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Heterosis and combining ability for weight of mature larvae and filament length of fifteen hybrids raised by half (6 × 6) diallel cross in silkworm, *Bombyx mori* L.

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ABSTRACT:

The investigation was carried out to evaluate fifteen hybrids raised by half (6 × 6) diallel cross involving six silkworm varieties of *Bombyx mori* viz. B(I)J, BB(O), N(I)K(P), BN(mn)M, HTHRB-3 and 95/14 in order to estimates of heterosis and combining ability. Observations were made on two economically important traits namely; weight of mature larvae and filament length over four rearing seasons in Bangladesh. Considerable amount to heterosis was obtained in the crosses where parents BB(O), B(I)J and HTHRB-3 were involved in different seasons. The gca quantities of the parents varied from season to season. The parents exhibit a significant gca effect for majority of the characters in all the rearing seasons. The overall gca quantities confirmed that the developed varieties B(I)J, BB(O) and HTHRB-3 and were the best general combining parents. It is evident from the results that cross 4, "B(I)J×HTHRB-3" and cross 8, "BB(O)×HTHRB-3" exhibited the best performance.

Key word: Heterosis, combining ability, weight of mature larvae, filament length, silkworm

Introduction

From the beginning in the history of sericulture efforts have been made to increase the productivity of silk through the improvement of silkworm breeds. Silkworm breeding is the genetic improvement in the economic value of the population. To improve the economic value and to exploit it commercially, silkworm breeders are engaged in selecting the combination of crosses giving emphasis on economic improvement of the traits. Genetic study regarding the inheritance of quantitative traits is a primary need to success the selection or hybridization programs. However, phenotypic variation of quantitative traits cannot only be due to the genetic effect but also environmental effect (Sarkar, 2018). Therefore, some experimental designs and mating designs as well as statistical analysis were developed to obtain sufficient information on the nature of gene on important economic traits and evaluation of heterosis for the commercial exploitation of hybrid vigour in plant and animal.

Research on the development of multivoltine silkworm breeds and bivoltine hybrids and tremendous results on these aspects have been achieved in tropical countries (Kumar *et al.*, 1980; Abadzhieva, 1983; Nacheva and Petkov, 1990; Kitahara *et al.*, 1990; Ahmed and Park, 1990; Jayaswal *et al.*, 1992; Lakshmi *et al*, 2012, Saha *et al.*, 2013; Zhang *et al.*, 2018; Sajgotra and Gupta, 2018; Gunduz and Şahan, 2019). As a result, in this century a good number of productive hybrids were isolated through heterosis study and the silkworm breeders in Indian have recommended their commercial exploitation (Datta *et al*., 2000a, b; Singh *et al*., 2000; Suresh *et al*., 2000; Narayanaswamy *et al*., 2000; Datta *et al*., 2001; Ravindra *et al*., 2001; Singh *et al*., 2001; Suresh *et al*., 2002). For the commercial exploitation of hybrid vigour of mulberry silkworm, *B. mori* in Bangladesh have also been discussed by a number of workers (Rashid *et al.*, 2011; 2013b; Hasan, 2011; Rahman *et al.*, 2015).

The combining ability analysis based on diallel crossing plan has been applied later in poultry as well as silkworm breeding to evaluate the general and specific combining abilities for different economic traits by a number of investigators (Redman and Shoffner, 1961; Yao, 1961; Warden *et al.*, 1965, Siddiqui and Sengupta 1993, Haque *et al.*, 1998; Rashid *et al.*, 2011, 2013b). In Bangladesh very scanty or no concrete attempt have been made to explore hybrid vigour in either the non-mulberry or mulberry silkworms though it is needed for the survival of the silk industry in the country. Some multivoltine and their cross combinations for commercial use are reported by Salam *et al.* (1980 a,b) who suggested that in adverse rearing seasons this may be used instead of rearing pure breeds. Heterosis over mid-parent and super-dominance with respect to the fecundity and fertility of *B. mori* was also noted by Rahman (1986) who recommended four cross combinations for commercial egg-production. Some other preliminary works on the existence of heterosis among the crosses of the available varieties were reported for commercial exploitation (Rahman, 1989; Rahman *et al.*, 1996; Ali and Kamal, 1998; Haque *et al.*, 1998; Rashid *et al.*, 2011, 2013b).

Materials and Methods:

The material of this research work contains six varieties of silkworm, *Bombyx mori* L. viz. BI(J), BB(O), N(I)K(P), BN(mn)M, HTHRB-3 and 95/14. The eggs of these races were collected from the Germplasm Maintenance Centre at Sakowa, Boda, Panchagarh, Bangladesh.

Experiment conducting area

The present investigation was carried out in a Laboratory of Germplasm Maintenance center at Sakowa, Boda, Panchagarh as it is one of the most important Germplasm Maintenance center in Bangladesh and surrounding area is very much important for silkworm rearing for its suitable climatic conditions.

Climatic conditions

Temperature and humidity for different rearing season:

Rearing seasons (Local name)	Code name	Average temperature(^{0}C)	Relative humidity (%)	Rearing period
Bhaduri	S-1	30±1.5	86±1.5	2 August to-23 August 2013
Chaita	S-2	28±1.5	88± 2	8 March to 30 April, 2014
Jaistha	S-3	26±1.5	84±1.5	20 May to 12 June, 2014
Agrahyoni	S-4	22±1.5	85±1.5	10 October to 02 November, 2014

Experimental design

A total of 15 hybrid combinations and parents were developed through half diallel crossing pattern. The experiment was conducting in three replications in four rearing seasons. Observation on weight of mature larvae (WML) and filaments (FL) length are carefully recorded.

Analysis of Heterosis and Combining ability

Estimates of heterosis were calculated by using the following formula:

Heterosis (%) over better parent (BP)= $\frac{\bar{F}_1 - \overline{BP}}{\overline{BP}} \times 100$; and

Heterosis (%) over mid -parent (MP) = $\frac{\bar{F}_1 - \overline{\text{MP}}}{\overline{\text{MP}}} \times 100$;

Test of significance of heterosis was done through 't' test and finally, calculated 't' value was compared with tabulated value of 't' at error degree of freedom.

The general and specific combining ability effects and variances were estimated following Griffings (1956a) Method I. In the model II the experimental material is to be regarded as the population about which inference are to be made.

Results:

The mean performance of parents for weight of mature larvae and filament length in different rearing seasons have been shown in Table 1. The estimates of heterosis over mid and better parents for the characters studied have been presented in Tables 2-3. The results obtained are as follows:

Weight of mature larvae:

The ranged of heterosis over mid-parent were -11.11 to 30.50 % in S-1, -13.00 to 27.54% in S-2, -5.62 to 22.50 % in S-3 and -7.32 to 16.13 % in S-4 rearing seasons. Of the fifteen crosses, in S-1 (positive: 10; negative: 3); in S-2 (positive: 11; negative: 3) and S-3 (positive: 11; negative: 3) and in S-4 (positive: 11; negative: 4) showed significant heterosis over their respective mid parents. The other crosses for all the four seasons did not show either positive or negative significant heterosis respectively. But in case of heterosis over better parents a few hybrids exhibited significant positive results in different rearing seasons. Of the fifteen crosses, in S-1 (positive: 3; negative: 9); cross in S-2 (positive: 5; negative: 9) and S-3 (positive: 5; negative: 6) and crosses in S-4 (positive: 2; negative: 10) showed significant heterosis over their respective better parents. The other crosses for all the four seasons did not show either positive or negative significant heterosis respectively (Table 2).

Filament length:

Of the fifteen crosses, thirteen crosses in S-1 (positive: 12; negative: 2); eleven crosses in S-2 (positive: 12; negative: 0) and S-3 (positive: 12; negative: 0) and nine crosses in S-4 (positive: 8; negative: 1) showed significant heterosis over their respective mid parents. On the other hand, the magnitude of heterosis over better parents was very low towards the positive direction. The values ranged from -23.20 to 1.83 %, -26.12 to 4.13, -22.12 to 0.88 % and -20.89 to 6.25 % in S-1, S-2, S-3 and S-4 rearing seasons respectively. For heterosis over better parents, among fifteen crosses, nine crosses in S-1 (positive: 0; negative: 13); eleven crosses in S-2 (positive: 0; negative: 11) and S-3 (positive: 0; negative: 13) and nine crosses in S-4 (positive: 1; negative: 13) showed significant results. The other crosses for all the four seasons did not show either positive or negative significant heterosis respectively (Table- 3).

General combining ability

The general combining ability effect of individual parents with their corresponding standard error for weight of mature larvae and filament length have been shown in Table 4. In general, the expression of gca varies from season to season in most of the cases. For WML, the varieties B(I)J and 95/14 showed highly significant results (P<0.01) in all the four rearing seasons. But BB(O) showed significant results only in S-1 and S-3. The results for FL revealed that BI(J), BB(O) and HTHRB-3 were positively significant in all of the seasons (except in HTHRB-3 for S-2). Majority of the other parents showed negatively significant results.

Specific combining ability:

Specific combining ability for these characters in respect of four different rearing seasons has been presented in Table 5. The results revealed that both the positive and negative specific combining ability effects were noted and some of the crosses were significant.

For WML, two crosses in S-1, five crosses in S-2, four crosses in S-3 and three crosses in S-4 and in FL five crosses in S-1; four crosses in S-2 and S-3 and no crosses in S-4 showed significant positive sca effect. Among which majority of the crosses were the resultant of at least one good combining parent. In some cases, exceptional results were observed which were cross 10 in S-1 and S-2; cross 14 in S-2, S-3 and S-4 for WML and cross 14 in S-1; 10 and 14 in S-2 and cross 12 in S-3 for FL. It might have a risen due to genetic interactions (Table -5).

Discussion

In a hybridization program, identification of parents is a prerequisite for maximum exploitation of heterosis. To achieve the goal, it is necessary to understand the combining ability of parents, which help in the selection of suitable parents for hybridization. Commercial utilization of hybrid vigor had revolutionized the production of maize in U.S.A. and other countries (East and Hays, 1912; Ahmed, 2013 and Nuaimi, *et al,* 2019). The phenomenon of heterosis or hybrid vigor was applied to gear up the production of yield and yield contributing traits in other crops and economically important animals like egg production of chickens (Batra *et al.,* 1973; Ayyagari *et al.*, 1979; Gu *et al.,* 2019) and milk production in cattle (Acharya and Bhat, 1983; Prata *et al.,* 2015; Daltro *et al,* 2019). Along with during the present days for commercial cocoon production, only hybrid vigour in *B. mori* for economic traits has been exploited in all the countries following the success in the Japanese sericulture. In recent years, many studies on heterosis have also been carried out in silkworm (Zhang *et al*., 2018; Angotra *et al*., 2018; Sajgotra and Gupta., 2018).

In the present investigation, heterosis, general and specific combining abilities have been observed in fifteen crosses among the six varieties with genetic diversity, different geographical origin and voltinism for two economically important traits of *B. mori* in four different rearing seasons. Different crosses showing heterosis was not consistent over characters as well as their extent of heterosis varied from one season to another. Similar findings have been reported by Sengupta *et al.* (1971), Rahman (1986), Strunnikov (1986), Subba Rao and Sahai (1989), Datta *et al.* (2001), Lakshmi *et al.* (2012) and Saha *et al.* (2013). In general, considerable amount to heterosis was obtained in the crosses where parents BB(O), B(I)J and HTHRB-3 were involved in different seasons. These three breeds showing heterosis in majority of the crosses were picked from diverse genetic origin. These observations are in conformity with the previous findings that greater heterosis is obtained between the crosses of parents of different regions than crosses between closely related parents in silkworm (Narayanan *et al.*, 1964; Anonymous, 1985; Gamo *et al.*, 1985; Tayade, 1987; Govindan *et al.*, 1987; Rahman, 1989; Datta *et al.*, 2001; Farooq *et al.*, 2002) as well as other crops (Ahmed, 2013; Nuaimi *et al.*, 2019) and animals (Prata *et al.*, 2015; Daltro *et al.*, 2019). Falconer (1960) earlier also reported this view that the amount of heterosis of a cross depends on the square of the differences of gene frequencies between the populations or lines and therefore, heterosis is not expected where the parental populations do not differ in gene frequencies. The parents BB(O), B(I)J and HTHRB-3 exhibit significant gca effect for the characters in all most cases. These good general combiners could effectively be utilized in the future hybridization programmes for developing high yielding varieties but it would be difficult to develop pure line with yielding ability equal to F_1 hybrid, because much of the yielding ability of F_1 appear to be due to the non-additive type of genetic variance. On the evaluation merits of magnitude of heterosis, estimates of general combining ability and specific combining ability, the crosses "BB(O)×HTHRB-3" (cross No.8), "BB(O)× N(I)K(P)" (cross No. 6), "B(I)J×HTHRB-3" (cross No. 4) and "B(I)J×N(I)K(P)" (cross No. 2) exhibited the best performance. These varieties can be utilized for commercial exploitation for silk production after field trial.

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Table 1: Mean performance of parents in Bhaduri (S-1), Chaita (S-2), Jaistha (S-3) and Agrahyoni (S-4) rearing seasons.

Characters	Seasons	BIJ	BBO	N(I)K(P)	BN(MN)M	HTHRB-3	95/5
WML	S-1	33.67	28.67	24.67	22.33	21.00	32.33
	S-2	35.67	33.00	27.00	23.33	22.67	33.67
	S-3	32.33	27.67	25.00	22.33	21.67	31.67
	S-4	36.33	34.00	27.67	25.00	24.00	34.33
FL	S-1	584.07	662.22	391.11	358.15	520.00	473.33
	S-2	738.89	844.44	513.33	382.56	628.89	564.44
	S-3	650.00	753.33	440.00	418.89	617.33	508.56
	S-4	818.89	728.89	521.33	527.78	678.89	536.53

Table 2. Heterosis (%) over mid-parent (MP) and better parent (BP) in four seasons for weight of mature larvae of *B. mori*.

crosses	Heterosis in % over							
	S-1		S-2		S-3		S-4	
	MP	BP	MP	BP	MP	BP	MP	BP
$P_1 \times P_2$	-0.53	-7.92**	4.85**	0.93	5.56**	-2.06	2.37*	-0.92
$P_1 \times P_3$	8.57**	-5.94**	5.32**	-7.48**	8.14**	-4.12*	3.13*	-9.17**
$P_1 \times P_4$	-1.19	-17.82**	10.73**	-8.41**	-2.44*	-17.53**	3.26*	-12.84**
$P_1 \times P_5$	10.98**	-9.90**	5.14**	-14.02**	2.47*	-14.43**	2.76*	-14.68**
$P_1 \times P_6$	-10.86**	-18.29**	-0.96	-4.63**	-2.08	-2.08	-2.83*	-4.63**
$P_2 \times P_3$	16.25**	0.11	5.56**	-4.04*	6.33**	0.12	4.86**	-2.02
$P_2 \times P_4$	3.27*	-15.05**	-2.96*	-17.17**	2.67*	-8.33**	-5.08**	-15.15**

P2 × P5	22.15**	-2.15	11.38**	-6.06**	18.92**	4.76**	10.34**	-3.03*
P2 × P6	-3.83**	-8.33**	-13.00**	-12.12**	-5.62**	-6.67**	-7.32**	-6.86**
P3 × P4	30.50**	17.95**	17.88**	9.88**	16.90**	10.67**	5.06**	-4.60**
P3 × P5	25.55**	10.26 **	23.49**	13.58**	17.14**	9.33**	16.13**	3.45*
P3 × P6	-11.11**	-20.83**	-7.69**	-12.50**	-4.71**	-10.00**	-6.45**	-14.71**
P4 × P5	16.92**	15.15**	27.54**	27.54**	3.03*	13.33**	14.29**	7.69**
P4 × P6	12.20**	-4.17*	18.13**	5.21**	11.11**	0.11	15.73**	0.98
P5 × P6	22.50**	2.08	18.34**	4.17*	22.50**	8.89**	10.86**	-4.90**

Table 3. Heterosis (%) over mid-parent (MP) and better parent (BP) in four seasons for filament length of *B. mori*.

crosses	Heterosis in % over							
	S-1		S-2		S-3		S-4	
	MP	BP	MP	BP	MP	BP	MP	BP
P1 × P2	8.22**	1.83	11.07**	4.13*	8.31**	0.88	7.25**	1.36
P1 × P3	6.87**	-21.31**	5.52**	-21.76**	7.65**	-22.12**	1.01	-17.34**
P1 × P4	7.95**	-23.20**	11.27**	-26.12**	10.40**	-21.68**	5.61**	-13.16**
P1 × P5	5.27**	-12.25**	5.88**	-14.25**	7.31**	-9.73**	0.92	-7.71**
P1 × P6	3.54**	-17.48**	7.45**	-17.62**	15.47**	-9.61**	0.16	-16.54**
P2 × P3	11.81**	-11.22**	2.27	-18.31**	8.94**	-12.16**	8.67**	-9.02**
P2 × P4	4.25**	-19.82**	13.76**	-17.90**	12.99**	-10.51**	7.53**	-9.51**
P2 × P5	3.63**	-7.65**	14.66**	-0.63	3.76**	-3.90*	12.71**	6.25**
P2 × P6	4.87**	-10.23**	2.24	-15.27**	0.73	-14.11**	4.31**	-11.61**
P3 × P4	2.32	-0.02	17.08**	2.16	0.23	-2.17	-2.14	-3.75*
P3 × P5	3.82*	-9.62**	5.54**	-1.18	4.88**	-10.09**	0.91	-8.25**
P3 × P6	-2.83*	-19.75**	6.93**	-5.54**	19.01**	-8.47**	6.82**	-14.39**
P4 × P5	7.04**	-10.19**	9.63**	-9.11**	8.73**	-8.65**	-7.73**	-15.66**
P4 × P6	9.31**	-13.16**	12.87**	-12.39**	5.43**	-20.72**	-1.89	-20.89**
P5 × P6	-5.67**	-10.47**	-1.58	-3.73*	-2.10	-10.63**	3.01*	-5.15**

*P< 0.05 and **P< 0.01

Table 4. Estimates of general combining ability effects of the parents for weight of mature larvae and filament length in *B. mori*.

Parents	Seasons				
	Character	**S-1**	**S-2**	**S-3**	**S-4**
B(I)J	WML	1.4963**	2.0833**	2.5000**	2.3148**
	FL	50.1720**	68.8735**	59.7275**	89.3833**
BB(O)	WML	0.5755	0.8333*	-0.2222	1.3148**
	FL	90.2983**	129.3272**	93.6747**	75.7074**
N(I)K(P)	WML	-1.0662*	-1.1667**	-1.1389**	-1.4074**
	FL	-49.8221**	-63.4691**	-66.3836**	-61.1907**
BN(mn)M	WML	-1.0690*	-1.1667**	-1.8056**	-1.7130**
	FL	-68.3496**	-100.3210**	-74.4299**	-64.3111**
HTHRB-3	WML	-1.0968*	-1.6111**	-1.1667**	-1.9074**
	FL	4.2674*	2.8179	14.6654**	14.3463**
95/14	WML	1.1602*	1.0278**	1.8333**	1.3981**
	FL	-26.5659**	-37.2284**	-27.2540**	-53.9352**
SE ($\hat{g}i$)	WML	0.391	0.300	0.362	0.257
	FL	1.927	3.096	3.256	3.061

*P< 0.05 and **P< 0.01

Table 5. Estimates of specific combining ability for Weight of mature larvae in *B. mori*.

Cross No.	Crosses	Characters	Seasons			
			S-1	**S-2**	**S-3**	**S-4**
1	**$P_1 \times P_2$**	WML	0.1157	0.3889	1.1944	0.3241
		FL	8.8867*	22.4969**	6.6123	3.9870
2	**$P_1 \times P_3$**	WML	1.2546	0.0556	0.2778	0.8796
		FL	8.1922	13.6821	-1.3293	-5.7815
3	**$P_1 \times P_4$**	WML	0.0880	0.7222	0.9444	0.0185
		FL	8.3323	5.4228	11.1614	15.7833
4	**$P_1 \times P_5$**	WML	0.7824	0.5000	-0.5278	0.3796
		FL	9.5657*	-1.5494	13.3994	-3.4852
5	**$P_1 \times P_6$**	WML	-4.0995**	-1.9722*	-0.6944	-2.0926**
		FL	-2.3602	7.1080	36.2633**	-1.8148
6	**$P_2 \times P_3$**	WML	1.6782	1.4722*	1.5000	0.5463
		FL	26.6956**	-21.8827**	-17.2765*	1.8944
7	**$P_2 \times P_4$**	WML	-1.4884	-1.1944	-2.1667*	-0.8148
		FL	-6.6288	9.4136	41.6031**	14.6815

8	**$P_2 \times P_5$**	WML	1.3727	1.2500	2.5278**	1.3796*
		FL	0.7172	61.4414**	6.1355	48.4685
9	**$P_2 \times P_6$**	WML	-0.3843	-2.0556**	-2.6389**	-1.5926*
		FL	5.0505	-8.9568	-6.4062	2.3056
10	**$P_3 \times P_4$**	WML	2.8171**	1.6389*	2.0833*	0.2407
		FL	-9.1010*	20.6543*	-28.9497**	-3.8648
11	**$P_3 \times P_5$**	WML	-1.4884	-0.0833	-1.0556	-0.0648
		FL	16.8005**	-16.0401*	10.0660	-4.1889
12	**$P_3 \times P_6$**	WML	-2.2454*	-1.2222	-1.5556	-0.8704
		FL	-16.9958**	11.6173	61.3744**	17.0370
13	**$P_4 \times P_5$**	WML	1.1782	1.5833*	-0.0556	0.4074
		FL	1.2540	5.5895	20.8901*	-31.6241
14	**$P_4 \times P_6$**	WML	1.7546	2.7778**	1.7778*	2.9352**
		FL	27.6428**	24.0247**	-15.8015*	-2.5648
15	**$P_5 \times P_6$**	WML	3.7824**	2.0556**	3.6389**	1.2963*
		FL	-23.4557**	-24.3920**	-41.8414**	-10.5556
	SE ($\hat{s}$ij)	WML	0.894	0.685	0.825	0.586
		FL	4.396	7.063	7.428	6.981