Indian Journal of Agricultural Sciences **84** (12): 1477–85, December 2014/Article

Inheritance of seedling heat tolerance and maturity traits in diallel F_1 hybrids of pearl millet (*Pennisetum glaucum*)

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Received: 16 January 2013; Revised accepted: 28 July 2014

ABSTRACT

A half-diallel mating system involving ten parents was used in the present study to determine the nature of gene action and genetic parameters in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. The Vr–Wr graph indicated over dominance for emergence rate, number of leaves/seedling, seedling height, fresh weight/seedling, dry weight/seedling, panicle emergence, number of effective tillers/plant, plant height, ear weight/plant, dry fodder yield/plant, grain yield/plant and total biological yield/plant. Partial dominance was observed for seedling thermo-tolerance index and ear length. The epistasis was found to be absent for emergence rate, seedling thermo-tolerance index, seed to seedling thermo-tolerance index, ear length, seedling height and plant height. The additive component of variance (D) had a significant presence for STI and SSTI in both the stress environments. The effect of over dominance was also reflected by higher degree of overall dominance effect (h^2) for both these characters. The h^2 component was significant for germination, emergence rate, number of leaves/seedling, seedling height, fresh weight/seedling, dry weight/seedling, 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 in all the three environments, while, for the remaining characters and environments it was non-significant. The inter relationship of the H_1 and H_2 parameters is reflected in the allied genetic parameter $H_2/4H_1$ index that estimates the proportion of genes with positive/negative effects, showing dominance in the parents. The value of this index was less than the expected values of 0.25 for all the characters in all the three environments indicating the asymmetrical distribution of dominant genes having positive and negative effects in parents. The ratio h^2/H_2 denotes the number of gene groups exhibiting dominance. The value of this ratio indicated one group of genes for STI, SSTI, germination, and number of effective tillers/plant. The character panicle emergence indicated two gene groups exhibiting dominance. Three gene groups were shown by the characters, i.e. seedling height, fresh weight/seedling and dry weight/seedling. The characters, ear weight/plant (stress environments), dry fodder yield/plant and grain yield/plant (stress environments) exhibited four gene groups. Five gene groups were exhibited by the characters, namely, plant height, ear length and total biological yield/plant.

Key words: Diallel analysis, Gene action, Genetic dissection, Pearl millet, *Pennisetum glaucum*, Supra-optimal temperature tolerance

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a robust, diploid, cross-pollinated crop with immense genetic diversity. It is the most important staple crop of millions of people in the semi-arid and arid regions of Asia and sub-Saharan Africa (Rachie and Majmudar 1980, Rai *et al.* 1999). With its ability to adapt to diverse agro-ecological conditions, pearl millet may have unique position in the world agriculture (Govila 2001). It is a multipurpose cereal grown for grain and stover. It shall continue to play a prominent role in the integrated agricultural and livestock economy, particularly in rainfed areas due to its drought hardiness and tolerance to high temperature (Singh 1993). Although pearl millet shows considerable environmental adaptation to the marginal areas, its yield is not only low but also highly variable. Stand establishment of pearl millet continues to be a severe constraint to successful production under subsistence farming conditions in the semi-arid tropics (Soman *el al.* 1987). Failure to obtain adequate plant populations is often associated with adverse weather conditions occurring at critical times during the germination and seedling establishment process. The temperature is one of the key climatic factors and has profound effect on the growth and development of the pearl millet (Pearson 1975, Fussell *el al.* 1980, Squire 1989, Khalifa and Ong 1990, Yadav *el al.* 2006). The soil temperatures in farmers' field in India and Africa commonly exceed 45° C and as high as 68°C have been recorded (Peacock 1977, Soman *et al.* 1981, Peacock and Ntshole 1976, Singh 1993, Yadav *et al.* 2006). There is some concern that the currently available hybrids are not as well adapted to harsh growing conditions, as they are to more favourable ones (Kelley *et al.* 1996). Hybrids show their potential yield and thus their superiority

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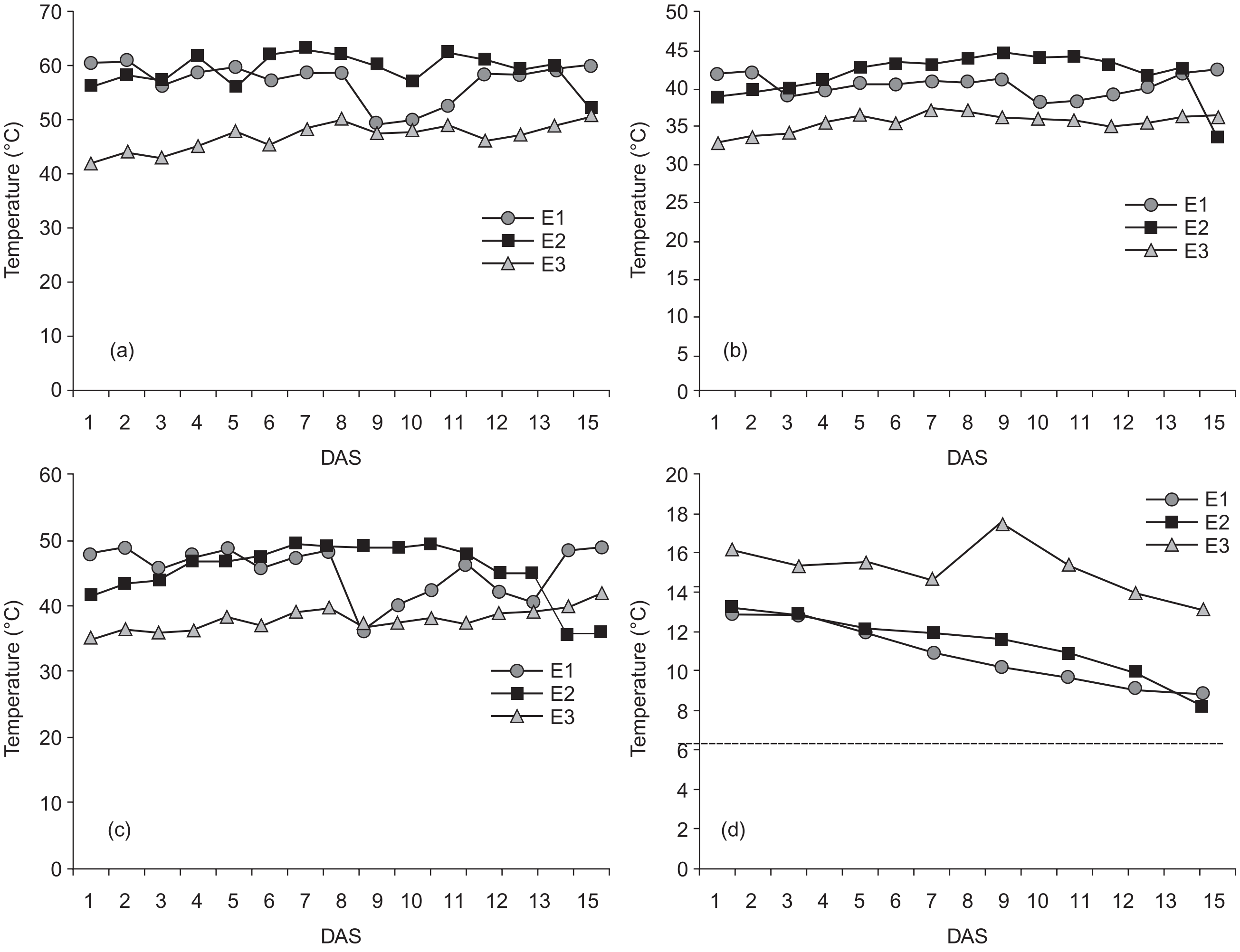

Fig 1 a) Soil surface temperature, b) Air temperature, c) Temperature 5cm above the soil surface and d) Soil moisture status in three environments

is best under favourable growing conditions. There are also reported cases of landraces which originate from arid regions, out yielding hybrids under stress conditions (Weltzien and Witcombe 1989, Yadav and Weltzien 1998). Farmers in arid regions frequently report low grain yield under heat and drought environtments is one of the major disadvantages of modern varieties (Kelley *et al.* 1996, Weltzien *et al.* 1998, Yadav *et al.* 2001).

An understanding of the genetic basis of supra-optimal temperature tolerance and identification of parents which are superior would be helpful in achieving such improvements. Supra-optimal temperature tolerance is a complex character involves a number of component traits which are likely to be quantitative in nature and the importance of supra-optimal temperature tolerance as a breeding objective is likely to increase in future. Diallel analysis for these parameters could furnish interesting information, which would be helpful in particular situations to understand the type of gene action involved in the expression of a character. It can identify genotypes possessing the most dominant and recessive alleles responsible for the expression of certain character, and also, provide information on narrow and broad sense heritability associated with the characters.

The purpose of this study was to investigate the nature and magnitude of different types of gene actions in controlling the inheritance of supra-optimal temperature tolerance and related traits at seedling stage and maturity traits from crosses of parental inbred differing in their responses to supra-optimal temperature and to suggest breeding strategies for the improvement thereof.

MATERIALS AND METHODS

Ten genotypes of pearl millet were selected on the basis of different response to supra-optimal temperature tolerance (Peacock *et al.* 1993). Of these, 7 heat 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 3 susceptible genotypes (H77/29-2, 77/245 and 1305) were crossed in a half-diallel mating system (excluding reciprocals). The 45 F_1 hybrids produced were tested for performance of seedling and maturity traits including fodder and grain yield in randomized block design with 3 replications under supra-optimal temperature exposure at seedling stage in 3 environments (two heat stress and one non-stress) during May–July. Each genotype was grown in

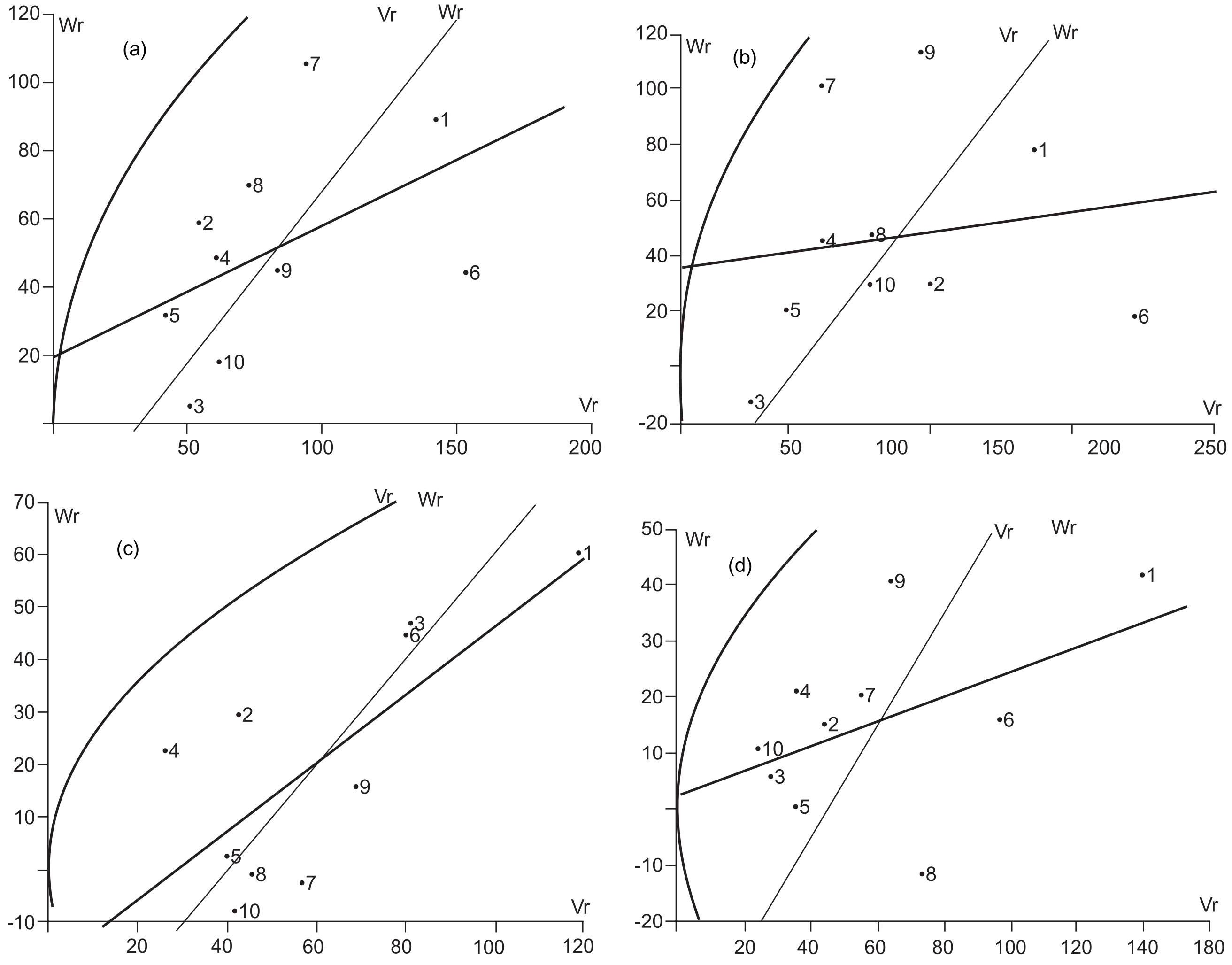

Fig 2 V_r–W_r graph for STI (a, b) and SSTI (c, d) in E_1 and E_2

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. For heat tolerance at seedling stage, two indices, i.e. seedling thermo-tolerance index (STI) (Peacock *et al.* 1993) and seed to seedling thermo-tolerance index (SSTI) (Singh 1993, Yadav *et al.* 2011) were applied to evaluate the hybrids and parents. Initially, emphasis of observation centred on germination, survival and mortality of the seedlings and later on maturity traits.

The experiment was conducted in the research area of Department of Genetics and Plant Breeding, CCS Haryana Agricultural University, Hisar (Lat: 29° 10'N, Long: 75° 46'E, and 215.2 m above mean sea level), located in subtropical region of Haryana, India. Standard agronomic package of practices were taken to raise the crop. The soil surface temperature was measured by a soil thermometer between 2:00 pm and 2:30 pm daily (Fig 1). 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), germination (%), emergence rate (ER), number of leaves/ seedling (two weeks stage), seedling height (two week stage), seedling fresh weight (g) (four week stage), seedling dry weight (g) (four week stage), panicle emergence (days), effective tillers/ plant, plant height (cm), ear length (cm), ear weight (g)/plant, dry fodder yield (g)/plant, grain yield (g)/plant and total biological yield (g)/plant. The data were recorded on 10 random plants per replication. Analysis of variance for Randomized Block Design (RBD), diallel analysis of Hayman's graphical and numerical approach (Hayman 1954a,b), among the various characters were calculated in relation to thermo-tolerance indices.

RESULTS AND DISCUSSION

Seedlings had to survive in a really high temperature at soil contact level at farmer's field. The excessive heat (soil temperature up to 63.0°C in E_2) about 18°C higher than the normal atmospheric temperature (Fig 1a) was responsible for mortality of seedlings. Many seedlings were found desiccated at the point of contact with soil 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

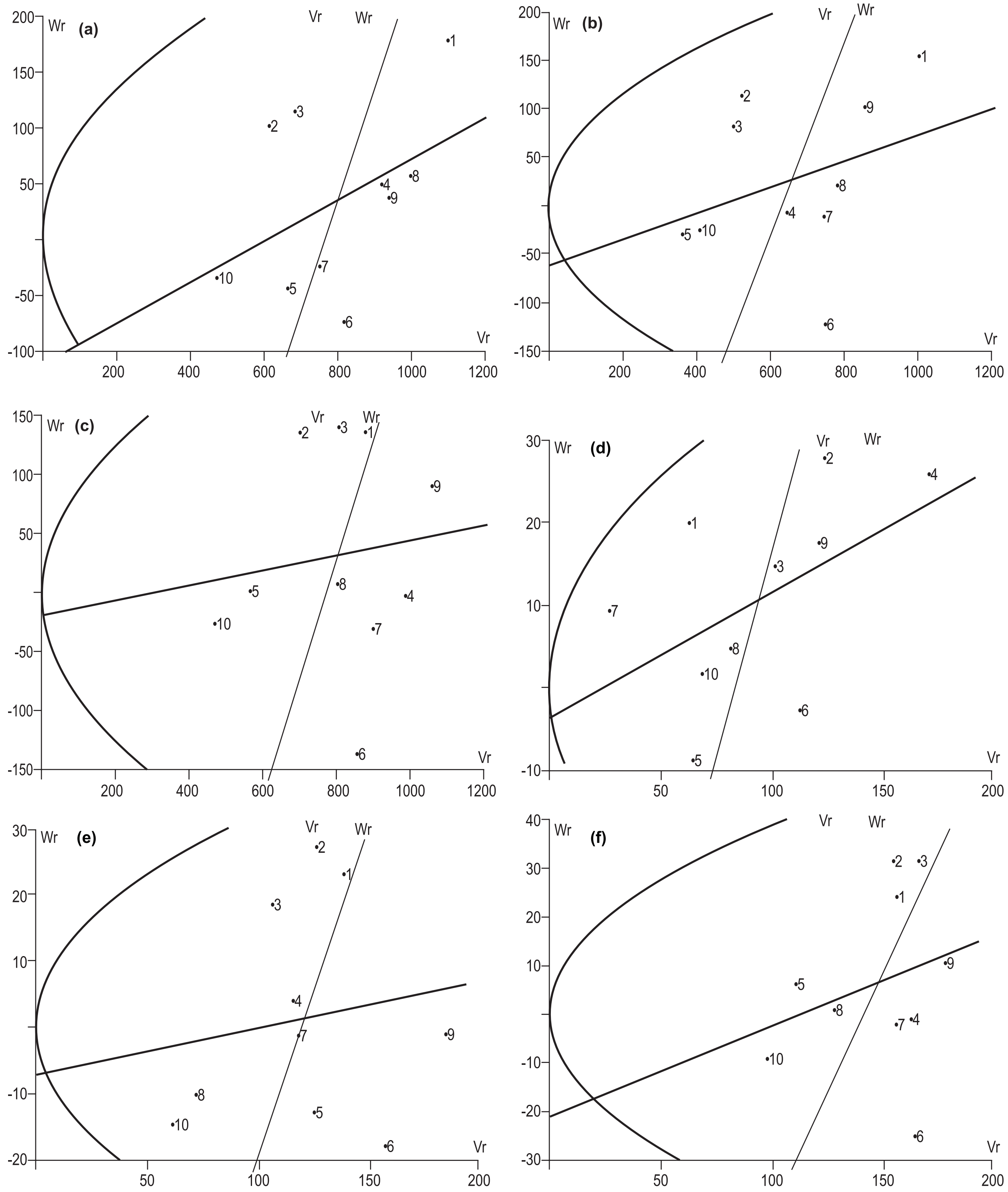

Fig 3 V_r–W_r graph for dry fodder yield/plant (a-c) and grain yield/plant (d-f) in E_1, E_2 and E_3

1c). During the experiment, moisture level remained above the permanent wilting point (Fig 1d). The analysis of variance for thermo-tolerance and maturity traits in three different environments (two stressed and one normal) was carried out and the results showed significant genotypic differences for all the characters in all the three environments. Significance of the mean squares associated with parents vs. hybrids indicated presence of average heterosis for all the characters.

Graphical approach

The graphical approach of analysis is mainly based on

Table 1 Estimates of Y–intercept (a), slope (b) and test of additivity for presence of epistasis

Parameter	Characters														
	STI	SSTI	Germi-nation	Rate of emer-gence	No. of leaves	Seedling height	Fresh weight	Dry weight	Panicle emergence	Effective tillers	Plant height	Ear length	Ear weight	Dry fodder yield	Grain yield	Total biological
a (Y–intercept)	19.143	–18.387	0.318	–8.139	–0.001	–2.589	1.627	0.065	–0.175	–0.005	–189.659	0.307	–16.054	–112.560	–3.728	–213.492
	35.774	2.584	4.629	–5.007	–0.275	–0.845	–57.254	–0.204	0.511	–0.013	–376.404	2.234	–37.038	–60.613	–7.127	–196.041
			7.498	–4.193	–1.659	5.748	–415.419	–3.340	–4.091	–0.053	–258.579	–0.229	–20.632	–18.586	–21.138	–55.432
b (slope)	0.386	0.646	0.262	0.845	0.244	0.582	0.058	0.004	0.709	–0.004	0.343	0.689	0.156	0.186	0.153	0.185
	0.111	0.222	0.089	0.589	0.408	0.409	0.078	0.035	0.175	0.140	0.679	0.575	0.204	0.135	0.071	0.172
			–0.030	0.844	0.329	–0.347	0.453	0.462	0.344	0.142	0.652	0.856	0.166	0.064	0.190	0.073
T^2	0.430	0.393	15.251**	0.408	21.801**	0.693	21.982*	42.437*	5.849*	27.947**	9.481*	0.747	18.988*	9.900**	24.905*	8.997*
	0.794	7.570**	14.022**	28.346**	3.852*	3.271	127.232**	111.262**	2.253	13.765**	3.828*	0.621	1.380	9.398**	6.141*	4.614*
			6.410*	0.946	22.913**	4.183*	7.527**	3.590	0.259	0.008	4.226*	0.005	4.444*	4.264*	1.064	3.290
H : b = 0	1.520	3.191*	2.440	6.747*	2.614	2.882*	0.589	0.059	7.907	0.044	2.782	4.047*	1.521	1.414	1.673	1.360
	0.431	1.554	0.759	10.011*	2.545	2.434	1.797	0.762	0.840	1.197	6.068*	2.777	0.891	0.991	0.447	1.004
			0.192	8.138	3.786*	2.128	3.690*	2.956	1.256	0.418	5.705*	4.465*	0.958	0.355	0.786	0.378
H : b = 1	2.413*	1.746	6.870**	1.236	8.108*	2.074	9.606*	13.557*	3.250*	11.326*	5.319*	1.830	8.249*	6.193*	9.293*	5.981*
	3.456*	5.438*	7.739**	6.999*	3.699*	3.522*	21.250*	20.733*	3.971*	7.329*	2.863*	2.052	3.473*	6.361*	5.818*	4.835*
			6.525**	1.505	7.727*	8.261*	4.452*	3.448*	2.390*	2.532*	3.042*	0.750	4.806*	5.230*	3.357*	4.817*

$^{\#}$Upper values for E_1, middle values for E_2 and lower values for E_3, Significant at P = 0.05, **Significant at P = 0.01

the information drawn from the Vr–Wr graphs, which shows a regression between variance of progenies in a parental array and covariance between parents and offspring in that array. In the Vr–Wr graphs, array points for parents H77/833-2, H77/29-2, G73-107, 77/245, CVJ-2-5-3-1-3, 1305, (77/371×BSECT CP-1), 96AC-93, Togo-II and 99HS-18 have been designated as 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10, respectively.

Coefficient of regression for STI was significantly different from zero and non-significant from unity in both the environments (E_1 and E_2), indicating absence of epistasis. The Vr, Wr graphs (Fig 2 a, b) showed partial dominance in both the stress environments. The parents 3, 5 (G73-107 and CVJ-2-5-3-1-3) in both environments appeared to have an excess of dominant genes, while, the parents 1, 6 (H77/833-2 and 1305) had maximum of recessive genes. The rest of the parents indicated to have almost equal proportion of dominant and recessive genes in them. The array points were found scattered along the regression line, indicating wide genetic diversity for STI. SSTI in E_1 the coefficient of regression was not significantly different form zero as well as unity, indicating the possible absence of epistasis, whereas epistasis was present in E_2 (Table 1 and 2). The V_r, W_r graphs (Fig 2 c, d) exhibited over dominance in E_1 and partial dominance in E_2. The array points 10, 5 (99HS-18 and CVJ-2-5-3-1-3) possessed maximum number of dominant genes and parents 1, 6 (H77/833-2 and 1305) possessed relatively more number of recessive genes in both environments. The well scattered array points along the regression line indicated genetic diversity. The differences in results due to variability in genetic and environment have been reported in wheat by Dere and Yildirim (2006). The information regarding degree of dominance, test of additivity and parental order of dominance for all the characters have been summarized in Table 2 and 3.

Hasan *et al.* (1996), Krishnaiah *et al.* (2002) and Khan and Khan (2005) reported the importance of both additive and non-additive type of gene action for the inheritance. The grain yield (g)/plant Vr, Wr graphs (Fig 3) showed over dominance as the regression line intercepted the Wr–axis below the origin in all the three environments. The well scattered array points along the regression line indicated genetic diversity among the parents.

The array 7, 5 (77/371×BSECTCP-1 and CVJ-2-5-3-1-3) in E_1, the array points 10, 8 (99HS-18 and 96AC-93) in E_2 and in E_3 the array points 10, 5 (99HS-18 and CVJ-2-5-3-1-3) showed more number of dominant genes, while, the array points 4, 2 (77/245 and H77/29-2) in E_1, the array points 9, 1, 2 (Togo-II, H77/833-2 and H77/29-2) in E_2 and in E_3 the array 3, 9, 2, 1 (G73-107, Togo-II, H77/29-2 and

Table 2 Degree of dominance, epistasis and parental order of dominance for different characters

Characters	Degree of dominance			Epistasis			Parental order of dominance		
	E_1	E_2	E_3	E_1	E_2	E_3	Dominant	Recessive	Others
STI	Partial	Partial		Absent	Absent		3, 5	1, 6	2, 4, 7, 8, 9, 10
SSTI	Over	Partial		Absent	Present		10, 5	1, 6	2, 3, 4, 7, 8, 9
Germination	Partial	Partial	Partial Dom.	Present	Present	Present	8, 3	1	2, 4, 5, 6, 7, 9, 10
Rate of emergence	Over	Over	Over Dom.	Absent	Present	Absent	8, 5, 7, 10	2, 6	1, 3, 4, 9
No. of leaves/ seedling	Over	Over	Over Dom.	Present	Present	Present	3, 10, 5, 7	6, 2, 4	1, 8, 9
Seedling height	Over	Over	Partial Dom.	Absent	Absent	Present	5, 8,4	6	1, 2, 3, 4, 7, 8, 9, 10
Fresh weight/ seedling	Partial	Over	Over Dom.	Present	Present	Present	6, 1	4	2, 3, 5, 7, 8, 9, 10
Dry weight/ seedling	Partial	Over	Over Dom.	Present	Present	Present	8	6, 1, 9	2, 3, 4, 5, 7, 10
Panicle emergence	Over	Partial	Over Dom.	Present	Present	Present	7	3, 6	1, 2, 4, 5, 8, 9, 10
Effective tillers/plant	Over	Over	Over Dom.	Present	Present	Present	3	6	1, 2, 4, 5, 7, 8, 9,10
Plant height	Over	Over	Over Dom.	Present	Absent	Absent	5, 1	9, 10	2, 3, 4, 6, 7, 8
Ear length	Partial	Partial	Over Dom.	Absent	Absent	Absent	5, 7	8, 4	1, 2, 3, 6, 9, 10
Ear weight/plant	Over	Over	Over Dom.	Present	Present	Present	10	2	1, 3, 4, 5, 6, 7, 8, 9
Dry fodder yield/plant	Over	Over	Over Dom.	Present	Present	Present	10, 5	1, 9	2, 3, 4, 6, 7, 8
Grain yield/plant	Over	Over	Over Dom.	Present	Present	Present	10, 5	2, 9, 1	3, 4, 6, 7, 8
Total biological yield/plant	Over	Over	Over Dom.	Present	Present	Present	10, 5	1, 9	2, 3, 4, 6, 7, 8

H77/833-2) showed more number of recessive genes for grain yield/plant in them. The Vr–Wr graphs indicated over dominance for emergence rate, number of leaves, seedling height, fresh weight, dry weight, panicle emergence, effective tillers, plant height, ear weight, dry fodder yield, grain yield and total biological yield. Partial dominance was observed for STI, germination and ear length. The epistasis was found to be absent for emergence rate, STI, SSTI, ear length, seedling height and plant height (Table 2). The array points were found scattered along the regression line, indicating wide genetic diversity among the parents for all the characters studied.

Numerical approach

The additive component of variance (D) had a significant presence for STI and SSTI in both the stress environments. At the same time the dominance component of variance (H_1) for these characters was not only significant but also in higher magnitude. This effect of over dominance was also reflected by higher degree of overall dominance effect (h^2) for both these characters. The covariance between D and H_1 showed a symmetrical distribution of dominant and recessive alleles for SSTI which was however shown to be asymmetrical for STI due to its significant mean squares. The proportion of dominant genes was also higher over the recessive genes in parents for both STI and SSTI. It was also seen that proportion of dominant genes with positive effect was higher than those with negative effects in control of STI and SSTI. Only one dominant gene appears to be responsible for expression of STI and SSTI. Narrow sense heritability (h^2_{ns}) for STI was estimated as 39 % and 28% for E_1 and E_2 and 37% and 26% respectively for SSTI.

The estimates of D were significant for emergence rate, panicle emergence, plant height and ear length in all the three environments. The characters, number of leaves/ seedling, seedling height were significant in two stress environments, while, the characters fresh weight/seedling, dry weight/seedling and effective tillers/plant showed significant D value only in E_3. For the remaining characters, i.e. germination, ear weight/plant, dry fodder yield/plant, grain yield/plant and total biological yield/plant, D value was non-significant. The two dominance components, H_1 and H_2 are interlinked and together reflect the contribution of genes with positive effects and those with negative effects. Both these H_1 and H_2 components were significant for all the traits in all the three environments except for number of effective tillers/plant. The magnitude of H_1 was higher than that of D for all the (except the ear length in E_2) indicating a preponderance of non-additive gene effects in the inheritance of these characters. Yadav *et al.* (2011) also reported non-additive component for all the characters and suggested hybrid breeding. However, additive genetic effects appear to be more pronounced in genetic control of grain yield/plant and ear length in maize (Haq *et al.* 2009).

The h^2 component, which reflects net dominance of genes (as the algebraic sum over all the loci in the heterozygous phase in all the crosses), was significant for germination, emergence rate, number of leaves, seedling height, fresh weight, dry weight, panicle emergence, number of effective tillers, plant height, ear length, ear weight, dry

Table 3 Genetic parameters for different characters

Genetic variance component	STI	SSTI	Germination	Emergence rate	No. of leaves/ seedling	Seedling height	Fresh weight/ seedling	Dry weight/ seedling	Panicle emergence	Effective tillers/ plant	Plant height	Ear length	Ear weight/ plant	Dry fodder yield/plant	Grain yield/ plant	Total biological yield/plant
D (Additive	193.161*	60.602*	16.101	43.156*	3.482*	2.603*	7.744	0.122	13.313*	0.021	456.261*	6.722*	33.18	78.015	10.605	187.096
effect)	229.356*	57.859*	20.562	8.581*	2.128*	4.142*	33.047	0.237	7.066*	0.141	530.989*	12.367*	43.913	57.997	8.913	179.963
			21.169	32.744*	4.435	2.75	443.496*	4.279*	24.420*	0.287*	367.961*	11.584*	49.411	68.746	13.652	221.103
	313.485*	216.063*	105.727*	80.098*	11.656*	21.442*	193.052*	3.851*	22.019*	1.119	3298.191*	8.746*	656.101*	3110.412*	339.360*	5842.912*
H_1 (Dominance	440.438*	232.345*	115.161*	34.787*	6.835*	17.358*	3092.264*	25.727*	29.515*	0.906	2851.594*	11.137*	717.622*	2564.172*	477.422*	5395.716*
effect)			144.523*	49.381*	30.712*	79.162*	4532.592*	39.055*	99.166*	1.452*	2033.408*	15.167*	742.711*	3125.955*	570.427*	6798.573*
	182.869*	38.245	-1.581	52.719*	4.308	1.621	-2.609	-0.026	0.989	0.081	574.31	2.346	27.935	16.449	-20.217	136.059
F (Mean cov.	272.067*	52.322	11.763	20.061*	2.687	4.402	56.392	0.391	6.940	0.221	769.235*	4.274*	100.882	6.508	12.96	223.613
of D & H_1)			18.052	47.114*	5.661	8.94	525.394	3.468	33.279*	0.630*	530.747*	0.397	59.82	11.581	1.298	170.077
	242.416*	181.913*	86.246*	61.786*	9.660*	20.752*	167.039*	3.696*	18.105*	0.872*	2887.823*	8.300*	557.859*	2695.446*	302.985*	4994.586*
H_2	331.183*	201.346*	101.515*	18.925*	5.397*	16.080*	2785.773*	23.341*	22.457*	0.660*	2367.494*	10.240*	589.321*	2167.276*	427.867*	4497.222*
			113.949*	30.007*	26.418*	69.181*	4058.554*	35.830*	79.667*	0.904*	1675.760*	13.322*	657.962*	2643.239*	500.072*	5851.731*
h^2 (Overall	3.744	50.591*	57.329*	214.367*	38.066*	56.026*	308.850*	7.078*	55.829*	0.016*	15198.321*	28.661*	1922.075*	11404.485*	995.314*	22697.064*
dominance effect)	0.198	16.747	21.008	32.271*	19.838*	68.155*	7437.132*	68.129*	34.830*	0.133*	11614.782*	42.517*	2088.571*	8401.513*	1424.975*	18871.279*
			45.839*	133.257*	92.499*	144.259*	11330.007*	91.883*	114.240*	0.061	8045.172*	62.390*	3092.474*	9979.659*	2036.408*	24186.592*
E (Environmental	3.889	2.332	0.96	4.477*	0.132	1.023*	0.613	0.018	1.725*	0.041	13.097	0.745*	5.666	12.032	2.257	17.31
component)	3.532	2.092	1.131	3.815*	0.223	0.553	2.328	0.021	1.701	0.019	20.862	0.539*	3.162	7.149	1.529	10.806
			2.617	3.844*	0.461	0.959	10.109	0.08	2.283	0.027	18.83	0.757*	4.939	8.708	1.528	17.181
Allied genetic parameters																
	1.274	1.888	2.563	1.362	1.83	2.87	4.993	5.612	1.286	7.387	2.689	1.141	4.447	6.314	5.657	5.588
Mean degree	1.386	2.004	2.367	2.013	1.792	2.047	9.673	10.411	2.044	2.534	2.317	0.949	4.043	6.649	7.319	5.476
of dominance			2.613	1.228	2.631	5.365	3.197	3.021	2.015	2.25	2.351	1.144	3.877	6.743	6.464	5.545
:: of Genes with +/-	0.193	0.21	0.204	0.193	0.207	0.242	0.216	0.24	0.206	0.195	0.219	0.237	0.213	0.217	0.223	0.214
effects in parents	0.188	0.217	0.22	0.136	0.197	0.232	0.225	0.227	0.19	0.182	0.208	0.23	0.205	0.211	0.224	0.208
			0.197	0.152	0.215	0.218	0.224	0.229	0.201	0.156	0.206	0.22	0.221	0.211	0.219	0.215
:: of Dom & rec	2.183	1.401	0.962	2.625	2.022	1.243	0.935	0.964	1.06	1.735	1.611	1.361	1.209	1.034	0.712	1.139
genes in parents	2.497	1.583	1.275	3.768	2.088	1.701	1.193	1.172	1.633	1.894	1.909	1.445	1.794	1.017	1.221	1.256
			1.39	3.829	1.64	1.869	1.455	1.31	2.022	2.904	1.885	1.03	1.37	1.025	1.015	1.149
Va (Additive	40.68	28.254	18.581	4.375	0.585	0.837	18.182	0.151	8.119	0.093	146.159	2.411	51.744	238.266	33.599	449.681
gene effects)	33.272	18.268	11.222	2.191	0.44	0.509	141.573	1.116	3.592	0.083	122.927	4.495	35.666	224.192	22.754	427.422
			16.845	2.502	1.534	1.896	196.07	2.018	5.32	0.103	97.431	6.516	37.17	269.941	41.354	498.934
	60.604	45.478	21.561	15.447	2.415	5.188	41.76	0.924	4.526	0.218	721.956	2.075	139.465	673.861	75.746	1248.647
Vd (Dominance	82.796	50.336	25.379	4.731	1.349	4.02	696.443	5.835	5.614	0.165	591.873	2.56	147.33	541.819	106.967	1124.305
deviations)			28.487	7.502	6.605	17.295	1014.639	8.958	19.917	0.226	418.94	3.331	164.49	660.81	125.018	1462.933
h^2 / H_2 (No. of	0.015	0.278	0.665	3.469	3.941	2.7	1.849	1.915	3.084	0.019	5.263	3.453	3.445	4.231	3.285	4.544
dominant gene	0.001	0.083	0.207	1.705	3.676	4.238	2.67	2.919	1.551	0.201	4.906	4.152	3.544	3.877	3.33	4.196
blocks)			0.402	4.441	3.501	2.085	2.792	2.564	1.434	0.067	4.801	4.683	4.7	3.776	4.072	4.133
h^2 (Heritability in	0.387	0.371	0.452	0.18	0.187	0.119	0.3	0.138	0.565	0.264	0.166	0.461	0.263	0.258	0.301	0.262
narrow sense)	0.278	0.258	0.297	0.204	0.219	0.1	0.168	0.16	0.329	0.311	0.167	0.592	0.192	0.29	0.173	0.274
			0.351	0.181	0.178	0.094	0.161	0.182	0.193	0.288	0.182	0.615	0.18	0.287	0.246	0.252

Upper values for E_1, middle values for E_2 and lower values for E_3,*Significant at P = 0.05, **Significant at P = 0.01

fodder yield, grain yield and total biological yield. Similar findings were also reported in wheat by Dere and Yildirim (2006).

The sign of the parameter 'F' which is the mean covariance of additive and non-additive effects in the arrays is used to determine the relative frequency of dominant to recessive alleles in the parental population. The value of parameter F was significant and positive for emergence rate, panicle emergence (E_3), plant height (E_2 and E_3) and ear length (E_2), indicating the excess of dominant genes among the parents for these characters. None of the character the value of F was significant and negative. For the remaining characters, the value of F was non-significant and thus, indicating equal proportion of dominant and recessive genes. The significant values of the environmental component of variance (E) were recorded for panicle emergence (E_1) and ear length in all the three environments.

Allied genetic parameters

The inter relationship of the H_1 and H_2 parameters is reflected in the allied genetic parameter $H_2/4H_1$ index that estimates the proportion of genes with positive/negative effects, showing dominance in the parents. The value of this index was less than the expected values of 0.25 for all the characters in all the three environments indicating the asymmetrical distribution of dominant genes having positive and negative effects in parents (Table 3). However, this ratio showed a slight deviation from symmetrical distribution of dominant genes with positive and negative effects for the characters, germination in E_2 (0.220), seedling height in E_1 and E_2 (0.242 and 0.232), fresh weight in E_2 and E_3 (0.225 and 0.224), dry weight (0.240, 0.227 and 0.229) in E_1, E_2 and E_3, ear length (0.237, 0.230 and 0.220), ear weight in E_3 (0.221) and grain yield (0.223 and 0.224) in E_1 and E_2. Hassan *et al.* (1996) also detected asymmetrical distribution of positive and negative alleles among parents in wheat. However, in maize the parental lines are supported to contain equal number of dominant and recessive genes for grain yield and ear length (Haq *et al.* 2009).

The mean degree of dominance $(H_1/D)^{0.5}$ indicated over dominance for germination, emergence rate, number of leaves, seedling height, fresh weight, dry weight, panicle emergence, effective tillers, plant height, ear length (E_1 and E_3), ear weight, dry fodder yield, grain yield and total biological yield, while, partial dominance was observed for ear length (E_2). None of the characters showed complete dominance in any environment.

Regarding proportion of dominant and recessive genes in parents positive F value caused the ratio $(4DH_1)^{0.5}+F/(4DH_1)^{0.5}-F$ to be greater than unity for germination (E_2 and E_3), emergence rate, number of leaves, seedling height, fresh weight (E_2 and E_3), dry weight (E_2 and E_3), panicle emergence, effective tillers, plant height, ear length, ear weight, dry fodder yield, grain yield (E_2 and E_3) and total biological yield in all the three environments, indicating that these characters were controlled by more of dominant genes in the parents. The negative sign of F causing the ratio to be less than unity indicating that germination, fresh weight, dry weight, grain yield in E_1 were controlled by an excess of recessive genes.

The ratio h^2/H_2 denotes the number of gene groups exhibiting dominance. The value of this ratio indicated one group of genes for STI, SSTI, germination, and effective tillers in all the environments (Table 3). The characters, i.e. emergence rate (E_1), fresh weight (E_1), dry weight (E_1) and panicle emergence (E_2 and E_3) indicated two gene groups exhibiting dominance. Three gene groups were shown by the characters, i.e. seedling height (E_1 and E_3), fresh weight (E_2 and E_3) and dry weight (E_2 and E_3). The characters, emergence rate (E_1), number of leaves, panicle emergence (E_1), ear length (E_1), ear weight (E_1 and E_2), dry fodder yield (E_2 and E_3) and grain yield (E_2 and E_3) exhibited four gene groups. Five gene groups were exhibited by the characters, namely, emergence rate (E_3), seedling height (E_2), plant height (E_2 and E_3), ear length (E_2 and E_3), ear weight (E_3), dry fodder yield (E_1), grain yield (E_3) and total biological yield in all the three environments and the only character, plant height exhibited six gene groups in environment (E_1). Patil and Jadeja (2009) reveal that alleles controlling the grain yield in stress and non-stress environments are partial different. The estimates of narrow-sense heritability (h^2_{NS}) were high for panicle emergence (E_1) and ear length (E_2 and E_3). Contrarily, the heritability estimates were low for rest of the characters.

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