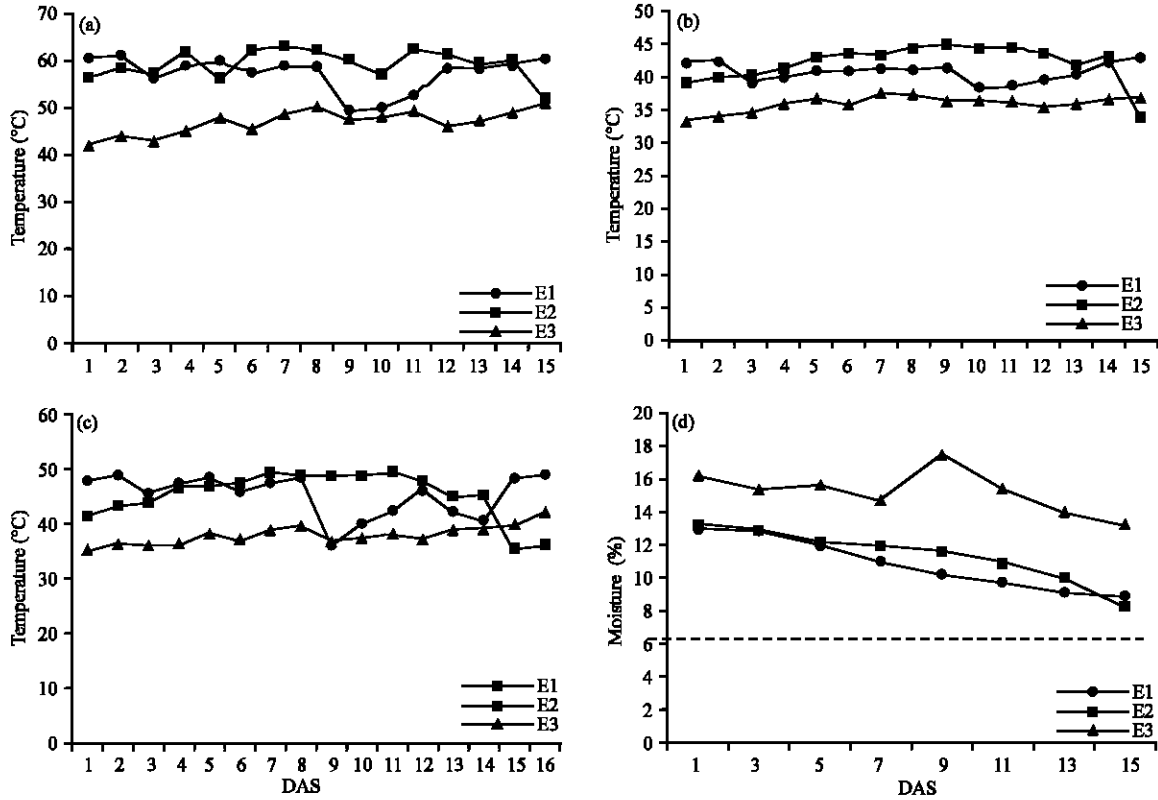


Fig. 1(a-d): (a) Soil surface temperature (b) Air temperature (c) Temperature 5 cm above the soil surface and (d) Soil moisture status in different environments

were found desiccated at the point of contact besides the desiccation at the tips. The temperature around the tip level (5 cm above the soil surface) also reached up to 50°C (Fig. 1c). It could, therefore be concluded that the seedlings had to survive in a really high temperature. The moisture level remained above the permanent wilting point (Fig. 1d). Therefore, drought effect was not in the play. The Seedling Thermo-tolerance Index (STI) of the hybrids ranged from 53 to 82. Among the hybrids 'H77/29-2×77/245' and 'H77/833-2×96AC-93' were identified as highly tolerant genotypes. Seed to Seedling Thermo-tolerance Index (SSTI) which was expected to be more rigorous index deviated the values from STI according to variation in germination under normal environment (E₃). The reductions in values were not strictly proportional to the STI. SSTI values ranged between 46 and 73. The analysis of variance for ten different characters in three different environments (two stressed and one normal) was carried out and the results showed significant genotypic differences for all the characters (Table 2). Significance of the mean squares associated with parents vs. hybrids indicated presence of average heterosis for all the characters. The results obtained from analysis of variance for combining ability revealed that both additive (GCA) and non-additive (SCA) genetic variances were highly significant in all the three environments and pooled basis played an important role in the genetic control of the maturity traits. Showemimo *et al.* (2006) and Mahdy *et al.* (2011) reported similar observations in sorghum with emphasis on quantitative and complex traits like yield and yield components. Krishnaiah *et al.* (2002) reported the importance of both additive and non-additive type of gene action for the

Table 2: Analysis of variance (pooled) for half-diallel for different characters

| Source of variation | | D.F | STI | SSTI | Panicle emergence | Effective tillers | Plant height | Ear length | Ear weight | Dry fodder yield | Grain yield/plant | Biological yield/plant |
|----------------------------|-----|------------|-------------|------------|-------------------|-------------------|--------------|------------|-------------|------------------|-------------------|------------------------|
| Environments | 2 | 47160.73** | 108068.12** | 13305.75** | 10.98** | 96007.59** | 418.30** | 3568.02** | 8301.47** | 4205.32** | 8870.16** | |
| Blocks within Environments | 6 | 7.93 | 7.56 | 12.91 * | 1.47** | 292.55** | 3.81 | 8.84 | 55.28 | 5.27 | 54.69 | |
| Treatments | 54 | 417.24** | 236.65** | 103.84** | 1.67** | 7267.45** | 66.48** | 1724.50** | 8302.74** | 1069.47** | 16911.37** | |
| Parents | 9 | 855.52** | 232.61** | 105.27** | 1.13** | 3800.26** | 95.18** | 382.33** | 661.12 | 89.64** | 1814.16** | |
| Hybrids | 44 | 336.38** | 235.45** | 72.32** | 1.81** | 2233.96** | 39.55** | 828.16** | 4944.16** | 542.43** | 9089.94** | |
| Parents Vs. Hybrids | 1 | 30.59 * | 325.58** | 1478.07** | 0.54** | 259945.22** | 993.00** | 53242.98** | 224854.65** | 33077.94** | 496929.08** | |
| Treatment×Environments | 18 | 122.58** | 80.45** | 24.07** | 0.41** | 306.90** | 3.35** | 109.81** | 100.26** | 121.60** | 248.48** | |
| Parent×Environments | 18 | 217.14** | 68.02** | 23.13** | 0.24** | 211.87** | 1.48 | 19.24 | 18.41 | 12.90** | 43.11 | |
| Hybrids×Environments | 88 | 105.81** | 82.59** | 23.79** | 0.44** | 284.72** | 3.53** | 123.95** | 109.39** | 138.64** | 280.94** | |
| Parent vs. Hybrids×Env. | 2 | 9.76 | 98.31** | 44.88** | 0.64** | 2138.31** | 12.22** | 303.04** | 435.17** | 349.70** | 668.95** | |
| Error | 324 | 7.41 | 4.37 | 5.58 | 0.06 | 48.35 | 2.01 | 13.86 | 27.38 | 5.31 | 45.12 | |
| Total | 494 | 268.30 | 483.94 | 74.30 | 0.38 | 1285.47 | 11.06 | 236.16 | 981.75 | 164.06 | 1969.11 | |
| GCA | 9 | 329.60** | 161.80** | 72.41** | 1.02 | 1692.71** | 78.25** | 491.85** | 3194.66** | 362.37** | 5952.85 | |
| SCA | 45 | 100.98** | 62.30** | 27.06** | 0.46 | 2568.44** | 10.94** | 591.43** | 2682.16** | 355.32** | 5573.98 | |
| Environments | 2 | 15720.24** | 36022.71** | 4435.25** | 3.66 | 32002.53** | 139.43** | 1189.34** | 2767.16** | 1401.77** | 2956.72 | |
| GCA×Environments | 18 | 90.62** | 52.92** | 13.13** | 0.11 | 165.48** | 2.11** | 36.89** | 24.45** | 40.59** | 64.63 | |
| SCA×Environments | 90 | 30.91** | 21.60** | 7.00** | 0.14 | 89.66** | 0.92 * | 36.55** | 35.22** | 40.52** | 86.47 | |
| Error | 324 | 2.47 | 1.46 | 1.86 | 0.02 | 16.12 | 0.67** | 4.62 | 9.13 | 1.77 | 15.04 | |

*Significant at p = 0.05, **Significant at p = 0.01

inheritance. Chotaliya *et al.* (2010) reported that majority of superior crosses were obtained from high x high or high x low general combiners in pearl millet.

Combining ability effects

General combining ability: Hybridization is the most potent technique for breaking the yield ceiling and evolving varieties having high yield potential. Success in any breeding programme involving hybridization depends on the choice of parents. Selection of parents based on their performance per se alone, may not always be a sound procedure, since phenotypically superior genotypes may yield inferior hybrids and/or poor recombinants in the segregating generations. It is, therefore, essential that parents should be selected on the basis of their genetic worth. High GCA-effects of the parents are mainly due to additive and additive×additive type of gene action which is fixable in the segregating generations. Thus, to enable isolation of superior segregates in the subsequent generations, selection of parents for hybridization should be made on the basis of their GCA-effects (Krishnaiah *et al.*, 2002; Banerjee and Kole, 2009).

The parent ‘CVJ-2-5-3-1-3’ emerged as the best general combiner for seedling thermo-tolerance index (STI) and parent ‘(77/371×BSECT CP-1)’ for Seed to Seedling Thermo-tolerance Index (SSTI) which exhibited highest GCA effect (Table 3). The parent ‘CVJ-2-5-3-1-3’ was also good general combiner for plant height, ear head length, dry fodder yield and total biological yield. The parents ‘(77/371×BSECT CP-1)’, ‘CVJ-2-5-3-1-3’ and ‘96AC-93’ showed the good GCA for both STI and SSTI. Two parents ‘1305’ and ‘77/245’ were identified as poor general combiners. For panicle emergence the negative values of GCA are considered favourable as an indication of earliness. The parents H77/833-2 (77/371×BSECT CP-1) and 96AC-93 on pooled basis had significant and negative GCA effects and were, therefore, considered as good general combiners for earliness whereas, ‘H77/29-2’ and ‘G73-107’ were good general combiners for lateness. Positive and significant highest GCA effects for number of effective tillers/plant were recorded for the parent ‘1305’ and ‘H77/833-2’ followed by ‘CVJ-2-5-3-1-3’ whereas the parent ‘99HS-18’ was poorest for effective tillers. CVJ-2-5-3-1-3, H77/29-2, Togo-II and G73-107 had significant and positive GCA effects indicating good general combining abilities for plant height in pearl millet.

The parent CVJ-2-5-3-1-3 was found to be the most desirable in respect of the ear length as it possesses highest positive GCA effect. The parent Togo-II, 1305 and G73-107 also showed significant positive GCA effects as well. High significant and positive GCA effects were recorded for

Table 3: Estimates of GCA effects (pooled)

| Parents | STI | SSTI | Panicle emergence | Effective tillers | Plant height | Earhead length | Earhead weight | Dry fodder yield | Grain yield | Biological yield |
|-------------------|---------|---------|-------------------|-------------------|--------------|----------------|----------------|------------------|-------------|------------------|
| H77/833-2 | 3.51** | 1.15** | -1.68** | 0.22** | -4.36** | -0.90** | -1.89** | -6.99** | -2.06** | -8.88** |
| H77/29-2 | -1.81** | 0.82** | 1.85** | -0.05 | 8.94** | -0.34 | -4.58** | -12.37** | -3.40** | -16.95** |
| G73-107 | 0.78* | 2.46** | 1.63** | 0.08* | 4.65** | 0.57** | 1.22* | 2.21** | 0.49 | 3.43** |
| 77/245 | -8.37** | -4.30** | -0.14 | -0.05 | -8.97** | -1.09** | -1.03* | -0.23 | -0.64* | -1.26 |
| CVJ-2-5-3-1-3 | 5.03** | 2.02** | -0.22 | 0.12** | 9.78** | 3.02** | 1.92** | 11.30** | 1.49** | 13.22** |
| 1305 | -6.77** | -6.67** | 0.39 | 0.22** | -6.50** | 1.04** | 5.65** | 12.71** | 5.78** | 18.36** |
| 77/371×BSECT CP-1 | 3.77** | 3.27** | -1.94** | -0.04 | -2.25* | -1.33** | -4.88** | -5.81** | -3.96** | -10.69** |
| 96AC-93 | 2.34** | 2.11** | -1.63** | -0.01 | 1.46 | -1.42** | 1.11* | -4.05** | -0.18 | -2.95** |
| Togo-II | -1.15** | -0.90** | 1.60** | -0.16** | 4.68** | 1.46** | 5.25** | 12.74** | 4.38** | 17.99** |
| 99HS-18 | 2.66** | 0.05 | 0.15 | -0.33** | -7.44** | -1.01** | -2.76** | -9.50** | -1.91** | -12.27** |

*Significant at p = 0.05. **Significant at p = 0.01

the parents 1305 and Togo-II for ear weight/plant on pooled basis. For dry fodder yield the parents Togo-II was identified as best general combiner whereas, 1305 and CVJ-2-5-3-1-3 appeared to be close runners up. The estimate of General Combining Ability (GCA) effects in respect of grain yield/plant indicated that parents 1305 and Togo-II exhibited high positive GCA effects. The parents 1305, Togo-II and CVJ-2-5-3-1-3 were the most desirable parents in respect of the total biological yield/plant (excluding roots).

Specific combining ability: The magnitude of SCA effects, of course differed for specific crosses in different environment but the direction (+ve or -ve) generally remained the same. On pooled basis ten cross combinations, namely, 'H77/29-2×1305', 'H77/29-2×CVJ-2-5-3-1-3', '1305×99HS-18', '(77/371×BSECT CP-1)×Togo-II', '1305×96AC-93', 'H77/833-2×96AC-93', 'G73-107×77/245', 'G73-107×1305', 'H77/833-2×77/245' and 'G73-107×(77/371×BSECT CP-1)' showed high significant positive values of specific combining ability effects for STI on pooled basis (Table 4). As regards the SCA effects for SSTI the results were almost similar to STI. On pooled basis top ten cross combinations i.e., H77/833-2×96AC-93, 1305×96AC-93, 1305×99HS-18 (77/371×BSECT CP-1)×Togo-II, H77/29-2×CVJ-2-5-3-1-3, H77/833-2×(77/371×BSECT CP-1), G73-107×(77/371×BSECT CP-1), G73-107×77/245, H77/833-2×H77/29-2 and H77/29-2×Togo-II were identified as the crosses having the positive significant SCA effects for SSTI. While the cross H77/833-2×1305 was identified as the poorest specific cross combination for SSTI.

The best specific cross for STI 'H77/29-2×1305' involves both the susceptible parents whereas, crosses H77/29-2×CVJ-2-5-3-1-3, 1305×99HS-18, 1305×96AC-93, G73-107×77/245, G73-107×1305, H77/833-2×77/245 and which involve one of the susceptible parents among top ten for STI. Similarly, crosses 1305×96AC-93, 1305×99HS-18, H77/29-2×CVJ-2-5-3-1-3, G73-107×77/245, H77/833-2×H77/29-2 and H77/29-2×Togo-II involve one of the susceptible parents for SSTI. It is a re-assertion of the fact the heat tolerant genes are also contributed by parents with poor performance per se. This indicates a complex nature of gene distribution and the control system for the trait. The contribution of positive genes by the poor performer has a special significance in plant breeding. We can expect the genes being disbursed in large germplasm and coming from any parent. This would also suggest that in absence of particular sources, the trait could be tested in hybrids as a qualifying standard.

Of the 10 F₁ hybrids each for STI and SSTI showing significant and positive SCA-effects, eight hybrids for STI and seven hybrids for SSTI involved one or both of the parents having low GCA-effect for the trait. This indicates that diversity in parental GCA effects played an important role for the production of hybrids with significant positive SCA-effects for STI and SSTI in pearl millet. The diversity in parental GCA-effects was necessary for the development of specific combinations with high value. This kind of superiority of High×Low crosses might involve dominant×recessive type of gene interaction and, therefore, might tend to be unfixable. Crosses involving at least one parent with high GCA-effect could produce good segregates, only if, the additive genetic system present in the good general combiner and the complementary epistatic effects in the other act in the same direction to maximize the desirable plant attribute (Chotaliya *et al.*, 2010).

Remaining crosses have significant and positive SCA-effects involving both the parents with high GCA-effects for STI and SSTI. Superiority of such hybrid might be due to additive and additive×additive type of interaction which is fixable. Therefore, more heat tolerant genotypes could be obtained in the segregating generations of these crosses. In such a situation the estimation of

Table 4: Estimates of SCA effects (pooled) for maturity traits

| Genotypes | STI | SSTI | Panicle emergence | Effective tillers | Plant height | Ear head length | Ear head weight | Dry fodder yield | Grain yield/plant | Biological yield/plant |
|-------------------------------|----------|----------|-------------------|-------------------|--------------|-----------------|-----------------|------------------|-------------------|------------------------|
| H77/833-2×H77/29-2 | 3.75** | 6.40** | -2.30* | 0.26** | -12.74** | 0.44 | 0.39 | 3.25 | -2.32** | 3.64 |
| H77/833-2×G73-107 | 4.63** | 2.73** | -0.63 | -0.05 | 0.16 | -0.14 | 3.12* | -8.47** | 0.18 | -5.34* |
| H77/833-2×77/245 | 8.02** | 0.44 | 1.36 | -0.10 | 6.94** | 0.22 | 2.60 | 5.30** | 2.96** | 7.90** |
| H77/833-2×CVJ-2-5-3-1-3 | -1.73 | 1.53 | -1.78 | 0.08 | 0.03 | 0.86 | 5.46** | 15.02** | 6.98** | 20.49** |
| H77/833-2×1305 | -22.84** | -16.75** | -2.83** | 1.23** | 3.93 | 2.17** | 15.78** | 51.58** | 11.18** | 67.37** |
| H77/833-2×(77/371×BSECT CP-1) | -1.06 | 8.37** | -2.95** | -0.07 | 2.98 | -0.52 | 6.32** | 1.56 | 4.47** | 7.88** |
| H77/833-2×96AC-93 | 11.16** | 14.70** | -0.81 | -0.14 | 6.48* | -0.07 | 3.47* | -5.53** | -0.45 | -2.07 |
| H77/833-2×Togo-II | -5.00** | -3.82** | -0.05 | -0.33** | 32.68** | 0.42 | 7.66** | 18.83** | 5.62** | 26.49** |
| H77/833-2×99HS-18 | -12.89** | -2.64** | 1.52 | 0.19* | 28.82** | 2.20** | 4.57** | 13.34** | 6.15** | 17.90** |
| H77/29-2×G73-107 | -1.84 | 0.28 | 1.18 | 0.28** | 4.00 | -0.88 | -5.54** | -12.52** | -2.94** | -18.06** |
| H77/29-2×77/245 | 2.82** | 3.37** | -0.28 | -0.09 | -8.03** | 0.32 | 1.51 | 5.24** | -0.75 | 6.75** |
| H77/29-2×CVJ-2-5-3-1-3 | 14.04** | 9.68** | 0.14 | -0.48** | 15.60** | 1.12* | 1.35 | 7.53** | 2.37** | 8.88** |
| H77/29-2×1305 | 14.67** | 3.24** | -2.36** | 0.50** | 1.18 | 1.38* | 21.47** | 39.82** | 15.46** | 61.30** |
| H77/29-2×(77/371×BSECT CP-1) | -1.01 | -0.87 | -1.37 | -0.27** | 11.61** | 0.73 | 7.53** | 11.53** | 3.12** | 19.06** |
| H77/29-2×96AC-93 | -9.28** | -8.19** | -1.12 | -0.01 | 1.01 | 1.20* | 7.06** | 6.87** | 8.77** | 13.93** |
| H77/29-2×Togo-II | 1.53 | 5.81** | -2.02* | 0.26** | 31.92** | 1.22* | 5.34** | -11.25** | 2.46** | -5.91* |
| H77/29-2×99HS-18 | -3.03** | -4.18** | -1.12 | -0.08 | 21.69** | -0.40 | 9.47** | 16.15** | 7.16** | 25.62** |
| G73-107×77/245 | 11.85** | 6.89** | -1.83* | 0.11 | -2.57 | 0.86 | 0.97 | 19.66** | -0.28 | 20.63** |
| G73-107×CVJ-2-5-3-1-3 | -3.09** | -1.01 | -4.86** | 0.11 | 11.22** | 0.16 | 5.75** | -0.79 | 5.99** | 4.96 |
| G73-107×1305 | 10.32** | 1.21 | 2.42** | 0.00 | 3.22 | 1.10* | 11.75** | 12.96** | 8.67** | 24.70** |
| G73-107×(77/371×BSECT CP-1) | 5.33** | 8.20** | -3.81** | -0.07 | 11.37** | 0.30 | 6.21** | 22.30** | 1.77* | 28.52** |
| G73-107×96AC-93 | -1.53 | -0.04 | 2.10* | 0.25** | 25.56** | 1.60** | 8.99** | 15.52** | 8.37** | 24.50** |
| G73-107×Togo-II | -10.14** | -9.79** | -2.02* | -0.16 | 36.42** | 1.00 | 9.57** | 17.23** | 8.76** | 26.80** |
| G73-107×99HS-18 | -6.23** | -2.66** | -4.68** | 0.14 | 21.87** | 0.43 | 6.47** | 31.63** | 4.92** | 38.11** |
| 77/245×CVJ-2-5-3-1-3 | 1.19 | 2.93** | 0.02 | 0.53** | 6.21* | 0.46 | 24.76** | 38.93** | 18.74** | 63.69** |
| 77/245×1305 | 4.50** | 1.83* | -2.15* | -0.13 | 1.21 | -0.66 | 6.27** | 10.00** | 6.79** | 16.27** |
| 77/245×(77/371×BSECT CP-1) | -4.73** | -1.87* | -1.38 | -0.10 | 11.99** | 0.35 | -10.91** | -26.77** | -7.55** | -37.69** |
| 77/245×96AC-93 | -4.61** | -1.69* | -2.24* | -0.49** | 9.01** | -0.11 | 11.34** | 15.63** | 8.70** | 26.97** |

Table 4: Continue

| Genotypes | STI | SSTI | Panicle emergence | Effective tillers | Plant height | Ear head length | Ear head weight | Dry fodder yield | Grain yield/plant | Biological yield/plant |
|-----------------------------------|---------|----------|-------------------|-------------------|--------------|-----------------|-----------------|------------------|-------------------|------------------------|
| 77/245×Togo-II | -5.83** | -2.14** | -1.14 | 0.20* | 31.22** | 3.10** | 0.91 | 16.41** | 1.20 | 17.31** |
| 77/245×99HS-18 | -4.16** | -2.71** | -2.02* | -0.07 | 26.79** | 1.42** | -1.98 | -8.80** | 0.84 | -10.78** |
| CVJ-2-5-3-1-3×1305 | -0.97 | 0.49 | -2.73** | 0.05 | 2.37 | 1.26* | 0.21 | 13.50** | -1.66 | 13.71** |
| CVJ-2-5-3-1-3×(77/871×BSECT CP-1) | -7.81** | -13.29** | -1.07 | 0.50** | -3.06 | -1.28* | 11.22** | 12.28** | 7.87** | 23.50** |
| CVJ-2-5-3-1-3×96AC-93 | 2.72** | 2.85** | 1.51 | -0.21* | 19.43** | 1.73** | 4.06** | 14.18** | 3.81** | 18.23** |
| CVJ-2-5-3-1-3×Togo-II | -2.87** | -2.95** | 2.06* | 0.16 | 16.73** | -0.08 | -6.99** | 3.54 | -4.01** | -3.46 |
| CVJ-2-5-3-1-3×99HS-18 | 0.78 | 3.09** | -2.16* | -0.36** | 5.25 | -1.03* | -5.04** | 11.22** | -3.26** | 6.18* |
| 1305×(77/871×BSECT CP-1) | -8.06** | -2.22** | -1.46 | 0.15 | 9.92** | 0.15 | 0.83 | 10.68** | 1.22 | 11.51** |
| 1305×96AC-93 | 13.75** | 12.51** | -3.99** | -0.24* | 11.77** | -1.48** | -3.33* | -12.11** | -4.53** | -15.43** |
| 1305×Togo-II | -2.40* | -1.46 | 5.22** | 0.13 | 15.02** | 1.98** | 15.90** | 7.93** | 13.29** | 23.82** |
| 1305×99HS-18 | 14.30** | 10.55** | -2.10* | -0.78** | 19.82** | 2.10** | 1.88 | 1.22 | 3.33** | 3.10 |
| (77/871×BSECT CP-1)×96AC-93 | 0.07 | -4.38** | -0.78 | -0.50** | 17.02** | 2.42** | 1.84 | 5.05* | 3.58** | 6.89** |
| (77/871×BSECT CP-1)×Togo-II | 13.94** | 9.90** | -0.23 | 0.26** | 14.40** | 0.35 | 16.29** | 39.97** | 11.53** | 56.26** |
| (77/871×BSECT CP-1)×99HS-18 | 4.04** | 4.68** | 3.11** | -0.30** | 11.69** | 1.67** | -4.85** | -15.16** | -3.59** | -20.01** |
| 96AC-93×Togo-II | -5.24** | -6.68** | -0.87 | 0.51** | 8.23** | 0.17 | 8.87** | 50.15** | 5.92** | 59.01** |
| 96AC-93×99HS-18 | -2.14* | 0.75 | 2.81** | -0.28** | 25.75** | 1.72** | -5.68** | -16.47** | -3.47** | -22.16** |
| Togo-II×99HS-18 | -7.00** | -7.26** | 1.02 | 0.09 | -29.96** | 0.11 | 7.15** | 4.00* | 6.06** | 11.15** |

*Significant at p = 0.05; **Significant at p = 0.01

GCA and SCA assume added significance. Pure additive action at individual loci was coupled with favourable additive×additive interaction could produce heterotic combinations. Also, the heterosis was related to GCA of parents and SCA of crosses. Therefore, superior recombinants with high STI and SSTI could be isolated from these crosses as these involved both the parents with high GCA effects, although the chances would depend on linkage relationship. It was a matter of enormous importance that the best specific cross 'H77/29-2×1305' had resulted from the two susceptible parents. That would mean the genes for heat tolerance are distributed across the parents.

For panicle emergence the negative values of SCA indicates for early flowering. The cross G73-107×CVJ-2-5-3-1-3 was identified as best specific cross combination for earliness followed by G73-107×99HS-18 and 1305×96AC-93 on pooled basis whereas, specific cross 1305×Togo-II was identified for extreme lateness. Among the crosses exhibiting significant positive SCA effects for number of effective tillers/plant H77/833-2×1305 showed highest positive SCA effects. The SCA effects for plant height revealed that 29 cross combinations showed significant and positive SCA effects on pooled basis. The cross G73-107×Togo-II showed highest significant and positive SCA effects for tallness followed by H77/833-2×Togo-II, H77/29-2×Togo-II and 77/245×Togo-II whereas, the cross combination Togo-II×99HS-18 was identified for dwarfness. The magnitude of SCA effects for ear length revealed that seventeen crosses exhibited significant positive SCA effects on pooled basis. The cross combination 77/245×Togo-II was identified as best specific combiner followed by (77/371×BSECT-CP-1)×96AC-93 and H77/833-2×99HS-18 for ear length.

Among 27 crosses which showed significant positive SCA effects for ear weight /plant, cross combinations 77/245×CVJ-2-5-3-1-3 showed highest SCA effects followed by H77/29-2×1305 (77/371×BSECT CP-1)×Togo-II, 1305×Togo-II and H77/833-2×1305. For dry fodder yield/plant a consideration of SCA effects revealed that out of 45 cross combinations, 31 crosses exhibited significant positive SCA effects. The cross H77/833-2×1305 appeared as best specific combination for dry fodder yield. The estimate of specific combining ability (SCA) effects in respect of grain yield/plant indicated that 29 crosses exhibited significant positive SCA effects. The cross 77/245×CVJ-2-5-3-1-3 identified as best specific cross combination followed by H77/29-2×1305, 1305×Togo-II (77/371×BSECT CP-1) ×Togo-II and H77/833-2×1305 for grain yield/plant. The magnitude of SCA effects for total biological yield g plant⁻¹ revealed that 32 cross combinations exhibited significant positive SCA effects. The cross H77/833-2×1305 was identified as best specific cross combination.

Estimates of the GCA-effects of 10 parental genotypes for all characters revealed that none of the parents had good general combining ability for all the maturity traits studied. Therefore, to determine the best combiner across the characters, each parent was given a score for each trait based on their GCA-effects. A score of '+1' was assigned for significant GCA-effect in desirable direction, while '-1' for significant GCA-effect in undesirable direction. A score of '0' was assigned for non-significant GCA-effect (Banerjee and Kole, 2009). The scores revealed that CVJ-2-5-3-1-3 appeared as best overall general combiner followed by G73-107, whereas, the parent 99HS-18 and 77/245 were the poorest overall general combiners.

Nature of gene action: The relative magnitudes of the respective variances for GCA and SCA (Table 5), however, showed that the later was more important for the traits, such as, Seedling Thermo-tolerance Index (STI), Seed to Seedling Thermo-tolerance Index (SSTI), panicle emergence, number of effective tillers/plant, plant height, ear length, ear weight/plant, dry fodder yield/plant, grain yield/plant and total biological yield/plant indicating that non-additive genetic variance (dominance variance) was mainly responsible in the inheritance of these traits.

Table 5: Genetic components (pooled) for different characters

| Genetic components | STI | SSTI | Panicle emergence | Effective tillers/plant | Plant height | Ear length | Ear weight | Dry fodder yield | Grain yield/plant | Biological yield/plant |
|--------------------|--------|--------|-------------------|-------------------------|--------------|------------|------------|------------------|-------------------|------------------------|
| σ^2_g | 9.09 | 4.45 | 1.96 | 0.03 | 46.57 | 2.16 | 13.53 | 88.49 | 10.02 | 164.94 |
| σ^2_s | 32.84 | 20.28 | 8.40 | 0.15 | 850.77 | 3.42 | 195.60 | 891.01 | 117.85 | 1852.98 |
| σ^2_l | 349.28 | 800.47 | 98.52 | 0.08 | 710.81 | 3.08 | 26.33 | 61.29 | 31.11 | 65.37 |
| σ^2_{gl} | 7.35 | 4.29 | 0.94 | 0.01 | 12.45 | 0.12 | 2.69 | 1.28 | 3.23 | 4.13 |
| σ^2_{sl} | 28.44 | 20.14 | 5.14 | 0.12 | 73.55 | 0.25 | 31.93 | 26.09 | 38.75 | 71.43 |
| σ^2_e | 2.47 | 1.46 | 1.86 | 0.02 | 16.12 | 0.67 | 4.62 | 9.13 | 1.77 | 15.04 |
| σ^2_A | 18.17 | 8.91 | 3.92 | 0.06 | 93.14 | 4.31 | 27.07 | 176.97 | 20.03 | 329.88 |
| σ^2_D | 32.84 | 20.28 | 8.40 | 0.15 | 850.77 | 3.42 | 195.60 | 891.01 | 117.85 | 1852.98 |
| σ^2_p | 89.27 | 55.07 | 20.26 | 0.35 | 1046.03 | 8.77 | 261.91 | 1104.48 | 181.64 | 2273.46 |
| h^2_{ns} | 0.20 | 0.16 | 0.19 | 0.16 | 0.09 | 0.49 | 0.10 | 0.16 | 0.11 | 0.15 |
| GCA/SCA ratio | 0.28 | 0.22 | 0.23 | 0.19 | 0.05 | 0.63 | 0.07 | 0.10 | 0.09 | 0.09 |

Mahdy *et al.* (2011) also reported non-additive effects of genes for these traits in sorghum. Izge *et al.* (2007) reported panicle emergence, number of effective tillers/plant, plant height, grain yield non-additive gene genetic variance whereas, panicle length, no. of seeds/panicle and 1000 grain weight were predominantly under the control of additive genetic effects. Chotaliya *et al.* (2010) also observed non-additive gene action for grain yield/plant and fodder yield/plant but additive for plant height, ear length and ear weight. However, for number of effective tillers both additive and non-additive gene action were reported by them.

The preponderance of non-additive interaction as seen in this analysis is also some times caused due to presence of epistasis and/or a correlated gene distribution. A further bias may also be caused due to interaction of non-additive variance with the environment. Realizing that individual components of genetic variance also interact with environment and can thus be biased, it becomes important to evaluate these interactions also. Both the additive and dominance components can interact with changes in the environment. Predictability factor calculated from GCA and SCA variances reflects the degree to which character is transmitted to the progeny. The closer is the ratio to unity, the greater is the predictability of progeny performance based on the GCA-effect. Higher the involvement of additive gene actions in the inheritance of character, better will be the transmission of the trait to the progeny (Banerjee and Kole, 2009).

The $\sigma^2_{GCA}/\sigma^2_{SCA}$ ratio was low for Seedling Thermo-tolerance Index (STI), seed to seedling thermo-tolerance index (SSTI), panicle emergence, number of effective tillers, plant height, ear weight, dry fodder yield, grain yield and total biological yield, the low ratio as well as the higher magnitude of dominance component of variance (σ^2_D) than additive component of variance (σ^2_A) would confirm that most of the characters were predominantly under the control of non-additive genetic variance. This should facilitate the success of hybrid breeding by making use of the expected heterosis. The heterosis breeding has been the hallmark of genetic improvement of pearl millet for grain productivity and other traits. The results in this investigation suggest that hybrid breeding could probably hold true for thermo-tolerance too. However, the reverse was true for panicle emergence and ear length where there was a preponderance of additive genetic variance. Here the pedigree breeding for these two characters would expect to be more successful.

The additive and dominance components were used for the estimation of heritability in broad sense as well as narrow sense. Expected in the estimates narrow sense heritability were also very high for these characters. The selection in the segregating population is expected to be really effective. These estimates for STI, SSTI and panicle emergence were of moderate magnitude which

Table 6: Pooled correlation coefficients among various characters in all the three environments

| Characters | STI | SSTI | Panicle emergence | Effective tillers | Plant height | Ear length | Ear weight | Dry fodder yield | Grain yield/plant | Biological yield/plant |
|------------------------------|-------|---------|-------------------|-------------------|--------------|------------|------------|------------------|-------------------|------------------------|
| STI | 1.000 | 0.837** | -0.215 | -0.211 | 0.030 | -0.007 | -0.043 | -0.101 | -0.111 | -0.084 |
| SSTI | | 1.000 | -0.247 | -0.268* | 0.184 | -0.017 | -0.066 | -0.129 | -0.144 | -0.112 |
| Panicle emergence | | | 1.000 | -0.150 | -0.269* | 0.022 | -0.329* | -0.337* | -0.280* | -0.341* |
| Effective tillers/plant | | | | 1.000 | -0.012 | 0.170 | 0.366** | 0.405** | 0.323* | 0.401** |
| Plant height | | | | | 1.000 | 0.650** | 0.603** | 0.596** | 0.619** | 0.610** |
| Ear length | | | | | | 1.000 | 0.608** | 0.671** | 0.648** | 0.664** |
| Ear weight/plant | | | | | | | 1.000 | 0.910** | 0.984** | 0.957** |
| Dry fodder yield/plant | | | | | | | | 1.000 | 0.907** | 0.991** |
| Grain yield/plant | | | | | | | | | 1.000 | 0.950** |
| Total biological yield/plant | | | | | | | | | | 1.000 |

*Significant at p = 0.05; **Significant at p = 0.01

also indicated good chances of effective selection. The values of broad sense heritability (h^2_{bs}) for most other characters were quite high. This would be of little significance or for the fixation of genes is concerned but would certainly suggest the adoption of heterotic breeding as a method. The analysis of genetic components overwhelmingly supported the method of hybrid breeding as the principal approach for genetic improvement in pearl millet.

Correlations: The pooled correlations among the characters were calculated (Table 6) around heat tolerance indices (STI and SSTI) with a view to find, whether, there was any association of these characters with maturity traits. Correlation coefficients were calculated while evaluating the diallel progenies which also included the seedling thermo-tolerance indices (STI and SSTI) and other morphological and agronomic characters. It was observed that STI and SSTI recorded highest significant correlation among themselves as they are related indices for heat tolerance. While evaluating the diallel progenies it was also seen that the heat tolerance indices STI and SSTI were not showing any perceptible correlation with either of the maturity traits except negative correlation with effective tillers/plant. The stress period was terminated by irrigating the field experiment after 15 days from date of sowing when the seedlings get established and further mortality stopped due to heat. Moreover, the soil moisture was depleting near to the permanent wilting point and drought stress could also come into play along with heat stress to further continue the experiment. Since, experiment proceeded without any stress after the establishment of seedling (Peacock *et al.*, 1993), the pearl millet plants show great resilience and recovery. The main impact of supra-optimal temperature at germination and seedling stage was observed on the seedling survival and resulted in poor plant stand/population of pearl millet. Poor crop stand reduces the productivity (fodder and grain) drastically, whereas, after seedling establishment no impact of supra-optimal temperature at seedling stage was observed on later growth stages. Hence the early heat effects could have no impact on its later growth and development as most of maturity traits were observed on per plant basis.

Maturity traits showed significant correlation among themselves. Panicle emergence had a significant but negative correlation with plant height, ear weight/plant, dry fodder yield/plant, grain yield/plant and total biological yield/plant. Whereas, grain yield/plant showed significant correlation with number of effective tillers/plant, plant height, ear length, ear weight/plant, dry fodder yield/plant and total biological yield/plant. These results are in agreement with findings of

Harer and Karad (1998), Kulkarni *et al.* (2000), Yadav *et al.* (2001), Alam *et al.*, 2001 and Chaudhry *et al.* (2003). Patil and Jadeja (2009) revealed that alleles controlling the grain yield in stress and non stress environment are partially different therefore, need to select in target environments to improve the performance of the genotypes.

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