

Evaluation of General and Specific Combining Ability in Newly Synthesized Inbred Lines of Bivoltine Silkworm *Bombyx mori* L.

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Eight bivoltine inbred lines of silkworm *Bombyx mori* L. viz., AP8, AP10, AP17 and AP18 with marked female and plain male larvae and AP1, AP54, AP71 and AP72 with all plain larvae synthesized from Chinese commercial hybrids were evaluated for their general combining ability (gca), specific combining ability (sca) and reciprocal effects for eight quantitative traits. The line AP18 was found to be best general combiner by virtue of significant positive and positive gca effects for seven out of eight traits studied followed by the lines AP10, AP8 and AP17. Seven hybrids recorded significant positive and positive sca effects for all the traits under study reflecting the interaction of alleles, additive and non additive gene action and dominant effects expressed by genes. Among the 28 reciprocal hybrids, AP54×AP18 and AP1×AP17 revealed significant reciprocal effects for the six traits followed by AP54×AP8 for five and AP10×AP71 for four traits.

Key words: Silkworm, Bivoltine, Inbred Lines, Hybrids, Combining Ability

Introduction

The diallel cross system (Griffing, 1956) is one of the best approaches in assessing the parents for their ability to combine. For improving the economic characters identification of parental races through combining ability is essential for

utilizing them for further breeding programmes or for identification of potential hybrids. Since, majority of the traits of economic and commercial importance in silkworm are quantitative in nature, the combining ability estimates of breeding lines on such traits draw more importance and attention. The genetic worth of the pure lines can be determined by evaluating their general and specific combining abilities. A comparison of the performances of different inbred lines for hybridization work can be best made on the basis of concept of the two combining abilities. The study of combining ability for traits, which are polygenic in nature, is complex since many genes are usually involved. However, it provides information about the gene action and prospective parents, which may combine well to produce the potential hybrid. Several workers (Bhargava *et al.*, 1992; Chandrashekharaiyah, 1994; Datta and Pershad, 1988; Gamo and Hirabayashi, 1983; Goel, 2008; Kobayashi *et al.*, 1968; Krishnaswami *et al.*, 1964; Malik *et al.*, 1999; Ramesh Babu *et al.*, 2005; Sarkar *et al.*, 1991; Satenahalli *et al.*, 1989; Subba Rao and Sahai, 1989) studied combining ability both in cross breeds or bivoltine hybrids of mulberry silkworm varieties, which were introduced in India for commercial exploitation as early as 1922 (Datta, 1984).

Even though large number of bivoltine hybrids has been developed and introduced for commercial exploitation, most of them did not show consistent performance in the field. Therefore, there is a need to develop more and more new bivoltine hybrids which can sustain in the field to improve productivity and quality of silk. In light of the above, newly developed lines were used for practical application of diallel analysis to understand combining ability, a detailed study is carried out to understand the combining ability and to identify the potential hybrids involving eight newly synthesized bivoltine breeds of silkworm *Bombyx mori* L. viz., AP1, AP8, AP10, AP17, AP18, AP54, AP71 and AP72 following complete diallel method.

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Table 1. Analysis of variance for GCA, SCA and reciprocal effects

Source of Variation	DF	Fecundity	Hatching	Cocoon Yield/ 10000 Larvae (No)	Cocoon Yield/ 10000 Larvae (Wt.)	Pupation Rate	Cocoon Weight	Cocoon Shell Weight	Cocoon Shell Ratio
GCA	7	1238.26**	2.743**	73592.8**	3.894**	11.512**	0.036**	0.002**	2.054**
SCA	28	668.98**	5.890**	187616.7**	1.471**	11.261**	0.008**	0.001**	1.176**
Reciprocal	28	282.04**	3.937**	62530.7**	0.784**	6.408*	0.005**	0.003**	0.441**
Error	126	42.83	0.143	19099.2	0.117	3.687	0.001	0.0001	0.118
$\sigma^2 g$		74.714	0.162	3405.800	0.236	0.489	0.002	0.00013	0.121
$\sigma^2 s$		626.152	5.747	168517.600	1.354	7.573	0.007	0.001	1.058
h^2 (NS) ¹⁾		0.159	0.040	0.032	0.207	0.072	0.300	0.172	0.153
h^2 (BS) ²⁾		0.827	0.749	0.811	0.802	0.629	0.785	0.829	0.823
Predictability Ratio		0.119	0.028	0.020	0.174	0.065	0.308	0.131	0.114

¹⁾Heritability (Narrow sense).

²⁾Heritability (Broad sense).

Materials and Methods

Eight bivoltine inbred lines of silkworm *Bombyx mori* L. viz., AP8, AP10, AP17, AP18 all with marked female and plain male larvae and AP1, AP54, AP71 and AP72 with all plain larvae, synthesized from the Chinese commercial hybrids, formed the materials for the present study. The lines were crossed in 8×8 diallel pattern to obtain 56 F1s including reciprocal crosses. To evaluate the inbred lines, the larvae of all the combinations were reared with three replications each by following improved rearing technology of silkworm both for chawki (young silkworms) and adults. To minimize the effect of climatic conditions on rearing performance, the rearing was carried out under controlled conditions with temperature of 27~28°C and relative humidity of 80~85% during first three instars and temperature of 23~25°C and relative humidity of 70~75% during 4th and 5th instars. Data was recorded for eight economically important traits viz., fecundity (number of eggs per laying), hatching (%), cocoon yield by number per 10000 larvae, cocoon yield by weight per 10000 larvae, pupation rate (%), single cocoon weight (g), single shell weight (g) and cocoon shell ratio (%). The data was analyzed using statistical software "INDOSTAT" as per the standard statistical procedure of Diallel analysis, Method-1, suggested by Griffing (1956).

Results and Discussion

With good parental stocks the hybrids are vigorous but not always. Some parental stocks though not being good, F1 hybrids produced may be outstanding as a result of dif-

ferent levels of combining abilities. Hence, the choice of the hybrid combinations is the reflection of its combining ability (Chandrashekharaiyah, 1994).

Analysis of variance for combining ability revealed highly significant differences ($P < 0.01$) for general combining ability (gca), specific combining ability (sca) and reciprocal effects for all the traits studied (Table 1) indicating the genetic diversity of the parental breeds/hybrids and role of additive gene action for the traits studied. Predominant role of non-additive gene action in the control and inheritance of all the eight traits is evidenced from the high estimates of sca variance ($\sigma^2 s$) and predictability ratio ($\sigma^2 g / \sigma^2 s$), which is less than one for all the traits. Similar results were obtained by other studies (Bhargava *et al.*, 1992; Chandrashekharaiyah, 1994; Goel, 2008; Hosseini and Etebari, 2005; Nanjundaswamy, 1997; Ramesh Babu *et al.*, 2005).

General combining ability (gca) effects

Parental lines possessing high gca are generally preferred for population development and for initiation of pedigree breeding as it is heritable and can be fixed. Parental lines with high gca produce high heterosis as gca consists of additive effects and additive \times additive type of interaction (Bandopadhyay, 1990; Singh *et al.*, 2003). From the results of the general combining ability effects (Table 2) of the 08 parental lines, the line AP18 was found to be best general combiner by virtue of significant positive and positive gca effects for all the traits except cocoon shell ratio. The line was closely followed by AP10 AP8 AP17, which registered significant positive to positive gca effects for seven, six and five out of eight traits respectively. Hence, the lines AP18, AP10 and AP8 by virtue of their positive gca

Table 2. General combining ability of parental lines

Line	Fecundity	Hatching	Cocoon Yield/ 10000 Larvae (No)	Cocoon Yield/ 10000 Larvae (Wt.)	Pupation Rate	Cocoon Weight	Cocoon Shell Weight	Cocoon Shell Ratio
AP17	5.125*	0.342*	-11.786	-0.181	0.364	-0.01	0.009*	0.651*
AP71	-2.562	0.017	93.047*	-0.091	0.974*	-0.023	-0.002	0.147
AP1	-16.333	-0.647	-60.515	-0.934	-0.685	-0.093	-0.017	0.148
AP72	4.292*	0.247*	-0.703	0.015	-1.510	0.002	-0.003	-0.212
AP18	7.458*	0.191*	86.713*	0.655*	0.913*	0.059*	0.01*	-0.113
AP8	7.542*	0.249*	4.692	0.242*	-0.049	0.024*	0.005*	-0.035
AP54	-9.688	-0.661	-110.433	-0.214	-0.433	-0.005	-0.011	-0.610
AP10	4.167*	0.262*	-1.015	0.507*	0.427	0.046*	0.01*	0.024
CD 5% (Gi) ¹⁾	3.028	0.174	63.95	0.158	0.888	0.013	0.003	0.159
CD 5% (Gi-Gj) ²⁾	4.579	0.264	96.69	0.239	1.343	0.020	0.004	0.240

¹⁾ Critical difference (gca of ith parent for a trait).

²⁾ Critical Difference (difference in gca of ith and jth parent for a trait).

indicate their superiority, ability to combine with most of the breeds and are expected to produce promising hybrids with improved performance for their respective traits. The parental lines AP71 and AP72 exhibited significant positive and positive gca for 4 traits each. However, none of the parents was found good general combiner for all the quantitative traits. It is evidenced from the findings that for inheritance of traits in respective line, additive gene has played major role as observed by Singh *et al.* (2003).

The parental lines AP54 followed by AP1 were recorded to be poor combiners. Contribution of at least one good combiner in the hybrid combination is expected to yield transgressive segregants in the later generation, which on exploitation may yield lines with increased merit. Similar results have been reported by many workers (Bhargava *et al.*, 1995; Chandrashekharaiah, 1994; Datta and Pershad, 1988; Gamo and Hirabayashi, 1983; Hosseini and Etebari, 2005; Krishnaswami *et al.*, 1964; Nanjundaswamy, 1997; Ramesh Babu *et al.*, 2005; Singh *et al.*, 2000; Subba Rao and Sahai, 1989) wherein they have identified good parents based on gca values.

Specific combining ability

Specific combining ability is another aspect to be evaluated in the hybrids to estimate their superiority. The magnitude of sca effects varied considerably among F1 hybrids (Table 3) exhibiting both positive and negative sca effects indicating the genetic diversity of the parental lines. The sca effects of the hybrids revealed the importance of both additive and non-additive gene action for the eight traits studied. Among the 28 F1 hybrids analyzed, seven hybrids *viz.*, AP1×AP10, AP1×AP54, AP8×AP54, AP17×AP18, AP17×AP72, AP71×AP10 and

AP72×AP18 recorded high positive and positive sca effects for all the traits under study reflecting the interaction of alleles, additive and non additive gene action and dominant effects expressed by genes, which play major role in the expression of hybrid vigour which is in conformity with the studies of Bandopadhaya (1990), Choudhary (2006) and Singh *et al.* (2003).

The hybrid combination AP17×AP10 and AP71×AP8 also registered significant positive and positive sca effects for seven traits. Out of these hybrid combinations with best sca effects, both the parental lines in the combination AP1×AP54 have been poor combiners indicating non-additive gene interaction. Additive×dominance gene action was revealed by the F1 hybrid combinations AP1×AP10, AP8×AP54, and AP18×AP54 wherein in each combination one of the parent *viz.*, AP10, AP8 and AP18 was good combiner.

Further, additive gene action was also evident in the combinations AP72×AP18, AP17×AP18, AP71×AP10, AP17×AP72, AP17×AP10, AP71×AP8 and AP17×AP71 for most of the traits, wherein both the parental lines involved in each of the combination were good combiners. The observations confirm the role of both additive and non-additive gene action expression. Subba Rao and Sahai (1989) have observed the importance of both additive and non-additive gene actions in the inheritance of cocoon shell, cocoon shell ratio and larval duration and additive genetic variance for cocoon yield, cocoon weight, filament length and denier. Predominant role of additive gene action was recorded for larval duration, cocoon shell weight and filament length (Razdan *et al.*, 1994) whereas Kumar *et al.* (1994) observed the importance of both additive and non-additive gene actions for effective rate of

Table 3. Specific combining ability effects

S. No.	F1 Combination	Fecundity	Hatching	Cocoon Yield/ 10000 Larvae (No)	Cocoon Yield/ 10000 Larvae (Wt.)	Pupation Rate	Cocoon Weight	Cocoon Shell Weight	Cocoon Shell Ratio
1	AP17 * AP71	8.02	1.114*	96.77	0.175	1.378	-0.010	-0.005	-0.162
2	AP17 * AP1	-1.72	1.398*	-244.34	-0.869	-3.309	-0.058	-0.022	-0.695
3	AP17 * AP72	13.33*	1.153*	250.51*	0.821	2.066	0.037*	0.019*	0.651*
4	AP17 * AP18	1.33	1.677*	164.10	0.284	1.188	0.011	0.004	0.054
5	AP17 * AP8	2.75	-0.432	90.78	0.092	0.047	-0.007	-0.002	-0.044
6	AP17 * AP54	10.81*	-0.888	-160.75	0.046	-0.512	0.032	-0.012	-1.146
7	AP17 * AP10	12.46*	-0.911	58.49	0.407	0.913	0.041*	0.018*	0.585*
8	AP71 * AP1	6.81	1.358*	-49.00	-0.452	-0.037	-0.023	-0.017	-0.761
9	AP71 * AP72	12.02*	0.993*	-69.81	0.166	0.175	0.028	0.006	0.049
10	AP71 * AP18	1.52	-1.319	-2.90	-0.518	-2.749	-0.060	-0.027	-0.962
11	AP71 * AP8	5.77	-0.487	154.12	0.621*	1.028	0.036*	0.020*	0.802*
12	AP71 * AP54	3.67	0.157	116.24	0.551*	0.630	0.04*	0.007	-0.065
13	AP71 * AP10	13.48*	0.778*	273.83*	0.747*	0.439	0.053*	0.031*	1.203*
14	AP1 * AP72	-0.04	0.602*	-361.25	-0.410	-5.985	0.020	0.011*	0.457*
15	AP1 * AP18	0.79	1.105*	280.33*	0.800	1.023	0.040*	-0.002	-0.652
16	AP1 * AP8	10.37*	0.227	61.68	0.261	2.709*	0.016	-0.005	-0.541
17	AP1 * AP54	6.94	0.305	385.64*	1.442*	4.058*	0.085*	0.024*	0.375
18	AP1 * AP10	13.25*	2.322*	131.39	1.121*	3.307*	0.105*	0.038*	0.955*
19	AP72 * AP18	7.33	1.348*	188.52*	1.477*	1.347	0.134*	0.027*	0.012
20	AP72 * AP8	5.25	1.220*	-75.79	-0.667	0.199	-0.058	-0.019	-0.440
21	AP72 * AP54	7.31	-0.034	156.66	0.336	0.533	0.021	-0.001	-0.248
22	AP72 * AP10	3.46	-0.523	12.24	-0.764	1.375	-0.087	-0.030	-0.799
23	AP18 * AP8	8.08	-0.585	-132.38	-0.654	-1.725	-0.041	-0.010	-0.097
24	AP18 * AP54	9.48*	-1.285	2.58	0.133	0.468	0.005	0.008*	0.493*
25	AP18 * AP10	4.46	-0.586	308.66*	0.049	2.633*	-0.055	-0.025	-0.788
26	AP8 * AP54	5.06	1.099*	133.77	0.228	1.457	0.001	0.002	0.117
27	AP8 * AP10	3.87	0.240	321.68*	0.581*	-1.118	0.005	-0.025	-1.504
28	AP54 * AP10	-1.89	1.466*	76.47	-0.584	-1.965	-0.060	-0.005	0.451*
	CD 5% (Sij) ¹⁾	8.09	0.467	170.90	0.423	2.370	0.0357	0.0080	0.425
	CD 5% (Sij-Sik) ²⁾	12.11	0.699	255.80	0.633	3.550	0.0534	0.0120	0.636
	CD 5% (Sij-Skl) ³⁾	11.21	0.647	236.80	0.586	3.290	0.0495	0.0111	0.589

¹⁾sca of hybrid of i^{th} and j^{th} parent.

²⁾difference in sca of the two hybrids involving ij^{th} and ik^{th} parents.

³⁾difference in sca of the two hybrids involving ij^{th} and kl^{th} parents.

rearing and filament length. Bhargava *et al.* (1995) have recorded predominant role of non-additive gene action for cocoon weight, cocoon shell weight, cocoon shell ratio, raw silk%, filament length, reelability and neatness. Similar predominant role of non-additive action in the inheritance of different traits has been studied by several workers (Malik *et al.*, 1999; Ramesh Babu *et al.*, 2005; Singh *et al.*, 2000). It is evident from the review paper

(Singh *et al.*, 2003) that various authors have registered contradictory results regarding role of additive and non-additive gene action for the control of various quantitative traits. These contradictory results regarding relative importance of additive and non-additive gene action may be due to genetic variability of different silkworm breeds utilized in the above studies. However, most of the economic traits including cocoon yield, cocoon weight,

Table 4. Reciprocal effects

S. No.	RF1 Combination	Fecundity	Hatching	Cocoon Yield/ 10000 Larvae (No)	Cocoon Yield/ 10000 Larvae (Wt.)	Pupation Rate	Cocoon Weight	Cocoon Shell Weight	Cocoon Shell Ratio
1	AP71 * AP17	6.33	-0.155	-48.83	0.060	-0.038	0.010	-0.007	-0.600
2	AP1 * AP17	23.50*	-0.598	272.83*	1.000*	1.293	0.064*	0.021*	0.525*
3	AP1 * AP71	7.00	0.453	-61.00	0.613*	0.722	0.070*	0.010*	-0.232
4	AP72 * AP17	2.50	-0.983	-173.50	-0.038	-1.167	0.029	0.019*	0.748*
5	AP72 * AP71	-4.50	-0.998	-177.68	-0.653	2.445*	-0.040	-0.017	-0.552
6	AP72 * AP1	-22.33	-1.870	-544.67	-1.122	-2.930	-0.028	-0.007	-0.072
7	AP18 * AP17	0.67	-0.038	39.83	0.215	-0.508	0.038*	0.028*	1.233*
8	AP18 * AP71	-11.83	1.460*	145.66	0.217	-0.055	0.001	-0.006	-0.357
9	AP18 * AP1	-25.00	-1.663	-39.67	-0.765	1.722	-0.081	-0.019	-0.202
10	AP18 * AP72	-10.17	0.870*	203.66*	-0.323	0.110	-0.065	-0.011	0.088
11	AP8 * AP17	-12.50	-3.063	-172.17	-0.473	-4.835	-0.014	-0.017	-0.833
12	AP8 * AP71	-17.17	-1.413	57.33	0.658*	-0.130	0.066*	0.015*	0.072
13	AP8 * AP1	-12.00	-1.267	38.67	-0.738	0.445	-0.086	-0.018	-0.060
14	AP8 * AP72	-5.50	1.290*	294.33*	0.013	1.777	-0.050	-0.014	-0.232
15	AP8 * AP18	1.83	-0.432	251.83*	0.387	2.833*	-0.012	-0.004	-0.120
16	AP54 * AP17	14.67*	-1.762	5.83	0.365	-0.778	0.046*	0.002	-0.427
17	AP54 * AP71	-0.50	-1.355	-76.33	-0.409	0.023	-0.031	-0.010	-0.210
18	AP54 * AP1	-4.33	1.302*	163.50	0.659*	0.257	0.040*	0.006	-0.112
19	AP54 * AP72	15.00*	2.467*	66.00	0.881*	-0.397	0.076*	0.003	-0.658
20	AP54 * AP18	14.67*	1.053*	291.00*	1.275*	2.582*	0.084*	0.001	-0.908
21	AP54 * AP8	14.67*	0.712*	5.50	0.647*	-1.888	0.067*	0.011*	-0.170
22	AP10 * AP17	1.17	-2.402	19.17	0.557*	0.483	0.066*	0.011*	-0.185
23	AP10 * AP71	-5.50	-1.695	109.67	0.760*	2.463*	0.040*	0.013*	0.238
24	AP10 * AP1	-12.50	0.102	108.33	0.279	0.745	0.012	0.001	-0.142
25	AP10 * AP72	3.33	-2.340	-92.00	-0.952	-0.378	-0.083	-0.025	-0.575
26	AP10 * AP18	6.83	-0.002	-72.50	-0.238	-0.330	-0.012	0.003	0.342
27	AP10 * AP8	11.67*	0.322	-127.83	-0.540	2.160	-0.034	-0.010	-0.250
28	AP10 * AP54	-3.67	-0.108	101.83	0.053	3.278*	-0.021	-0.005	-0.073
	CD 5% (Sij)	8.09	0.467	170.9	0.423	2.37	0.0357	0.0080	0.425
	CD 5% (Sij-Sik)	12.11	0.699	255.8	0.633	3.55	0.0534	0.0120	0.636
	CD 5% (Sij-Skl)	11.21	0.647	236.8	0.586	3.29	0.0495	0.0111	0.589

¹⁾sca (reciprocal effects) of hybrid of i^{th} and j^{th} parent.

²⁾difference in sca (reciprocal effects) of the two hybrids involving ij^{th} and ik^{th} parents.

³⁾difference in sca (reciprocal effects) of the two hybrids involving ij^{th} and kl^{th} parents.

cocoon shell weight and cocoon shell ratio, non-additive gene action was found predominant rather than additive gene action (Singh *et al.*, 2003). The present study supports the observations of predominant role of non-additive gene action for fecundity, hatching, cocoon yield by number, cocoon yield by weight, pupation rate, cocoon weight, shell weight and cocoon shell ratio as evidenced by predictability ratio of less than unity for all the traits under study (Table 2).

Reciprocal Effects

The significant difference between direct (F1) and reciprocal (RF1) hybrid combinations indicate the involvement of sex linked genes, which are known to cause differences in quantitative traits in reciprocal crosses in silkworm (Morohoshi, 1949; Murakami and Ohtsuki, 1989; Nagatomo, 1942). Analysis of variance for combining ability revealed highly significant differences ($p < 0.01$) for reciprocal effects for all the traits studied (Table 1). The four out of

eight parental lines viz., AP17, AP18, AP8 and AP10 with larval marking sex linked gene may be the major factor causing significant reciprocal effects for all the traits. The findings were in conformity with Chandrashekharaiiah (1994); Nanjundaswamy (1997), who have reported significant reciprocal effects for all the traits except one, studied by them and also in agreement with Ramesh Babu *et al.* (2005) who have registered significant reciprocal effects for all the traits studied.

Out of 28 reciprocal hybrid (RF1) combinations (Table 4), the AP54×AP18 and AP1×AP17 revealed significant reciprocal effects for the six traits viz., fecundity, hatching, cocoon yield by number, cocoon yield by weight, pupation rate and cocoon weight. The RF1 hybrids, AP54×AP8 for five traits, AP10×AP71 for four, AP54×AP72 and AP18×AP17 both for three traits, AP8×AP72 and AP54×AP1 for two traits each were recorded with significant reciprocal effects.

It was interesting to note that out of eight RF1 hybrids registered with significant reciprocal effects for more number of traits; four combinations were with poor general combiner viz., AP54 used as female parent. Based on the findings of Nakada (1972) and Tazima (1988), it is obvious that AP54 may carry a different type of Z chromosome along with W or cytoplasmic factors may be determining the differential manifestation. In the present findings, based on the reciprocal effects, it was difficult to attribute with certainty whether sex-linked genes, maternal effects or cytoplasmic factors were in major or partly involved in controlling the quantitative traits. The lines with positive gca could be used in future breeding programmes for improvement of respective traits. The crosses showing high sca/reciprocal effects involving parents with good gca could be exploited to produce promising hybrids with increased merit in the yield contributing characters.

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