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## Heterosis and Combining Ability Analysis among Indigenous and Newly Developed Bivoltine Silkworm, *Bombyx mori* L.

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### ABSTRACT

Heterosis and combining ability studies of the isolated variable multivoltine races and developed bivoltine races with high yield capacity and their eighteen combinations were evaluated in two commercial rearing seasons in Bangladesh. Appropriate statistical methods were employed to interpret data on the hybrid performance, general and specific combining ability of the hybrids. Analysis of variance for combining ability revealed larger mean squares. Here high  $\delta_{gca}^2/\delta_{sca}^2$  values for most of the characters reflected predominant additive gene action. Similarly, the variance of components of specific combining ability ( $\delta_{sca}^2$ ) of multivoltine×bivoltine were higher than those of general combining ability ( $\delta_{gca}^2$ ) for most of the characters in both the seasons indicating preponderance of non-additive gene action inheritance of all these traits. Among the combinations BSR-BN(B<sub>1</sub>)×BSRB-BB<sub>1</sub> and BSR-3×BSRB-BB<sub>2</sub> exhibited highly productive performance which could be recommended for commercial cocoon production in Bangladesh.

**Key words:** *Bombyx mori* L., heterosis, combining ability

### INTRODUCTION

In recent times among the various genetic principles and breeding techniques, utilization of heterosis is one of the major breakthroughs which contributed to the success of modern silkworm breeding. Hybrids obtained from genetically diverse inbred lines are usually vigorous, productive and sturdier than either the parents. As a result, introduction of hybrids, instead of pure strains is the target to increase production. As a result, preparation of suitable hybrids, selection of parents and knowledge on the nature as well as magnitude of gene action is of paramount importance to the breeders to have a sound breeding program. Combining ability has been used for the assessment of relative breeding potential of parental materials along with the genetic components involved in the inheritance of commercially important traits of *B. mori* (Kempthorne, 1957; Strunnikov, 1986; Subba Rao and Sahai, 1989; Satenahalli *et al.*, 1989a, b, 1990a, b; Sarkar *et al.*, 1991). In Bangladesh heterosis breeding in silkworm has not been properly exploited due to inadequate

information on the magnitude of heterosis of quantitative traits (Mahfuzar *et al.*, 1992; Rahman *et al.*, 1996; Rahman and Jahan, 1997; Ali and Kamal, 1998; Haque *et al.*, 2007). In the present study, an attempt was made to find out the magnitude of heterosis and combining ability in silkworm for characters contributing to yield.

### MATERIALS AND METHODS

**Materials:** A line×tester crossing design was followed where 6 lines of multivoltine (BSR-BN(M)-P<sub>1</sub>, BSR-BN(B<sub>1</sub>)-P<sub>2</sub>, BSR-BN(P)-P<sub>3</sub>, BSR-IDC-P<sub>4</sub>, BSR-3-P<sub>5</sub>, BSR-10-P<sub>6</sub> and 3 testers of bivoltine (BSRB-BB<sub>1</sub>-P<sub>7</sub>, BSRB-BB<sub>2</sub>-P<sub>8</sub> and BSRB-03(sl)-P<sub>9</sub>) silkworm *B. mori* L. were utilized for the experiment.

**Methods:** A total of 27 hybrid combinations and parents were developed through line×tester analysis technique (Kempthorne, 1957). The experiment was conducted in three replications in the two very important commercial rearing

seasons viz. Agrahyoni (October-November' 12-S<sub>1</sub>) and Chaita (February-March' 13-S<sub>2</sub>). The experimental rearing was conducted in a randomized block design and standard rearing techniques suggested by Krishnaswami (1978) were followed. Cocoons were harvested as per the schedule without any interruption. Observations on single cocoon weight, shell weight and Shell Ratio percentage (SR%) were carefully recorded. General and Specific Combining Ability (GCA and SCA) and their variations were calculated according to Kempthorne (1957). Heterosis over both mid-parent (MP) and better-parent (BP) were calculated for all the 18 crosses in both the seasons by using the following equation:

$$\text{Heterosis over mid-parent (MP)} = \frac{F_1 - \text{MP}}{\text{MP}} \times 100$$

$$\text{Heterosis over better-parent (BP)} = \frac{F_1 - \text{BP}}{\text{BP}} \times 100$$

The combining ability analysis was based on the procedure developed by Kempthorne (1957). In the first step, analysis of variance for different seasons were estimated to test the significance of differences among the genotypes, including crosses and parents (treatment). The treatment SS was further partitioned into various components like parents, crosses and parent vs. crosses. These components were calculated as follows:

$$\text{SS (cross)} = \frac{\sum \sum C_{ij}^2}{r} - \text{CF(crosses)}$$

and:

$$\text{SS (parents)} = \frac{\sum \sum P_{ij}^2}{r} - \text{CF(parents)}$$

Where:

- C<sub>ij</sub> = Observation i×jth cross
- P<sub>ij</sub> = Observation for the parents
- r = No. of replications

The SS (parents vs. crosses) was calculated by a generalized formula, as follows:

$$\text{SS (P vs. C)} = \frac{\left[ \sum^a (c \sum y) \right]^2}{n \sum^a c^2}$$

Where:

- n = No. of observations added in a sum
- c = Coefficient of contrast

- a = No. of groups
- y = Sum of entries in a contrasted set

Different components for line×tester ANOVA were obtained from the pooled data on line×tester. The estimates of general and specific combining abilities were calculated using the following equation:

$$\text{GCA (line)} = \frac{X_{i\dots}}{\text{tr}} - \frac{X_{\dots}}{\text{ltr}}$$

$$\text{GCA (tester)} = \frac{X_{j\dots}}{\text{lr}} - \frac{X_{\dots}}{\text{ltr}}$$

and:

$$\text{SCA} = \frac{X_{ij\dots}}{r} - \frac{X_i}{\text{tr}} - \frac{X_j}{\text{lr}} + \frac{X_{\dots}}{\text{ltr}}$$

Where:

- t = No. of testers
- l = No. of lines
- r = No. of replications

General and Specific Combining Ability (GCA and SCA) were calculated as:

$$\text{SE (GCA for line)} = (\text{MS}_e / r \times t)^{1/2}$$

$$\text{SE (GCA for tester)} = (\text{MS}_e / r \times t)^{1/2}$$

and:

$$\text{SE (SCA effects)} = (\text{MS}_e / r)^{1/2}$$

Where:

- MS<sub>e</sub> = Error mean sum of square

## RESULTS AND DISCUSSION

Results revealed that for cocoon weight and shell weight significant positive heterosis was expressed over better-parent in S<sub>1</sub> where for Shell Ratio percentage (SR%) only three crosses showed significant positive values (Table 1). The percentage of heterosis for single cocoon weight and shell weight over their respective better-parents ranged from 5.38-31.79 and 4.65-24.05 in S<sub>1</sub> while for SR%, the value ranged from 2.89-8.26 in the same season. Similarly, 17 crosses for single cocoon weight, 14 crosses for shell weight and none for SR%, exhibited significant positive values in S<sub>2</sub> season. The percentage of heterosis for single cocoon weight and shell weight over the same parent, ranged from 5.08-19.75 and 2.88-12.25. Results indicated that almost all the crosses for single cocoon weight, shell weight and SR%

Table 1: Heterosis in percentage over better-parent and mid-parent for three economic parameters in silkworm *Bombyx mori* L

Crosses	Heterosis percentage over Better-Parent (BP)						Heterosis percentage over Mid-Parent (MP)					
	S <sub>1</sub>			S <sub>2</sub>			S <sub>1</sub>			S <sub>2</sub>		
	Single cocoon weight	Single shell weight	SR (%)	Single cocoon weight	Single shell weight	SR (%)	Single cocoon weight	Single shell weight	SR (%)	Single cocoon weight	Single shell weight	SR (%)
P <sub>1</sub> ×P <sub>7</sub>	15.43**	2.33	-3.82*	14.66**	6.49**	-4.39*	30.11**	19.80**	2.17	27.21**	24.48**	11.09**
P <sub>1</sub> ×P <sub>8</sub>	20.10**	1.55	-2.24	17.01**	7.93**	-5.76**	32.94**	18.01**	2.67*	27.43**	23.23**	8.70**
P <sub>1</sub> ×P <sub>9</sub>	14.49**	11.64**	2.29	17.60**	7.21**	-3.05*	22.82**	19.80**	4.93**	28.90**	22.40**	9.35**
P <sub>2</sub> ×P <sub>7</sub>	18.70**	8.53**	-1.89	19.75**	12.25**	-1.92	29.70**	25.98**	4.84**	29.69**	28.35**	12.04**
P <sub>2</sub> ×P <sub>8</sub>	19.40**	2.33	-2.02	15.05**	7.93**	-3.22*	27.95**	17.92**	3.36*	21.79**	20.44**	9.73**
P <sub>2</sub> ×P <sub>9</sub>	31.79**	24.05**	4.20*	17.79**	7.93**	-2.18	38.61**	33.15**	7.58**	25.74**	20.44**	8.45**
P <sub>3</sub> ×P <sub>7</sub>	11.69**	0.00	-4.12*	8.60**	0.72	-6.16**	28.22**	19.00**	2.22	20.77**	17.98**	9.08**
P <sub>3</sub> ×P <sub>8</sub>	18.00**	2.33	-1.75	12.51**	6.49**	-2.65	32.94**	20.79**	3.63**	22.81**	21.73**	12.32**
P <sub>3</sub> ×P <sub>9</sub>	21.74**	17.07**	2.56	12.90**	3.60*	-4.34*	33.62**	27.96**	5.63**	24.05**	18.40**	7.90**
P <sub>4</sub> ×P <sub>7</sub>	10.52**	-2.33	-4.93**	5.08**	-1.44	-5.02**	23.36**	15.59**	3.20*	15.69**	15.99**	11.23**
P <sub>4</sub> ×P <sub>8</sub>	16.13**	0.78	-1.78	14.08**	5.77**	-5.95**	27.27**	18.28**	5.50**	23.60**	21.40**	9.35**
P <sub>4</sub> ×P <sub>9</sub>	24.78**	15.52**	2.22	11.93**	4.33*	-2.77	33.62**	25.45**	7.16**	21.90**	19.73**	10.55**
P <sub>5</sub> ×P <sub>7</sub>	5.38**	-8.53**	-6.40**	5.08**	-2.16	-7.17**	16.75**	7.35**	-0.19	15.35**	13.28**	6.31**
P <sub>5</sub> ×P <sub>8</sub>	18.94**	1.55	-1.83	17.20**	9.37**	-2.75	29.85**	18.10**	3.76**	26.87**	23.69**	10.61**
P <sub>5</sub> ×P <sub>9</sub>	21.74**	16.29**	2.89*	11.73**	2.88*	-3.93*	29.44**	25.27**	6.24**	21.34**	16.19**	6.78**
P <sub>6</sub> ×P <sub>7</sub>	-1.17	-8.53**	-4.47*	0.78	-4.33*	-6.27**	10.89**	8.60**	2.43*	10.39**	10.57**	7.15**
P <sub>6</sub> ×P <sub>8</sub>	19.87**	4.65**	-0.36	18.38**	10.81**	-2.67	32.63**	22.94**	5.86**	28.23**	25.14**	10.50**
P <sub>6</sub> ×P <sub>9</sub>	15.43**	21.72**	8.26**	8.80**	4.33*	-0.58	23.86**	32.79**	12.84**	17.95**	17.65**	10.45**

SR: Shell ratio, \*,\*\*Significant at 5 and 1% level, respectively

Table 2: Analysis of variance for combining ability of cocoon characters in silkworm *Bombyx mori* L.

Sources	df	Mean sum of square					
		S <sub>1</sub>			S <sub>2</sub>		
		Single cocoon weight	Single shell weight	SR (%)	Single cocoon weight	Single shell weight	SR (%)
Genotypes	26	0.13**	0.01**	13.87**	0.12**	0.01**	15.84**
Replications	2	0.0001	0.000024	0.33	0.002*	0.0001	0.22
Parents	8	0.04**	0.01**	22.02**	0.05**	0.01**	28.46**
Crosses	17	0.02**	0.0011**	1.94**	0.02**	0.001**	0.90**
Parents vs crosses	1	2.62**	0.16**	151.48**	2.54**	0.18**	168.97**
Lines	5	0.03**	0.0014**	3.03**	0.03**	0.0013**	0.46**
Testers	2	0.02**	0.0004**	0.39	0.01**	0.0009**	4.03**
Lines×testers	10	0.02**	0.0011**	1.71**	0.01**	0.0008**	0.49**
Error	52	0.0003	0.00003	0.40	0.0004	0.00003	0.09

\*,\*\*Significant at 5 and 1% level, respectively, tested against the error mean square, SR: Shell ratio, df: Degrees of freedom

showed significant positive heterosis over their mid-parents in both S<sub>1</sub> and S<sub>2</sub> seasons. The percentage of heterosis over their mid-parents ranged from 10.89-38.61, 7.35-33.15 and 2.43-12.84 in S<sub>1</sub> and 10.39-29.69, 10.57-28.35 and 6.31-12.32 in S<sub>2</sub> season, respectively for single cocoon weight, shell weight and SR% (Table 1).

The analysis of variance for combining ability (Table 2) revealed that the mean squares due to genotypes was highly significant, indicating much diversity among the present population. The significant results due to parent and crosses in all the characters exhibited the presence of sufficient diversity within parents and their hybrids. The lines and testers for all the characters, in both the seasons expressed high significance. Similarly, the other sources like parent vs. crosses and line×testers also exhibited high significance in both the seasons, indicating heterotic response.

Variance due to specific combining abilities for single cocoon weight, shell weight in both the seasons for all the characters highlighted predominant roles of non-additive gene action. Experimental data further expressed very high  $\delta_{gca}/\delta_{sca}$  in both the seasons, clearly indicating preponderance of additive gene action (Table 3).

The present investigation further indicated that the BSR-BN (B<sub>1</sub>) among all the lines showed significant positive GCA in both the rearing seasons for all the economic characters under consideration (Table 4) while BSR-BN(M) for cocoon weight and shell weight in S<sub>2</sub> followed by BSR-10 for SR% in S<sub>1</sub> were significant. Similarly, among the testers BSRB-BB<sub>2</sub> expressed significant positive GCA in both the seasons for cocoon and shell weight as well as for SR% in S<sub>2</sub> season, followed by similar trend in BSRB-BB<sub>1</sub> for SR% in S<sub>2</sub>.

Table 3: Components of variance for different characters in two rearing seasons

Characters	S <sub>1</sub>			S <sub>2</sub>		
	$\delta^2_{gca}$	$\delta^2_{sca}$	$\delta^2_{gca}/\delta^2_{sca}$	$\delta^2_{gca}$	$\delta^2_{sca}$	$\delta^2_{gca}/\delta^2_{sca}$
Single cocoon weight	0.0001	0.0049	0.024	0.0001	0.0045	0.027
Single shell weight	0.0000003	0.0004	0.0009	0.0000048	0.0003	0.0183
SR (%)	0.01	0.44	0.02	0.01	0.13	0.09

SR: Shell ratio

Table 4: Effect of general combining ability (GCA) of parents for three parameters in multivoltine×bivoltine silkworm, *B. mori* L.

Parents	Season	Mean sum of square			
		Single cocoon weight	Single shell weight	SR (%)	
Lines BSR-TI, BSR-BN(M)	P <sub>1</sub>	S <sub>1</sub>	-0.002	-0.004*	-0.27
		S <sub>2</sub>	0.06**	0.01**	-0.12
BSR-BN(B <sub>1</sub> )	P <sub>2</sub>	S <sub>1</sub>	0.09**	0.02**	0.43*
		S <sub>2</sub>	0.08**	0.02**	0.37**
BSR-BN(P)	P <sub>3</sub>	S <sub>1</sub>	-0.78**	-0.13**	-8.75**
		S <sub>2</sub>	-0.81**	-0.14**	-8.90**
BSR-IDC	P <sub>4</sub>	S <sub>1</sub>	0.004	-0.01**	-0.39
		S <sub>2</sub>	-0.04**	-0.01**	-0.16
BSR-3	P <sub>5</sub>	S <sub>1</sub>	-0.02**	-0.01**	-0.54*
		S <sub>2</sub>	-0.02**	-0.01**	-0.17
BSR-10	P <sub>6</sub>	S <sub>1</sub>	-0.08**	-0.001	0.97**
		S <sub>2</sub>	-0.06**	-0.01**	0.19
Testers					
BSRB-BB <sub>1</sub>	P <sub>7</sub>	S <sub>1</sub>	-0.02**	-0.004*	-0.15
		S <sub>2</sub>	-0.02**	0.001	0.28**
BSRB-BB <sub>2</sub>	P <sub>8</sub>	S <sub>1</sub>	0.04**	0.01**	0.01
		S <sub>2</sub>	0.02**	0.01**	0.26**
BSRB-03(s1)	P <sub>9</sub>	S <sub>1</sub>	-0.01*	-0.001	0.14
		S <sub>2</sub>	0.004	-0.01**	-0.55**
SE (Line)		S <sub>1</sub>	0.01	0.0018	0.21
		S <sub>2</sub>	0.01	0.0019	0.10
SE(Tester)		S <sub>1</sub>	0.004	0.0012	0.15
		S <sub>2</sub>	0.005	0.0013	0.07

SR: Shell ratio, \*,\*\*Significant at 5 and 1% level, respectively

The experimental results on Specific Combining Ability (SCA) exhibited both positive and negative effects in different characters where three crosses resulted in significant positive values in most of the characters in both seasons (Table 5) while 2 crosses showed significant positive values for two characters in the same S<sub>1</sub> season and the other for two characters in two separate seasons. Similarly, another 3 crosses exhibited significant positive values for single character, only in one season. Among the most encouraging combinations, only one cross (P<sub>2</sub>×P<sub>7</sub>) showed significant positive values for all the characters in both the seasons, followed by 3 crosses (P<sub>1</sub>×P<sub>7</sub>, P<sub>5</sub>×P<sub>8</sub> and P<sub>6</sub>×P<sub>8</sub>) which exhibited positive values for the same two characters like cocoon and shell weight in both the seasons.

Heterosis has been exploited by crossing the inbred lines of genetic diversity, geographical origin and voltinism in silkworm, *B. mori* L. In a hybridization programme, identification of parents is a prerequisite for maximum exploitation of heterosis. To achieve this goal, it is necessary to understand the combining ability of parents, which help in the selection of suitable parents for hybridization. This is because, high yielding parents may not necessarily transfer their superiority to the progenies in the hybrid crosses.

Selection of suitable parents and information on nature and magnitude on gene action of traits of economic importance determine the success of any crop improvement programme.

Under the multivoltine×bivoltine experiment, heterosis has been observed in a series of crosses of *B. mori* L. for different characters. Their range of heterosis varied from season to season. In this study a reasonable amount of heterosis was seen in their respective crosses, where BSR-BN (B<sub>1</sub>) followed by BSR-BN (M) and BSR-10 were involved as lines and BB<sub>1</sub> followed by BB<sub>2</sub> as testers. Similar findings have been reported by many silkworm breeders (Subba Rao and Sahai, 1989; Satenahalli *et al.*, 1989a, b; 1990a, b). Experimental results further indicated that, the high  $\delta^2_{gca}/\delta^2_{sca}$  values in S<sub>1</sub> for most of the characters showed predominantly an additive gene action, while the variance of component of specific combining ability ( $\delta_{sca}$ ) of multivoltine×bivoltine were higher than that of general combining ability ( $\delta_{gca}$ ) for most of the characters in S<sub>1</sub> and S<sub>2</sub> expressing preponderance of non-additive gene action in inheritance of all these traits. Non-additive gene actions governing the expression of some quantitative traits have been reported by some breeders in *B. mori* (Mahfuzar *et al.*, 1992; Rahman *et al.*, 1996). Additive and non-additive gene actions

Table 5: Specific combining ability effects for three parameters in multivoltine×bivoltine silkworm, *Bombyx mori* L.

Cross combinations	Seasons	Parameters		
		Single cocoon weight	Single shell weight	SR (%)
P <sub>1</sub> ×P <sub>7</sub>	S <sub>1</sub>	0.08**	0.02**	0.50
	S <sub>2</sub>	0.03*	0.01**	0.31
P <sub>1</sub> ×P <sub>8</sub>	S <sub>1</sub>	0.02*	0.001	-0.03
	S <sub>2</sub>	-0.04**	-0.01**	-0.36*
P <sub>1</sub> ×P <sub>9</sub>	S <sub>1</sub>	-0.10**	-0.02**	-0.48
	S <sub>2</sub>	0.01	-0.0002	0.06
P <sub>2</sub> ×P <sub>7</sub>	S <sub>1</sub>	0.03**	0.02**	0.80*
	S <sub>2</sub>	0.10**	0.03**	0.43*
P <sub>2</sub> ×P <sub>8</sub>	S <sub>1</sub>	-0.08**	-0.02**	-0.61
	S <sub>2</sub>	-0.09**	-0.02**	-0.22
P <sub>2</sub> ×P <sub>9</sub>	S <sub>1</sub>	0.05**	0.004	-0.19
	S <sub>2</sub>	-0.01	-0.01*	-0.22
P <sub>3</sub> ×P <sub>7</sub>	S <sub>1</sub>	0.02	0.005	0.27
	S <sub>2</sub>	0.02	0.001	-0.14
P <sub>3</sub> ×P <sub>8</sub>	S <sub>1</sub>	-0.02	-0.0007	0.15
	S <sub>2</sub>	-0.03*	-0.001	0.41*
P <sub>3</sub> ×P <sub>9</sub>	S <sub>1</sub>	-0.003	-0.004	-0.42
	S <sub>2</sub>	0.01	-0.0002	-0.27
P <sub>4</sub> ×P <sub>7</sub>	S <sub>1</sub>	0.002	0.003	0.06
	S <sub>2</sub>	-0.03*	-0.01	0.19
P <sub>4</sub> ×P <sub>8</sub>	S <sub>1</sub>	-0.04**	0.0004	0.33
	S <sub>2</sub>	0.01	-0.001	-0.36*
P <sub>4</sub> ×P <sub>9</sub>	S <sub>1</sub>	0.04**	-0.003	-0.39
	S <sub>2</sub>	0.01	0.01	0.17
P <sub>5</sub> ×P <sub>7</sub>	S <sub>1</sub>	-0.05**	-0.02**	-0.56
	S <sub>2</sub>	-0.04**	-0.01**	-0.33
P <sub>5</sub> ×P <sub>8</sub>	S <sub>1</sub>	0.02*	0.01**	0.45
	S <sub>2</sub>	0.05**	0.01**	0.44*
P <sub>5</sub> ×P <sub>9</sub>	S <sub>1</sub>	0.02*	0.01*	0.10
	S <sub>2</sub>	-0.01	-0.002	-0.11
P <sub>6</sub> ×P <sub>7</sub>	S <sub>1</sub>	-0.08**	-0.03**	-1.07*
	S <sub>2</sub>	0.08**	-0.02**	-0.47*
P <sub>6</sub> ×P <sub>8</sub>	S <sub>1</sub>	0.09**	0.01**	-0.29
	S <sub>2</sub>	0.10**	0.02**	0.10
P <sub>6</sub> ×P <sub>9</sub>	S <sub>1</sub>	-0.01	0.02**	1.37
	S <sub>2</sub>	-0.02	0.003	0.37*
SE(sca)	S <sub>1</sub>	0.01	0.003	0.36
	S <sub>2</sub>	0.01	0.003	0.18

SR: Shell ratio, \*,\*\*Significant at 5 and 1% level, respectively

of cocoon yield contributing characters in *B. mori* L. have been observed by many silkworm breeders (Goel *et al.*, 2010; Nagalakshamma *et al.*, 2010; Singh and Nirupama, 2012; Singh and Gangopadhyay, 2013). Predominant role of additive gene actions have been reported for cocoon weight (Islam *et al.*, 2005; Haque *et al.*, 2007), cocoon weight and shell weight (Mahfuzar *et al.*, 1992), cocoon weight, shell weight and SR% (Rahman and Jahan, 1997; Ali and Kamal, 1998). Results clearly indicate that the combinations BSR-BN (B<sub>1</sub>)×BSRB-BB<sub>1</sub> and BSR-3×BSRB-BB<sub>2</sub> for all the characters, followed by BSR-BN (M)×BSRB-BB<sub>1</sub> and BSR-10×BSRB-BB<sub>2</sub> for two characters in both the seasons exhibited encouraging results that may be released for further field trials. On satisfactory performance in the field, these combinations may be utilized for commercial cocoon production to increase the productivity of silk in Bangladesh.

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