

Gene effects for different metric traits under normal and high temperature stress environments in wheat (*T.aestivum* L. Em.Thell)

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Abstract

The present investigation was conducted to analyze gene effects for grain yield and its components under two different environments. Nine wheat genotypes were selected to generate the experimental material comprised six parental and segregating generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BS_1 of BC_1 of each of the following six crosses - PBW 343 x WH 283, PBW 343 x WH 542, PBW 343 x PBW 435, UP 2565 x UP 2425, EIGN 1 x Raj 3765 and EIGN 8 x UP 2425. Joint scaling tests revealed the presence of epistasis. Six parameter model revealed the significance of additive gene effects (d) for biological and grain yield and their components in most of the crosses. The relative magnitude of (h) was higher than (d) in all the crosses for most of the characters while additive x additive (i) effects appeared to be significant for grain yield per plant (E_1) and number of grain per spike (E_2) in PBW 343 x WH 283. Significant (i) type of interaction was recorded in PBW 343 x WH 542 for number of grain per spike (E_1), number of tillers per plant (E_2) in PBW 343 x PBW 435 and for 1000-grain weight in UP 2565 x UP 2425. Pedigree method and simple selection in crosses like PBW 343 x PBW 435, UP 2565 x UP 2425, PBW 343 x WH 283 and PBW 343 x WH 542 should be used for improvement of traits governed by additive and additive x additive gene effect.

1. Introduction

The terminal heat stress can be a problem in up to 40 per cent of the irrigated wheat growing areas in the developing world which cover 36 m ha (Reynold *et al.*, 2001). High temperature (> 30 °C) during grain filling stage is one of the major constraints in increasing productivity in wheat in tropical countries like India (Rane and Nagarajan, 2004). According to an estimate there are currently around 9 m ha of wheat in tropic and subtropics areas that experience losses due to high temperature stress. In India alone around 13.5 m ha of area is under heat stress (Joshi *et al.*, 2007). In India, incidences of high temperatures at the time of grain filling are more pronounced when sowing of wheat is delayed due to delay in harvest of highly remunerative preceding crops such as scented rice or cotton (Joshi *et al.*, 2002). Intensity of high temperature is likely to become much larger if current trends and future predictions about global warming continue. For improvement of heat tolerance, information on the genetic control of grain yield and associated characters under heat stress and identification of good combiner parents /crosses are primary requirements.

The information about gene effects including mean (m), additive gene effects (d), dominance gene effect (h), and three types of non-allelic gene interactions, viz., additive x additive (i), additive x dominance (j) and dominance x dominance (l) and nature of epistasis is useful in deciding breeding procedures to be adopted for the improvement of quantitative traits like yield and high temperature tolerance (Singh and Singh, 1992). This paper deals with the gene effects for important traits, contributing to grain yield under normal and heat stress conditions during grain filling stages (terminal heat stress), in six wheat crosses.

2. Material and Method

Experimental material: Nine genetically diverse homozygous genotypes of wheat (*Triticum aestivum* L. em. Thell) viz. PBW 343, WH 283, WH 542, PBW 435, UP 2565, UP 2425, EIGN1 and EIGN8 varying in their response to heat stress during grain filling stages were selected to generate the experimental material. Experimental material comprised six parental and

segregating generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BS_1 (Self of BC_1)) of each of the following six crosses 343 x WH 283, PBW 343 x WH 542, PBW 343 x PBW 435, UP 2565 x UP 2425, EIGN 1 x Raj 3765, EIGN 8 x UP 2425.

Layout of the Experiment: During the winter season 2006-07, the experimental material, i.e. six generation of six crosses, were grown in randomized block design (compact family block design) with three replications under two dates of sowing i.e. 1.12.2006 (E_1) and 4.1.2007 (E_2). The non-segregating generation, parents and F_1 's were grown in single row each and segregating generations F_2 and BS_1 in 10 rows each and BC_1 in three rows of 2.0 meter length. The row to row distance was kept 30 cm, whereas, plant to plant distance within row was 10 cm. All recommended package and practices to raise a good crop in field were observed.

Statistical procedures: Joint scaling test were carried out as per Cavalli (1952) as described by Mather and Jinks (1982).

3. Result and Discussion

Scaling Tests: Joint scaling test revealed the presence of epistasis for most of the characters in all the six crosses studied in normal and late sown environments except a few cases like in PBW 343 x WH 283 for number of grains per spike (E_1); in PBW 343 x WH 542 for days to 50 % flag leaf emergence (E_2), number of tillers per plant (E_2), biological yield per plant (E_1), grain yield per plant (E_1) and harvest index (E_1); in PBW 343 x PBW 435 for days to anthesis and number of tillers per plant (E_1), in UP 2565 x UP 2425 for days to 50% flag leaf emergence and days to anthesis (E_1); in EIGN 1 x Raj 3765 for number of tillers per plant (E_1) and in EIGN 8 x UP 2425 for number of grains per plant (E_1), where the goodness of fit for non-epistasis model was revealed. The individual scaling test and joint scaling test were by and large in complete agreement with each other in reflecting the presence of epistasis. Failure of simple additive dominance model in most of the cases for different characteristics revealed that genetic variation which could not be ascribed to additive and dominance effects rather revealed the presence of epistasis. Therefore, six parameter model was followed to estimate gene effects and digenic interaction.

Table 1. Estimate of components of generation mean for different traits in six crosses (six parameter Model).

Characters and Environment		m	d	h	i	j	l	X²3df	Types of epitasis
Days to 50% flag leaf emergence									
PBW 343 x WH 283	E ₁	81.627**	3.018**	-6.298**	-5.698**	-1.431	8.489*	8.793*	D
	E ₂	73.54**	-0.498	-2.809	-4.276**	-8.196**	3.191	62.223**	
PBW 343 x WH 542	E ₁	82.887**	-0.818*	3.078	6.444**	-5.302**	-24.902**	109.731**	
	E ₂	75.207**	-0.656	2.129	-1.204	-0.778	-0.551	5.274	
PBW 343 x PBW 435	E ₁	80.88**	1.484	6.022*	5.422*	-2.631	-17.964**	18.392**	D
	E ₂	71.733**	0.456	8.278**	9.311**	-4.089**	-21.622**	48.000**	D
UP 2565 x UP 2425	E ₁	79.82**	1.687**	6.147**	2.947	2.04	-7.04	4.618	
EIGN 1 x Raj 3765	E ₁	80.733**	-1.047	-2.207	-2.44	-14.427**	7.613*	109.791**	
	E ₂	74.26**	-2.631**	21.878**	16.311**	-8.796**	-17.862**	156.891**	D
EIGN 8 x UP 2425	E ₁	81.64**	1.88**	-0.987	-5.787**	4.827**	5.013	30.601**	
	E ₂	80.013**	1.318**	-20.378**	-23.578**	0.102	19.369**	181.452**	D
Days to anthesis									
PBW 343 x WH 283	E ₁	96.9**	3.156**	-5.956**	-6.356**	-2.089	10.444**	9.446**	D
	E ₂	80.7**	0.16	-2.12	-2.587	-10.347**	-1.76	165.176**	
PBW 343 x WH 542	E ₁	97.407**	-0.304	9.071**	12.138**	-4.076**	-32.569**	138.381**	D
	E ₂	83.127**	0.447	1.367	-1.133	-2.507*	-4.307	7.502**	
PBW 343 x PBW 435	E ₁	97.22**	1.211	2.342	3.276	-0.911	-11.698*	5.513	
	E ₂	79.153**	0.336	6.638**	7.071**	-1.129	-20.022**	26.472**	D
UP 2565 x UP 2425	E ₁	95.52**	0.778	3.976	0.542	-0.244	-2.831	0.767	
EIGN 1 x Raj 3765	E ₁	96.627**	0.68	-1.1	-0.133	-6.44**	3.96	27.040**	
	E ₂	82.32**	0.216	18.178**	16.778**	0.564	-26.702**	114.555**	D
EIGN 8 x UP 2425	E ₁	97.767**	0.316	0.491	-4.409**	0.031	1.018	15.103**	
	E ₂	87.027**	0.067	-24.673**	-21.573**	0.6	16.973**	178.805**	D
Number of tillers of plant									
PBW 343 x WH 283	E ₁	23.28**	-4.349**	0.522	2.689	-5.564	12.769	9.057**	
	E ₂	11.4**	-5.847**	-2.24	4.227	-9.693**	0.747	13.427**	
PBW 343 x WH 542	E ₁	23.707**	1.704	-4.791	-1.524	-0.991	31.022**	28.106**	D
	E ₂	16.713**	1.371*	3.616	-0.084	1.076	-3.151	3.503	
PBW 343 x PBW 435	E ₁	22.433**	2.289	-8.656	-4.889	4.911	14.511*	7.481	
	E ₂	13.773**	-0.756	-5.471*	-5.404**	2.489	4.382	16.865**	
UP 2565 x UP 2425	E ₁	27.573**	2.24	0.927	-1.44	8.28	-16.413	14.003**	
EIGN 1 x Raj 3765	E ₁	25.507**	-3.413**	2.6	-2.933	-9.227*	-2.96	7.062	
	E ₂	19.307**	-7.809**	-30.564**	-32.898**	-13.351**	42.302**	221.029**	D
EIGN 8 x UP 2425	E ₁	18.76**	-0.289	6.749	6.249	4.422	-30.138**	37.556**	
	E ₂	19.673**	7.433**	6.073*	1.907	17.067**	-42.04**	407.369**	D
Number of spikelets per spike									
PBW 343 x WH 283	E ₁	21.733**	-1.16**	1.253	1.52	-4.187**	-5.173*	30.047**	

Characters and Environment		m	d	h	i	j	l	X²3df	Types of epitasis
PBW 343 x WH 542	E ₂	17.833**	2.653**	-0.74	3.893**	4.44**	-26.653**	424.140**	
	E ₁	23.247**	0.009	-8.282**	-9.182**	-0.849	13.178**	110.053**	D
PBW 343 x PBW 435	E ₂	18.713**	-2.3**	6.247**	4.413*	-5.733**	-2.813	31.267**	
	E ₁	22.387**	0.54	-2.36*	-2.627**	-4.787**	-1.627	69.127**	
UP 2565 x UP 2425	E ₂	19.873**	0.724**	1.036	0.836	-2.818*	-8.231**	41.107**	
	E ₁	20.773**	0.127	4.253**	4.387**	-1.213	-9.2**	47.037**	D
EIGN 1 x Raj 3765	E ₁	21.567**	1.702**	4.284**	0.818	3.138**	-3.636*	28.247**	D
	E ₂	19.22**	-3.876**	-21.584**	-16.951**	-10.884**	24.156**	313.467**	D
EIGN 8 x UP 2425	E ₁	21.273**	0.056	7.951**	5.284**	-0.422	-14.596**	84.661**	D
	E ₂	13.353**	4.351**	25.229**	22.596**	5.569**	-16.138**	1507.883**	D
Number of grains per spike									
PBW 343 x WH 283	E ₁	70.307**	4.338*	-4.324	-9.724	1.476	6.356	5.996	
	E ₂	63.993**	-3.527	-49.087**	-39.32**	-7.653	26.733	50.317**	
PBW 343 x WH 542	E ₁	76.44**	-0.193	-20.74**	-15.507**	-3.653	6.12	26.681**	
	E ₂	71.387**	-8.96**	15.273	-12.427	-14.787	47.907*	8.447**	
PBW 343 x PBW 435	E ₁	78.353**	-0.147	-7.387	-22.453**	-0.027	10.16	40.980**	
	E ₂	79.833**	-3.109	-36.971**	-49.738**	-24.818*	69.542**	39.318**	D
UP 2565 x UP 2425	E ₁	73.173**	3.469	28.291**	20.724**	8.871	-59.94**	28.350**	D
	E ₁	67.867**	1.993	33.913**	16.813**	-3.28	-52.093**	28.395**	D
EIGN 1 x Raj 3765	E ₂	69.693**	-5.218**	-67.082**	-32.516**	-31.436**	-53.409**	779.483**	
	E ₁	69.18**	0.431	9.362	-0.871	-10.804*	-2.111	6.781	
EIGN 8 x UP 2425	E ₂	14.807**	58.564**	189.122**	156.356**	158.262**	-123.071**	1649.712**	D
	Plant height(cm)								
PBW 343 x WH 283	E ₁	96.633**	7.613**	10.04	8.373	19.493**	-27.413**	32.481**	
	E ₂	71.947**	-0.083	-46.207**	-38.287**	3.367	61.213**	148.518**	D
PBW 343 x WH 542	E ₁	97.667**	6.34**	-1.38	0.12	26.613**	-6.04	179.004**	
	E ₂	64.147**	0.314	4.662	14.029**	-9.304**	-21.911**	53.906**	
PBW 343 x PBW 435	E ₁	95.06**	-0.28	-11.347**	-12.213**	9.173**	22.187**	26.318**	D
	E ₂	72.593**	4.687**	-5.597	-5.08	6.14*	4.42	9.210**	
UP 2565 x UP 2425	E ₁	98.593**	0.656	7.571*	5.471	0.711	-22.049**	17.741**	D
	E ₁	97.967**	2.04	18.253**	13.12**	-0.053	-41.173**	92.847**	D
EIGN 1 x Raj 3765	E ₂	60.473**	3.562**	-27.028**	-8.794**	6.256**	8.828	15.855**	
	E ₁	93.12**	-4.007*	79.367**	76.867**	-9.28*	-142.413**	324.281**	D
EIGN 8 x UP 2425	E ₂	60.87**	-5.476**	17.549**	8.316	-5.884	21.689**	77.563**	
	Peduncle length(cm)								
PBW 343 x WH 283	E ₁	46.793**	5.102**	3.578	-2.622	15.271**	8.338	65.072**	
	E ₂	40.063**	0.848	-27.531**	-12.064**	5.229	10.942	35.749**	
PBW 343 x WH 542	E ₁	45.387**	0.698*	-8.764**	-7.298**	4.329**	-0.284	73.405**	
	E ₂	41.427**	-2.477**	-12.553**	-11.287**	-8.22**	12.467**	40.059**	D

Characters and Environment		m	d	h	i	j	l	X² 3df	Types of epistasis
PBW 343 x PBW 435	E ₁	48.153**	1.438**	-4.044**	-7.044**	4.742**	6.676**	40.569**	D
	E ₂	43.895**	0.823	-5.759*	-5.892**	3.313	0.339	26.469**	
UP 2565 x UP 2425	E ₁	46.647**	-1.709*	13.942**	5.276**	-6.084**	12.462	42.672**	D
	E ₂	47.867**	3.178**	6.689**	3.422*	5.289**	-18.444**	66.465**	
EIGN 1 x Raj 3765	E ₁	31.783**	5.557**	-19.38**	-7.58**	13.38**	4.827	26.344**	D
	E ₂	51.8**	1.147	16.473**	13.707**	-0.04	-25.213**	33.396**	
EIGN 8 x UP 2425	E ₁	33.53**	-0.48	4.59	0.44	9.74*	27.1**	44.575**	D
	E ₂								
Awn length(cm)									
PBW 343 x WH 283	E ₁	7.215**	0.111	-0.306	-0.799**	-0.098	2.017**	12.367**	D
	E ₂	6.364**	-0.771**	-3.966**	-2.243**	-0.468**	5.73**	284.586**	
PBW 343 x WH 542	E ₁	7.039**	-0.323**	-1.942**	-2.169**	-0.14	3.86**	55.685**	D
	E ₂	6.171**	-0.092	-0.223	0.05	-0.544**	0.801*	32.005**	
PBW 343 x PBW 435	E ₁	7.107**	0.723**	0.868*	2.252**	1.8**	-6.936**	180.801**	D
	E ₂	8.02**	-0.048	0.696*	-0.874**	1.298**	0.261	78.015**	
UP 2565 x UP 2425	E ₁	8.349**	0.51**	0.632	-1.064**	1.081**	0.088	20.420**	D
	E ₂	7.2**	-0.113	4.815**	4.252**	0.781	-6.457**	132.974**	
EIGN 1 x Raj 3765	E ₁	6.711**	0.222**	-2.029**	-2.606**	0.985**	4.92**	584.450**	D
	E ₂	8.767**	0.603**	-0.938*	-1.164**	0.993**	-2.207**	90.284**	
EIGN 8 x UP 2425	E ₁	6.169**	-0.127**	6.519**	5.746**	0.279*	-10.036**	3717.794**	D
	E ₂								
1000- grain weight(g)									
PBW 343 x WH 283	E ₁	37.582**	-1.304	24.32**	23.81**	-1.376	-46.061**	45.329**	D
	E ₂	27.99**	-7.18**	28.28**	21.84**	-18.952*	-46.06**	18.468**	
PBW 343 x WH 542	E ₁	37.42**	-0.212	22.334**	16.647**	-2.198	-20.241**	36.234**	D
	E ₂	28.35**	8.012**	34.39**	26.36**	15.871**	-60.436**	19.408**	
PBW 343 x PBW 435	E ₁	39.637**	4.088**	14.381**	11.401**	2.11	-11.628*	20.107**	D
	E ₂	34.45**	-1.582	5.068	14.171**	19.508	-44.91**	10.967**	
UP 2565 x UP 2425	E ₁	44.145**	-1.451	-18.143**	-11.333**	2.985	10.772	20.320**	D
	E ₂	38.627**	5.922**	22.325**	23.868**	17.478**	-54.226**	146.866**	
EIGN 1 x Raj 3765	E ₁	46.465**	-41.447**	89.182**	116.32**	-78.793**	-188.48**	398.852**	D
	E ₂	41.35**	-2.16**	16.01**	16.73**	2.531	-32.98**	38.756**	
EIGN 8 x UP 2425	E ₁	32.43**	-7.01**	26.38**	25.30**	141.55**	-54.85**	168.311**	D
	E ₂								
Biological yield per plant(g)									
PBW 343 x WH 283	E ₁	88.987**	-26.702**	109.30**	44.036*	-197.738**	19.31	103.982**	D
	E ₂	81.727**	-57.387**	69.13**	-57.733**	-66.573**	27.36	162.325**	
PBW 343 x WH 542	E ₁	107.053**	-8.682	-11.34	-0.804	-52.164**	-75.68**	7.250	D
	E ₂	96.953**	10.371**	-54.178**	-37.178*	-7.791	-145.06**	341.173**	
PBW 343 x PBW 435	E ₁	114.767**	11.964	-100.251**	-113.484**	34.396*	120.102**	47.348**	D
	E ₂	106.687**	-16.816**	-117.504**	-130.271**	-33.298*	88.262**	109.403**	
UP 2565 x UP 2425	E ₁	118.42**	-26.089**	42.942	16.809	-56.711**	-103.831*	17.748**	D
	E ₂								

Characters and Environment		m	d	h	i	j	l	X²3df	Types of epitasis
EIGN 1 x Raj 3765	E ₁	120.773**	-51.051**	92.764**	65.498*	-101.302**	-353.956**	124.638**	D
	E ₂	89.193**	-28.227**	-94.82**	-145.653**	-70.253**	171.267**	167.161**	D
EIGN 8 x UP 2425	E ₁	128.307**	1.176	12.478	-15.489	9.218	-154.982**	58.082**	
	E ₂	51.713**	-91.016**	105.422**	99.089**	-189.364**	-208.631**	184.483**	D
Grain yield per plant(g)									
PBW 343 x WH 283	E ₁	26.71**	-3.667*	15.125*	15.392**	-4.134	-5.516	15.130**	
	E ₂	10.789**	-5.548**	-19.012**	-17.516**	-9.21	42.63**	44.849**	D
PBW 343 x WH 542	E ₁	32.514**	-0.697	-5.63	-4.973	-17.181*	3.98	6.471	
	E ₂	15.581**	3.795**	-3.65	3.204	16.811**	-21.59**	475.246**	
PBW 343 x PBW 435	E ₁	30.551**	10.142**	9.938	13.415**	19.438**	-14.373	16.281**	
	E ₂	18.163**	0.806	-7.25	-7.471**	11.798**	-6.38	126.441**	
UP 2565 x UP 2425	E ₁	38.751**	-0.664	-2.067	-14.291	8.519	-12.951	28.474**	
EIGN 1 x Raj 3765	E ₁	31.728**	-1.857	52.258**	39.735**	0.987	-111.481**	62.813**	D
	E ₂	20.194**	-6.103**	3.414	-5.886	-18.472**	-5.711	77.550**	
EIGN 8 x UP 2425	E ₁	25.419**	2.201	21.575**	22.748**	6.135	-79.627**	80.926**	D
	E ₂	22.563**	-15.574**	-7.6*	-10.74**	-31.668**	1.214	88.564**	
Harvest index									
PBW 343 x WH 283	E ₁	32.56**	4.124	5.45	23.022**	45.582**	-52.07**	50.322**	
	E ₂	18.653**	-0.276	21.33	-17.618	-37.151	56.48**	18.429**	
PBW 343 x WH 542	E ₁	31.307**	2.847	-1.07	4.013	1.093	9.71	0.823	
	E ₂	20.187**	-5.796	12.58	9.156	24.209	29.59	12.309**	
PBW 343 x PBW 435	E ₁	29.293**	2.584	46.802**	56.236**	-1.964	-68.644**	101.763**	D
	E ₂	21.433**	-3.849	20.63*	27.742*	7.702	-53.39**	104.976**	D
UP 2565 x UP 2425	E ₁	35.153**	1.862	-0.049	-4.249	18.524*	-17.849	26.381**	
EIGN 1 x Raj 3765	E ₁	29.32**	4.309	28.358**	30.458**	19.484	-28.662**	25.131**	D
	E ₂	26.167**	3.027	36.313**	43.147**	0.253	-75.16**	79.097**	D
EIGN 8 x UP 2425	E ₁	30.433**	2.504	-24.031*	-13.498	1.676	-4.871	16.882**	
	E ₂	50.5**	9.76**	-55.787**	-60.987**	29.12**	62.64**	35.678**	D

3.1 Estimation of Gene Effects on Six Parameter Model

The characters which could not be explained on simple additive-dominance model were analysed on digenic epistatic model of Jinks and Jones (1958). Estimates revealed the significance of additive gene effects (d) for days of 50% flag leaf emergence, number tillers per plant, plant height, peduncle length, and number of spikelets per spike, number of grains per spike, awn length, biological yield per plant and grain yield per plant in most of the crosses. Dominance effects (h) were significant for days to 50% flag leaf emergence, days anthesis, plant height, peduncle length, number of tillers per plant, number of spikelets per spike, number of grains per spike, 1000-grain weight, awn length, biological yield per plant, grain yield per plant and harvest index in most of the crosses. Invariably, the relative magnitude of (h) was higher than (d) in all the crosses for most of the characters. The importance of additive as well as dominance effects for most of the traits in wheat has already been reported by a number of workers; (Baksh *et al.*, 2004; Prakash, 2005; Mostafavi *et al.*, 2005; Ismail *et al.*, 2006; Esmail, 2007 and Gurmani *et al.*, 2007).

The inheritance of quantitative traits become complex as the contribution of (h) to their inheritance becomes more (Mather and Jinks, 1982). Also the sign of (h) has enhancing effects on expression in that particular direction. The negative dominance effects were noticed for almost all the characters. The digenic, interaction, i, j and l were found important for most of the characters. But the type and magnitude of epistatic effect varied from characters to character and cross to cross.

Considering individual digenic epistatic effects, additive x additive (i) effects appeared to be significant for grain yield per plant (E_1), number of grain per spike (E_2), peduncle length (E_2) in PBW 343 x WH 283. Similarly, significant (i) type of interaction was recorded for number of grains per spike (E_1) in PBW 343 x WH 542 for number of grain per spike (E_1), peduncle length (E_2), number of tillers per plant (E_2) in PBW 343 x PBW 435 and for 1000-grain weight in UP 2565 x UP 2425. Additive x dominance (j) type of gene effects were found significant in PBW 343 x WH 283 for peduncle length (E_1), days to anthesis and number of tillers per plant (E_2); in PBW 343 x WH 542 for plant height (E_1), grain yield per plant (E_1) and days to anthesis (E_2); in PBW 343 x PBW 435 for plant height (E_2); in UP 2565 x UP 2425 for harvest index (E_1); in EIGN 1 x Raj 3765 for days to anthesis (E_1), number of tillers per plant (E_1) and grain yield per plant (E_2); in PBW 343 x WH 542 for number of tillers per plant (E_1) and number of grains per spike (E_2); in PBW 343 x PBW 435 for days to anthesis and number of tiller per plant (E_1); in UP 2565 x UP 2425 for plant height (E_1); in EIGN 8 x UP2425 for number of tillers per plant (E_1), biological yield per plant (E_1) and plant height (E_2).

The crop improvement for traits controlled by complementary type epistasis (i) are easily exploitable, whereas those controlled by duplicate epistasis are difficult to exploit since in case of former type the association between the two parameter is positive (Singh and Pawar, 2005). In the present study the estimate (h) and

(l) had opposite signs in majority of all the six crosses for different characters which revealed predominance of duplicate type of epistasis. The epistasis effects were also reported for biological yield per plant (Yadav *et al.*, 1988; Pandey and Singh 2003), grain yield per plant, harvest index and other metric traits (Sharma *et al.*, 2004).

In certain cases, like in PBW 343 x WH 283 and EIGN 8 x UP 2425 for number of grains per spike (E_1); PBW 343 x WH 542 for biological yield per plant (E_1), grain yield per plant (E_1), harvest index (E_1), days to 50% flag leaf emergence (E_2) and number of tillers per plant (E_2); PBW 343 x PBW 435 for days to anthesis (E_1), number of tillers per plant (E_1); UP 2565 x UP 2425 for days to anthesis (E_1) and EIGN 1 x Raj 3765 for number of tillers per plant (E_1), the additive-dominance model was found to be inadequate, when these were subjected to six parameter model and failed to show any of the significant gene effects. This may be due to the presence of higher order interaction or G x E interaction or linkage.

For some traits in particular crosses (Table 1), the additive-dominance model was found to be inadequate and in six parameter model failed to show significant gene effects. This may be due to the presence of higher order interaction or G x E interaction or linkage. Comparing estimates from the three parameters model joint scaling test to that of six parameter model it was observed that (d) and (h) from three parameter model were unquestionably biased due to the presence of epistasis. This might have led to the changes both in term of magnitude and direction of (h) and (d) in six parameter model. The estimates of (h) were more or less same for all the characters in both the models. The estimates of (d) and (h) were generally high in six parameter model. This discrepancy might be ascribed to relative change of C_{ii} (error component) terms in inverse matrix.

4. Conclusions

Estimates of gene effects in present study revealed significant additive gene effects (d) for days of 50% flag leaf emergence, number tillers per plant, plant height, peduncle length, and number of spike lets per spike, number of grains per spike, awn length, biological yield per plant and grain yield per plant in most of the crosses. Likewise additive x additive (i) effects were found for grain yield per plant (E_1), number of grains per spike (E_2), for number of grain per spike (E_1), peduncle length (E_2), number of tillers per plant (E_2) in PBW 343 x PBW 435, for 1000-grain weight in UP 2565 x UP 2425, peduncle length (E_2) in PBW 343 x WH 283 and for number of grains per spike (E_1) in PBW 343 x WH 542. Both the additive as well as additive x additive gene effects being fixable (Novoselovic *et al.*, 2004; Kaur and Singh, 2004) simple pedigree method followed by simple selection in crosses like PBW 343 x PBW 435, UP 2565 x UP 2425, PBW 343 x WH 283 and in PBW 343 x WH 542 will be useful for improvement of traits governed by such gene effects. However, for improvement of traits governed by dominance gene effects and, additive x dominance and dominance x dominance digenic interactions with prevalence of duplicate epistasis, some sort of intermating followed by selection in later generations will be advisable (Prakash, 2005; Singh and

Pawar, 2005) as release of additional genetic variability may express more additive and additive x additive effects.

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