

ADDITIVE AND NON-ADDITIVE GENE EFFECTS FOR QUANTITATIVE TRAITS THROUGH LINE X TESTER ANALYSIS IN MULBERRY SILKWORM

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ABSTRACT

Combining ability effects were studied for thirteen quantitative parameters in silkworm *Bombyx mori* through line x tester mating design. Three evolved multivoltine lines (MU₁, MU₁₁, MU₃₀₃) and one popular multivoltine race Pure Mysore were involved in the study and identified as females (lines) and two commercially popular bivoltine breeds (CSR₂ and NB₄D₂) along with two evolved bivoltine breeds of Mysore University (MG₄₀₈ and MU₈₅₄) were chosen as males (testers) and a total of sixteen hybrids were derived. All the twenty-four genotypes were reared under standard rearing conditions. Among the lines, MU₁ and MU₁₁ and the two testers MG₄₀₈ and NB₄D₂ exhibited significant +ve general combining ability (GCA) effects for most of the traits under study indicating the importance of additive gene action. Out of sixteen hybrids MU₁ x MG₄₀₈, MU₁₁ x CSR₂, MU₃₀₃ x MU₈₅₄ and PM x NB₄D₂ were found to be the best hybrid combinations with significant specific combining ability (SCA) effects confirming the importance of non-additive gene action. The ANOVA results based on the pooled data for thirteen economic traits revealed significant interaction among the testers, lines and between lines x testers. The developments of new hybrids through line x tester analysis are here in discussed.

INTRODUCTION

Silkworm *Bombyx mori*, a member of the order Lepidoptera is one of the popular silk producing insect in the world. Because of the inherent racial features with complimentary open genetic system, silkworm geneticists and breeders are constantly involved in synthesizing new gene combinations of silkworm with distinct quantitative traits for commercial exploitation to augment with the silk production. Hence, rich collection of silkworm races are maintained in the germplasm stations both in the tropical and temperate countries and these races are characterized and exploited through heterosis and hybrid vigour. But it is important that the extent of hybrid vigour depends on the inherent genetic endowment of a race and the amount of heterosis is the difference between the crossbreeds and inbred means. When inbred lines are crossed the progeny show an increase of those characters that previously suffered a reduction from inbreeding (Falconer, 1989). Hence, it is of paramount importance to select promising hybrids by crossing genotypes of inbred lines which are either purebreeds evolved for higher combining ability. For this purpose selected races/lines are crossed with a set of testers (line x tester) for evaluating general combining ability (GCA), specific combining ability (SCA) and genetic parameters. As a result, line x tester analysis has emerged as one of the quickest means of biometrical genetical tools to identify the genetic makeup of the parent material in the hybridization programme (Kempthorne, 1957). This method was successfully applied as one of the popular methods in

silkworm breeding in addition to diallel analysis both in tropical and temperate regions where sericulture is intensively practiced to identify the best combiners. (Harada, 1956; Narasimhanna, 1976; Kwon Yawl Chang *et al.*, 1981; Subba Rao, 1983; Gamo and Hirabayashi, 1983; Datta and Pershad, 1988; Bhanuprakash *et al.*, 1994; Liu *et al.*, 1994; Ramesh and Subramanya, 2009).

India, standing second place in the global silk production has all the capabilities to increase the silk production by many folds. The gifted tropical environment and introduction of elite hybrids for commercial exploitation may open up new avenues for the ever increase in the demand for silk production (Subramanya *et al.*, 1988; Chandrashekaraiiah, 1992; Rao *et al.*, 2004; Singh *et al.*, 2005). In the light of the above and realizing the importance of line x tester method, the present investigation was designed for the analysis of thirteen quantitative traits of each of the four lines and testers and sixteen hybrids with an objective to estimate effects due to general and specific combining abilities in the F₁ progenies derived by line x tester crosses.

MATERIALS AND METHODS

Selection of parents

Three improved multivoltine breeds namely MU₁, MU₁₁, MU₃₀₃ developed in the Department of Sericulture, University of Mysore and locally adapted popular multivoltine race "Pure Mysore" (Henceforth designated as PM) were selected as

female parents and denoted as lines. Four testers used as male components are bivoltine breeds viz., NB₄D₂, CSR₂, MU₈₅₄ and MG₄₀₈. Among the four testers, NB₄D₂ and CSR₂ are popular bivoltine breeds where as MG₄₀₈ and MU₈₅₄ are evolved bivoltine breeds of the University.

Crossing procedure: (lines x testers)

The line x tester mating between moths of each of the four lines and testers has resulted in the sixteen F₁ hybrid combinations. The details of the parents and the hybrids are presented in Table 1.

Table 1: Parental races and hybrids used in the line x tester analysis

Parents	Crosses	
Lines		
MU ₁	MU ₁ x CSR ₂	MU ₃₀₃ x CSR ₂
MU ₁₁	MU ₁ x NB ₄ D ₂	MU ₃₀₃ x NB ₄ D ₂
MU ₃₀₃	MU ₁ x MG ₄₀₈	MU ₃₀₃ x MG ₄₀₈
PM	MU ₁ x MU ₈₅₄	MU ₃₀₃ x MU ₈₅₄
Testers		
CSR ₂	MU ₁₁ x CSR ₂	PM x CSR ₂
NB ₄ D ₂	MU ₁₁ x NB ₄ D ₂	PM x NB ₄ D ₂
MG ₄₀₈	MU ₁₁ x MG ₄₀₈	PM x MG ₄₀₈
MU ₈₅₄	MU ₁₁ x MU ₈₅₄	PM x MU ₈₅₄

Rearing and assessment of quantitative traits

The eight parents and sixteen crosses were reared in a completely randomized design (CRD) of 300 larvae each replicated three times by following the standard rearing techniques of Yokoyama (1962) and Krishna swami (1978). Data on the thirteen quantitative traits namely fecundity, hatching percentage, larval weight, larval duration, yield/10,000 larvae brushed by number (Yield by number), yield/10,000 larvae brushed by weight (yield by weight), single cocoon weight, single shell weight, shell percentage, filament length, denier, renditta and pupation rate were recorded following the standard procedure.

Statistical analysis

The following statistical analysis was carried for line x tester analysis utilizing the procedure of Kempthorne (1957).

Analysis of variance (ANOVA): As a first step in the line x tester analysis, F values were estimated among the parents and crosses utilizing the pooled rearing data for one year.

Estimation of general combining ability effects

$$i. \text{ Lines } g_i = \frac{X_i}{tr} - \frac{X}{ltr}, \quad i=1 \text{ to } l$$

$$ii. \text{ Testers } g_j = \frac{X_j}{tr} - \frac{X}{ltr}, \quad j=1 \text{ to } t$$

Estimation of specific combining ability effects

$$\text{Hybrids } S_{ij} = \frac{X_{ij}}{r} - \frac{X_i}{tr} - \frac{X_j}{lr} + \frac{X}{ltr}$$

Where,

g_i = general combining ability of lines; g_j = general combining ability of testers; S_{ij} = specific combining ability effects for hybrids; l = Number of lines; t = Number of testers; r = Number of replications; X_i = Grand total of ith lines with "t" testers; X_j = Grand total of jth tester with "l" lines; X_{ij} = Performance of (i x j)th hybrid; X = Grand total

RESULTS

The mean values along with standard errors of four

Table 2: Mean values of the thirteen quantitative traits of the lines and testers

Parents	Fecundity (Nos.)	Hatching (%)	Larval dur. in (h)	Larval wt. in (g)	Yield by no.	Yield by wt. (kg)	Single cocoon wt (g)	Single shell wt (g)	Shell (%)	Shell ratio (%)	Filament length (m)	Denier	Renditta	Pupation rate (%)
Lines														
MU ₁	539.56	97.33	525.00	27.93	9521.4	12.06	1.287	0.206	15.90		551.11	2.081	10.61	94.22
MU ₁₁	537.78	97.34	529.44	27.95	9536.6	12.08	1.302	0.210	16.13		554.77	2.062	10.40	94.11
MU ₃₀₃	527.67	97.07	529.44	26.94	9491.2	11.60	1.261	0.200	15.75		542.33	2.061	11.00	93.11
Pure Mysore	432.33	97.61	634.00	22.76	9619.4	9.70	1.034	0.133	12.82		333.88	2.016	11.13	94.55
Mean	509.33	97.33	554.47	26.39	9542.1	11.36	1.221	0.184	15.15		495.52	2.055	12.54	93.99
SE	13.52	0.18	0.64	13.38	17.45	0.30	0.03	0.009	0.41		28.22	0.24	0.22	0.007
CD at 1 %	35.87	1.66	24.00	1.58	235.13	1.18	0.09	0.02	0.98		24.81	0.03	0.68	1.97
Testers														
MC ₄₀₈	569.11	97.63	550.11	39.65	9466.5	16.84	1.896	0.383	20.33		963.22	2.42	7.46	93.60
MU ₈₅₄	553.33	96.51	539.77	38.99	9360.1	16.09	1.783	0.346	19.40		950.22	2.44	8.97	92.62
CSR ₂	516.88	94.29	551.77	40.34	9266.1	16.07	1.920	0.398	20.72		1008.40	2.42	7.02	91.53
NB ₄ D ₂	552.00	96.87	541.77	38.14	9426.4	16.96	1.843	0.359	19.47		947.00	2.44	8.64	92.26
Mean	547.83	96.32	545.85	39.28	9379.8	16.49	1.860	0.371	19.98		967.21	2.43	8.02	92.50
SE	2.61	0.39	0.27	1.83	57.95	0.19	0.10	0.009	0.28		9.12	0.18	0.06	0.006
CD at 1 %	23.34	1.07	17.97	2.17	196.22	1.47	0.10	0.04	1.41		63.89	0.05	0.40	1.74

Table 3: Mean squares of analysis of variance for line x testers design for thirteen quantitative traits

Source of variations	df	Fecundity (Nos.)	Hatching (%)	Larval dur. in (h)	Larval in (g)	Larval Wt. by no.	Yield wt. (kg)	Single cocoon wt (g)	Single shell wt (g)	Shell ratio (%)	Filament length (m)	Denier	Renditta	Pupation rate (%)
Replications	2	20.29	0.3355	0.3695	0.7654	520.106	0.01342	0.00014*	0.0000	0.42473*	62.4634*	0.00003	0.00015	0.20525*
Treatments	23	2230.48*	3.5846	55.7186*	2091.28*	45703.56*	12.2473*	0.15812*	0.01246*	10.06671*	76155.86*	0.04250*	5.5177*	8.73645*
Parents	7	5767.56*	3.3957	148.77*	3756.55*	97673.29*	24.9131*	0.35741*	0.02872*	22.6318*	204750.46*	0.12182*	11.4400*	13.6395*
ParentsVs	1	34.02	0.6752	77.14*	456.46*	178928.93*	96.833*	0.9861*	0.05416*	34.1185*	63966.84*	161.178*	39.3784*	15.7785*
Crosses														
Crosses	15	726.28*	1.0141	10.8635*	823.78*	12569.32*	0.6975*	0.00991*	0.00209*	2.5995*	16957.64*	85.916*	0.4965*	5.9788*
Lines	3	23094.33*	2.7071	17.5355*	8501.98*	9526.41*	3.5549*	0.0494*	0.00458*	6.8603*	34978.81*	0.00159*	3.5653*	0.2222*
Testers	3	477.58*	13.3901*	3.8299*	111.144*	143600.74*	1.2546*	0.02961*	0.00396*	2.6609*	1963.95*	0.00058*	1.5237*	18.2562*
LinesxTesters	9	1100.88*	6.0775*	2.2092*	22.6154*	5633.00*	0.17826*	0.00191*	0.00025*	0.29593	2011.92*	0.00193*	0.08590*	2.4508*
Error	46	388.82	4.6899	0.0418	3.5110	994.74	0.01444	0.00010	0.00001	0.36391	31.0233	0.00009	0.00232	0.11829

Table 4: General combining abilities (GCA) of the lines and testers

Lines/ Testers	Fecundity (Nos.)	Hatching (%)	Larval dur. in (h)	Larval in (g)	Larval Wt. by no.	Yield wt. (kg)	Single cocoon wt (g)	Single shell wt (g)	Shell ratio (%)	Filament length (m)	Denier	Renditta	Pupation rate (%)
Lines (Female)													
MU ₁	3.000	-0.111	-3.201	-0.044	16.264	0.154	0.021	0.010	0.357	15.674	-0.012	-0.176	0.326
MU ₁₁	9.889	0.307	-4.451	1.815	23.847	0.372	0.037	0.004	0.403	20.257	-0.015	-0.166	0.660
MU ₃₀₃	6.083	0.348	-2.424	0.528	-21.097	-0.025	-0.002	-0.002	-0.069	7.618	-0.002	0.014	-0.868
Pure Mysore	-18.972	-0.544	10.076	-2.299	-19.014	-0.502	-0.056	-0.023	-0.691	-43.549	0.029	0.328	-0.118
SE	0.8393	0.0922	0.5409	0.0591	9.1047	0.0347	0.0029	0.0008	0.1741	1.6079	0.0027	0.0139	0.0993
Testers (males)													
MG ₄₀₈	6.861	0.002	-10.313	0.067	38.820	0.239	0.034	0.020	0.746	70.201	-0.042	0.279	0.521
CSR ₂	-1.111	0.223	25.326	0.720	-84.819	0.267	0.042	0.017	0.512	52.090	-0.035	-0.195	-1.757
MU ₈₅₄	-8.250	-0.398	-10.229	0.662	16.375	-0.070	0.031	-0.007	-0.060	-29.854	0.021	-0.048	0.299
NB ₄ D ₂	-14.000	0.173	-4.785	-1.449	29.625	-0.436	-0.045	-0.030	-1.198	-92.437	0.056	0.521	0.937
SE	0.8393	0.0922	0.5409	0.0591	9.1047	0.0347	0.0029	0.0008	0.1741	1.6079	0.0027	0.0139	0.0993

Table 5: Specific combining abilities in the new multi x bi hybrids

Hybrids	Fecundity (Nos.)	Hatching (%)	Larvaldur. in (h)	Larval Wt. in (g)	Yield by no.	Yield by. wt. (kg)	Single cocoon wt (g)	Single cocoon wt (g)	Single shell wt (g)	Shell ratio (%)	Filament length (m)	Denier	Renditta	Pupation rate (%)
PM X CSR ₂	4.333	-0.382	-0.057	-3.604	-74.209	-0.114	-0.018	-0.018	-0.008	-0.252	0.160	0.005	-0.017	-0.604
PM X NB ₄ D ₂	0.667	0.724	0.852	-1.049	21.681	0.384	0.021	0.021	0.012	0.444	43.576	-0.034	0.043	0.035
PM X MG ₄₀₈	-0.750	-0.688	-0.200	0.813	46.708	-0.239	-0.020	-0.020	-0.008	-0.202	-30.729	-0.006	-0.012	0.674
PM X MU ₈₅₄	-4.250	0.346	-0.595	3.840	5.819	-0.030	0.017	0.017	0.004	0.010	-13.007	0.03	-0.014	-0.104
MU ₁ X CSR ₂	-10.412	0.045	0.143	0.896	-5.042	-0.051	0.003	0.003	0.004	0.159	20.715	-0.011	-0.234	0.729
MU ₁ X NB ₄ D ₂	-4.306	-0.297	0.173	-1.437	-17.486	-0.126	-0.020	-0.020	-0.002	0.138	-1.535	-0.004	-0.108	-0.632
MU ₁ X MG ₄₀₈	7.833	0.208	0.823	-1.354	13.208	0.278	0.031	0.031	0.006	-0.013	-0.951	-0.001	0.160	0.007
MU ₁ X MU ₈₅₄	6.889	0.045	-1.139	1.896	9.320	-0.101	-0.015	-0.015	-0.008	-0.284	-18.229	0.016	0.182	-0.104
MU ₁₁ X CSR ₂	3.139	-0.147	-0.018	1.590	47.375	0.267	0.036	0.036	0.010	0.134	-8.179	-0.002	0.083	1.285
MU ₁₁ X NB ₄ D ₂	0.228	0.083	-0.300	1.479	-15.403	-0.164	-0.007	-0.007	-0.003	-0.078	-22.451	0.031	-0.102	0.035
MU ₁₁ X MG ₄₀₈	0.056	0.404	0.094	-1.215	-1.931	0.030	-0.008	-0.008	-0.001	0.042	9.299	-0.010	0.014	-0.660
MU ₁₁ X MU ₈₅₄	-3.222	-0.174	0.224	-1.854	-30.042	-0.133	-0.021	-0.021	-0.006	-0.099	22.132	-0.019	0.006	-0.660
MU ₃₀₃ X CSR ₂	2.944	0.484	-0.068	1.118	31.875	-0.102	-0.020	-0.020	-0.005	-0.041	-11.896	0.008	0.168	-1.410
MU ₃₀₃ X NB ₄ D ₂	3.611	-0.344	-0.725	1.007	11.208	-0.094	0.005	0.005	-0.008	-0.505	-19.590	0.007	0.168	0.562
MU ₃₀₃ X MG ₄₀₈	-7.139	0.077	-0.718	1.757	-57.986	-0.069	-0.003	-0.003	0.002	0.173	9.549	0.017	-0.162	-0.021
MU ₃₀₃ X MU ₈₅₄	0.583	-0.216	1.511	-3.882	14.903	0.265	0.019	0.019	0.010	0.373	21.938	-0.032	-0.174	0.868
SE	1.6786	0.1844	0.1182	1.0818	18.2094	0.0694	0.0059	0.0059	0.0017	0.3483	3.2158	0.0054	0.0298	0.1986

Table 6: Percent contribution of lines, testers and lines x testers for different quantitative traits in the silk worm *Bombyx mori*

Source	Fecundity (Nos.)	Hatching (%)	Larvaldur. in (h)	Larval Wt. in (g)	Yield by no.	Yield by. wt. (kg)	Single cocoon wt (g)	Single cocoon wt (g)	Single shell wt (g)	Shell ratio (%)	Filament length (m)	Denier	Renditta	Pupation rate (%)
Line	55.4871	41.2790	13.3502	65.2709	10.4370	47.6126	40.1570	40.1570	31.5891	23.7367	12.3155	13.0681	26.8423	17.5180
Testers	34.4077	18.7707	85.0027	22.5276	62.6737	37.0548	48.2777	48.2777	61.2993	69.4339	80.5659	71.2626	62.7783	57.8866
Lines X Testers	10.1052	39.9504	1.6472	12.2016	26.8893	15.3326	11.5654	11.5654	7.1316	6.8304	7.1186	15.6693	10.3794	24.5954

multivoltines designated as lines namely MU₁, MU₁₁, and MU₃₀₃ and PM and four bivoltine testers CSR₂, NB₄D₂, MG₄₀₈ and MU₈₅₄ for each of the thirteen quantitative traits such as fecundity, hatching percentage, larval weight, larval duration, yield by number, yield by weight, single cocoon weight, single shell weight, shell percentage, filament length, denier, renditta and pupation rate are presented in Table 2. Comparison of the mean values of the lines and testers showed significant genotypic differences for most of the quantitative traits under study (p < 0.05). The testers exhibited higher values for the traits of fecundity, larval weight, single cocoon weight, single shell weight, shell percentage, filament length where as the lines exhibited higher yield by number and pupation rate.

Table 3 reveals the data in regard to the analysis of variance for combining ability of lines, testers and line x tester. It is evident from the data that higher mean squares were observed for lines than testers for all the traits except hatching percentage, yield by number and pupation rate. Though there was not much difference between replications, yet significance differences were noticed between treatments, parents and parents x crosses.

The estimates of general combining abilities effects in each of the four multivoltine and bivoltine parents are recorded in Table 4. It is noteworthy that among four multivoltines MU₁₁ and MU₁ has emerged as good general combiners with high +ve GCA effects for ten and eight quantitative traits respectively followed by MU₃₀₃ for five traits and PM for three traits. Among bivoltine testers MG₄₀₈ ranked first exhibiting best +veGCA for eleven traits under study followed by CSR₂ for eight traits and MU₈₅₄ and NB₄D₂ for five traits each. Among the lines MU₁ and MU₁₁ and MG₄₀₈ and CSR₂ as testers exhibited highly significant +ve GCA effects.

Table 5 depicts the SCA effects of sixteen crosses. Out of sixteen crosses, the four crosses namely MU₁ x MG₄₀₈, MU₁₁ x CSR₂, PM x NB₄D₂ and MU₃₀₃ x MU₈₅₄ were found as the best specific combinations by exhibiting +veSCA for nine of the thirteen traits analyzed. It is evident that none of the crosses exhibited consistent SCA effects for all the thirteen quantitative traits analysed.

In Table 6 the percent contributions of lines, testers and interaction between line x tester for total variances for thirteen characters are recorded. Data from Table 6 clearly demonstrates that both males and females are substantially contributing for the expression of many of the traits under study.

DISCUSSION

Systematic animal and plant breeding programmes are being practiced since a long time in order to cope-up with increased productivity. In the breeding procedure several biometrical genetical tools are being frequently applied for evaluating the breeds. Among them line x tester analysis (Kempthorne, 1957) is very popular and effectively utilized to draw information on the general and specific combining abilities of parents and crosses respectively. In the present studies the genetic endowment contributed by three multivoltine lines namely, MU₁, MU₁₁ and MU₃₀₃ and a pure breed PM as female partners could be best understood in relation to the contributions made by male parents as testers namely NB₄D₂, CSR₂, MU₈₅₄ and MG₄₀₈ through combining ability studies. It is important that many silkworm breeders in several countries have successfully employed such a type of analysis in silkworm breeding programmes (Arunachalam, 1974; Sohn and Hong, 1986; Tayade, 1989; Sofi, 1994; Subramanya, 1996).

Scrutiny of the Table 2 on the mean values of the thirteen quantitative traits under evaluation both in the lines and testers have shown differential performances of multivoltine lines and bivoltine testers. Reference to Table points out that lines have higher survival rate than the testers. This is in conformity with the observations of Narasimhanna and Gururajan (1965) and Narasimhanna, (1976) who have demonstrated superiority of multivoltine breeds for viability traits compared to bivoltine breeds. The present findings are in conformity with the findings of the Yokoyama, (1962) who have demonstrated variability in the viability traits among different voltinistic traits. It is also clear from the data that the multivoltine lines though exhibited higher values for productivity traits compared to PM yet, there are significant differences for productivity traits ($p < 0.05$) between lines and testers wherein the bivoltines excel the multivoltine lines for these traits.

By virtue of the analysis of variance data presented in table-3, there is significant differences among parents ($p < 0.05$) justifying the selection of the lines and testers in the present investigation. Further, it is important to note from the data that the variance due to parents vs. crosses was highly significant for all the traits except fecundity and hatching percentage. Falconer (1989) proposed that genes that show no dominance ($d = 0$) are called additive genes are said to act additively. Based on this, it is possible to say that additive gene actions may be operating in the expression of these two traits. It is noteworthy from the results in Table 3 that the variance due to lines and testers was highly significant at 5% probability level for almost all the traits under study. Thus, a concordance of the ANOVA results based on the significant mean sum of errors indicates the involvement of non-additive gene action (dominance, additive x dominance, dominance x dominance) operating on the expression of the traits. The present results are in conformity with the findings of Satenahalli *et al.*, (1989 and

1990), Chauvan *et al.*, (2000) utilizing silkworm *Bombyx mori* who have demonstrated both additive and non- additive gene action for the expression of the quantitative traits in the life cycle of the silk moth. This aspect strongly supports the views of Comstock *et al.*, (1949), who proposed that both additive and non- additive gene effects play predominant role in any breeding programme.

Based on the general combining ability effects of the lines and testers presented in Table 4, it is clear that among lines MU₁₁ exhibited significant general combining ability effects for ten out of thirteen traits studied followed by eight traits in MU₁ and five traits in MU₃₀₃. On the other hand Pure Mysore has recorded significant ($p < 0.05$) general combining ability effects for only three traits. Quite contrary to the lines, the MG₄₀₈ as tester recorded +ve general combining ability effects for eleven traits followed by CSR₂ exhibited significant +ve general combining ability effects for eight out of thirteen traits under study. Similarly, MU₈₅₄ and NB₄D₂ recorded +ve general combining ability effects for five traits. Thus, higher +ve GCA effects for many of the traits under study among lines and testers underline the superiority of lines and testers and helped in the present investigations to draw the best general combiners. In a similar studies utilizing multivoltines as lines and bivoltines as testers, Datta and Pershad (1988), Subbarao and Sahai (1989), Narasimhanna, (1976), recorded more of +ve GCA effects for selected quantitative traits. Based on the GCA effects it is possible to conclude that MU₁₁ to be the best combiner with highest +ve GCA effects for ten out of thirteen traits where as MG₄₀₈ topped the list among testers with +ve GCA effects for eleven traits followed by CSR₂ for eight traits. This is a clear indication how additive gene action is playing major role in the expression of characters under study in these races.

Scrutiny of the Table 5, for SCA effects for thirteen traits under study among the hybrids have revealed that PM x NB₄D₂, MU₁ x MG₄₀₈, MU₁₁ x CSR₂ and MU₃₀₃ x MU₈₅₄ recorded +ve SCA effects for a maximum of nine out of thirteen traits. It is obvious that none of the hybrids exhibited consistent SCA effects for the entire thirteen quantitative traits under study. From the point of variable environmental conditions of tropics, the crosses MU₁₁ x CSR₂, MU₃₀₃ x MU₈₅₄ are very important since they ranked first for the pupation rate with high +ve SCA effects. The variable SCA effects were reported by many breeders both in bi x bi and multi x bi hybrids. As pointed out by Henderson (1964) the specific combining ability is the consequence of intra- allelic (dominance) and inter-allelic (Epistasis) gene action.

The proportional contribution of lines and testers calculated in percentage and their interaction to the total variance for different characters are presented in Table 6. It is evident from the table that the contribution of the females (lines) are noteworthy for fecundity, hatching percentage, larval weight and yield/number where as the males (testers) contributed for all the other traits with a maximum contribution of lines x testers for hatching percentage, yield/number and pupation rate. Thus based on the results from Table 6, the significant contributions and superiority of both the parents are noteworthy.

The overall picture that emerges out of the present studies is

that both additive genetic variance and predominant non-additive genetic variance would be very helpful for estimating combining ability analysis through line x tester analysis. The present findings is in conformity with the observations of Comstock *et al.*, (1949) wherein, more of non-additive type of gene action observed for many traits in addition to a few additive effects for known traits are important in any breeding programmes. Based on this, the four hybrids identified viz., $PM \times NB_4D_2$, $MU_1 \times MG_{408}$, $MU_{11} \times CSR_2$ and $MU_{303} \times MU_{854}$ may be utilized for predicting high yield by number and weight in the variable tropical environment.

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