

Studies on Analysis of Combining Ability in the Mulberry Silkworm, *Bombyx mori* L.

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Analysis of combining ability is a widely used biometrical tool to select promising parents and hybrids, to determine the kinds and relative magnitudes of genetic variability among hybrids as well as to forecast yield attributes in early breeding generations both in plants and animals. Various statistical approaches like Jinks and Hayman (1953), Griffing (1956), Kempthorne (1957) etc. have been extensively applied in plants. These approaches have also been tried in the mulberry silkworm, *Bombyx mori* L. In the present review, an attempt has been made to collect most of the studies carried out on combining ability in silkworm at one place and make it available to the scientists engaged in sericultural research.

Key words: *Bombyx mori* L., Breeding, Combining ability analysis, Diallel

Introduction

Combining ability analysis is the most widely used biometrical tool in determining promising parents and hybrids and detecting relative magnitude of genetic variability both by plant (Sprague and Tatum, 1942; Arunachalam, 1974; Baker, 1978; Kaushik *et al.*, 1984; Ram *et al.*, 1999; Sharma, 1999; Sood *et al.*, 2000) as well as animal breeders (Eisen *et al.*, 1983; Crusio, 1987; Falconer and Mackay, 1996). Analysis of combining ability has been used in eri silkworm, *Samia cynthia ricini* (Nagaraja and Govindan, 1994; Nagaraja *et al.*, 1996). In the mulberry silkworm, *Bombyx mori*, attempts have been

made to identify promising F₁ hybrids between multivoltine × multivoltine (Krishnaswami *et al.*, 1964; Pershad *et al.*, 1986; Kantaratanakul *et al.*, 1987; Chatterjee *et al.*, 1993; Sen *et al.*, 1995; Rao *et al.*, 1998), multivoltine × bivoltine (Datta and Pershad, 1988; Tayade, 1989; Kalpana and Sreerama Reddy, 1998; Datta *et al.*, 2001; Ravindra Singh *et al.*, 2001a, b), bivoltine bivoltine (Mingguan, 1982; Gamo, 1983; Gamo and Hirabayashi, 1983; Gamo *et al.*, 1985a, b; Hirabayashi and Gamo 1985; Jang and Sohn 1985; Eguchi *et al.*, 1986; Sohn and Hong, 1986; He *et al.*, 1989; Subba Rao and Sahai, 1989; Jeong, *et al.*, 1986, 1990; Niino *et al.*, 1990; Moon and Choi, 1992; Chung and Sohn, 1993; Kumar *et al.*, 1994; Liu *et al.*, 1994; Moon and Han, 1994; Razdan *et al.*, 1994a, b; Zhu and Weir, 1996; Ravindra Singh *et al.*, 2000) and bivoltine × univoltine silkworm breeds (Petkov, 1975; Petkov *et al.*, 1984). Performance of F₁ hybrids depends upon proper selection of suitable parents and genetic divergence between them. Parents possessing high general combining ability (GCA) are generally considered for population development and for initiation of pedigree breeding as it is heritable and can be fixed. Parents with high GCA produce high heterosis as GCA consists of additive effects and additive × additive type of interactions. Specific combining ability (SCA) consists of non-additive effects, dominant effects and other interactions (Bandyopadhyay, 1990). Specific combining ability is not heritable and therefore it cannot be utilised in pure line breeding. Hybrids with high SCA are useful for commercial exploitation. As pointed out by Jinks and Hayman (1953), diallel analysis is dependent upon homozygosity of the parents, whereas Dickinson and Jinks (1956) and Kempthorne (1957) opened that it is not necessary that parents should be homozygous. Sometimes, the performance of the parental breeds is good but their F₁ hybrids are not good. In such condition, combining ability analysis plays an important role in determining perspective parents / hybrids.

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Biometrical approaches followed in silkworm

A brief account of main biometrical approaches used for combining ability analysis in silkworm is mentioned below.

Haymans approach

This approach was developed by Jinks and Hayman (1953). Further developments about this approach have been described by Mather and Jinks (1971). In Haymans approach, there are two steps i) The analysis of variance and ii) Estimation of components of variation. This approach also provides other parameters like degree of dominance, proportion of positive and negative alleles, proportion of dominant and recessive genes, direction of influence of the dominant genes and the number of groups of genes controlling the characters. In silkworm, Haymans approach has been used by several workers (Krishnaswami *et al.*, 1964; Satenahalli *et al.*, 1989; Sarkar *et al.*, 1991).

Griffings approach

This approach was developed by Griffing (1956). In this approach, using a suitable model, the component variances due to general and specific combining abilities are estimated. Four methods have been suggested by Griffing, depending upon whether the set involves i) parents, F_1 s and reciprocals ii) parents and F_1 s only iii) F_1 s and reciprocals and iv) F_1 s only. According to Griffings approach, following mathematical model -1 is commonly used:

$X_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + l \sum \sum e_{ijkl}$, where μ is the population mean, g_i (g_j) denotes the GCA effect, s_{ij} and r_{ij} denote SCA and reciprocal effect and e_{ijkl} is the environmental effect associated with individual observation. The variances of GCA and SCA are calculated as follows:

$$V(g_i) = \frac{(n-1)}{2n^2} \sigma^2 e$$

$$V(s_{ij}) = \frac{(n-1)^2}{n} \sigma^2 e$$

Griffing approach has been extensively followed by many workers in silkworm (Pershad *et al.*, 1986; Datta and Pershad, 1988; Subba Rao and Sahai, 1989; Razdan *et al.*, 1994a, b; Kumar *et al.*, 1994; Rao *et al.*, 1998; Malik *et al.*, 1999).

Kemphornes Line \times Tester analysis

This approach was developed by Kemphorne (1957). In this method, 'l' lines are crossed to each of 't' testers and data generated on the parents (lines and testers) and their F_1 s are utilised to estimate various types of gene effects.

The method provides information on general combining ability of parents and the specific combining ability of the hybrids. In this method, less labour is required as compared to diallel analysis. Following formulae are used for analysis of general and specific combining abilities as suggested by Kemphorne (1957).

General Combining Ability:

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

$$b) \text{ Testers } g_j = \frac{X_j}{lr} - \frac{X}{ltr}, \quad j=1 \text{ to } t$$

Specific Combining Ability:

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

where, g_i = general combining ability of lines

g_j = general combining ability of testers

s_{ij} = specific combining ability of hybrids

l = number of lines

t = number of testers

r = number of replications

X_i = performance of i th line with t testers

X_j = performance of j th tester with l lines

X_{ij} = performance of ($i \times j$) th hybrid and

X = grand total

Some of the important studies concerned with the estimation of general and specific combining abilities, type of gene action and statistical methods followed, are given in Table 1.

Combining ability studies in multivoltine breeds / hybrids

Krishnaswami *et al.* (1964) have reported interaction of overdominance and epistatic in the expression of evaluated characters in a diallel analysis involving five indigenous multivoltine races *viz.*, Nistari, Mysore, Bulupolu, Sarupat and Nistid. Attempts were made to identify promising multivoltine silkworm breeds/ hybrids through combining ability analysis (Pershad *et al.*, 1986; Kantaratanakul *et al.*, 1987). Studies on genetic variability in multivoltine silkworm breeds on the basis of analysis of quantitative and qualitative characters were carried out (Rao *et al.*, 1991; Chatterjee *et al.*, 1993). Sen *et al.* (1995) have indicated that additive and non-additive effects of genes facilitate selection for the amelioration of multivoltine silkworm breeds.

Combining ability studies in multivoltine \times bivoltine F_1 hybrids

Combining ability analysis has been extensively used in silkworm for the selection of promising multivoltine \times bivoltine F_1 hybrids. Pershad *et al.* (1986) have reported

Table 1. Estimates of general and specific combining abilities (GCA and SCA) in the silkworm, *Bombyx mori*

Sl. no.	Characters	Status of component estimated	Type of gene action	Statistical approach followed	Reference
1	Hatching percentage, growth rate, cocoon weight and cocoon shell weight	Dominance greater than additive	Dominance more important than additive	Jinks and Hayman (1953)	Krishnaswami <i>et al.</i> (1964)
2	Fecundity, larval duration, pupal duration, cocoon yield, cocoon shell ratio and filament length	GCA equal to SCA	Additive and non-additive gene actions are equally important	Griffing (1956)	Pershad <i>et al.</i> (1986)
3	Fecundity, larval duration, pupal weight, cocoon shell ratio and filament length	GCA greater than SCA	Additive more important than non-additive	Griffing (1956)	Datta and Pershad (1988)
4	Larval weight, cocoon weight and cocoon shell weight Larval duration, cocooning and pupation	GCA greater than SCA SCA greater than GCA	Additive more important than non-additive Non-additive more important than additive	Jinks and Hayman (1953)	Sattenahalli <i>et al.</i> (1989)
5	Cocoon yield, cocoon weight, filament length and denier Cocoon shell weight, cocoon shell ratio and larval duration	GCA greater than SCA GCA equal to SCA	Additive gene action more important than non-additive Both additive and non-additive gene actions important	Griffing (1956)	Subba Rao and Sahai (1989)
6	Cocoon weight	GCA greater than SCA	Additive more important than non-additive	Mather and Jinks (1971)	Sarkar <i>et al.</i> (1991)
7	Effective rate of rearing and filament length	GCA equal to SCA	Both additive and non-additive gene actions important	Griffing (1956)	Kumar <i>et al.</i> (1994)
8	Larval duration, cocoon shell weight and filament length	GCA greater than SCA	Additive more important than non-additive	Griffing (1956)	Razdan <i>et al.</i> (1994a)
9	Cocoon weight, cocoon shell weight, cocoon shell ratio, raw silk percentage, filament length, reelability and neatness	SCA greater than GCA	Non-additive more important than additive	Griffing (1956)	Bhargava <i>et al.</i> (1995)
10	Cocoon breadth	SCA greater than GCA in favourable season and GCA greater than SCA in unfavourable season	Preponderance of non-additive genetic variance in favourable season and additive variance in unfavourable season	Kempthorne (1957)	Rahman and Jahan (1997)
11	Cocoon yield both by number and weight, cocoon weight, cocoon shell weight, cocoon shell ratio and filament length	SCA greater than GCA	Prominent role of non-additive gene action	Kempthorne (1957)	Rajalakshmi <i>et al.</i> (1997)
12	Cocoon weight, cocoon shell weight, cocoon shell ratio, larval duration and survival potential	GCA equal to SCA	Both additive and non-additive gene actions important	Griffing (1956)	Rao <i>et al.</i> (1998)
13	Cocoon weight, cocoon shell weight, cocoon shell ratio, effective rate of rearing and fifth instar larval duration	SCA greater than GCA	Prominent role of non-additive gene action	Griffing (1956)	Malik <i>et al.</i> (1999)
14	Cocoon weight, cocoon shell weight and cocoon shell ratio	SCA greater than GCA	Prominent role of non-additive gene action	Kempthorne (1957)	Ravindra Singh <i>et al.</i> (2000)

Table 1. Continued

Sl. no.	Characters	Status of component estimated	Type of gene action	Statistical approach followed	Reference
15	Fecundity, larval duration, cocoon yield both by number and weight, cocoon weight, cocoon shell weight and cocoon shell ratio	GCA equal to SCA	Both additive and non-additive gene actions important	Kempthorne (1957)	Datta <i>et al.</i> (2001)
16	Fecundity, hatching percentage, larval duration, cocoon yield both by number and weight, cocoon shell weight and cocoon shell ratio	GCA greater than SCA	Additive more important than non-additive	Kempthorne (1957)	Ravindra Singh <i>et al.</i> (2001a)
17	Fecundity, cocoon yield both by number and weight, cocoon weight, cocoon shell weight and cocoon shell ratio	SCA greater than GCA	Prominent role of non-additive gene action	Kempthorne (1957)	Ravindra Singh <i>et al.</i> (2001b)
18	Effective rate of rearing, cocoon weight, cocoon shell weight and cocoon shell ratio	GCA equal to SCA	Both additive and non-additive gene actions important	Kempthorne (1957)	Chauhan <i>et al.</i> (2000)
19	Fecundity, effective rate of rearing, cocoon weight, cocoon shell weight and cocoon shell ratio	GCA equal to SCA	Both additive and non-additive gene actions important	Kempthorne (1957)	Raghavendra Rao <i>et al.</i> (2002)

that both additive and non-additive gene actions are important in the inheritance of fecundity, larval duration, pupal duration, cocoon yield, cocoon shell ratio and filament length and environmental interaction is minimum in multivoltine \times bivoltine F_1 hybrids. Datta and Pershad (1988) observed that additive genes play more important role in the inheritance of fecundity, larval duration, pupation rate, cocoon shell ratio and filament length and they further confirmed that multivoltine \times bivoltine F_1 hybrids are superior to bivoltine \times multivoltine F_1 hybrids to obtain maximum cocoon yield. Preponderance of additive gene action was found for cocoon weight and cocoon shell weight whereas importance of non-additive gene action was observed in the inheritance of larval duration, cocooning and pupation (Sattenahalli *et al.*, 1989). Murakami and Ohtsuki (1989) have observed genetic variability in tropical races of silkworm. Sarkar *et al.* (1991) have observed additive genetic variance for cocoon weight in a diallel cross analysis of cocoon weight in hybrids involving multivoltine and bivoltine silkworm breeds.

It was interesting to note that during favourable season, non-additive genetic variance was important whereas additive genetic variance was important during unfavourable season for the inheritance of cocoon breadth (Rahman and Jahan, 1997). Rao *et al.* (1998) have reported importance of both additive and non-additive gene actions in the inheritance of cocoon weight, cocoon shell weight, cocoon shell ratio, larval duration and survival potential and they further indicated that some hybrids like Moria \times Dong 34, Hua 204 \times Guangnong should be tried in place

of Pure Mysore \times C. Nichi. Predominant role of additive gene action was recorded in the inheritance of fecundity, hatching %, larval duration, cocoon yield both by number and weight, cocoon shell weight and cocoon shell ratio (Ravindra Singh *et al.*, 2001a) whereas preponderance of non-additive gene action was observed for fecundity, cocoon yield both by number and weight, cocoon weight, cocoon shell weight and cocoon shell ratio in a Line \times Tester analysis study in sex-limited breeds of the silkworm with coloured cocoons (Ravindra Singh *et al.*, 2001b). Recently, Importance of both additive and non-additive gene actions in the inheritance of quantitative characters like fecundity, cocoon yield, cocoon weight, cocoon shell weight and cocoon shell ratio has been recorded (Datta *et al.*, 2001; Raghavendra Rao *et al.*, 2002).

Combining ability studies in bivoltine silkworm breeds / hybrids

Study on genetic divergence in bivoltine silkworm breeds was carried out to determine the magnitude of genetic diversity among breeds and to assess the importance of a set of quantitative characters (Jolly *et al.*, 1989). 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*

et al., 1994a) whereas Kumar *et al.* (1994) observed the importance of both additive and non-additive gene actions for effective rate of 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 gene action in the inheritance of different characters has been studied by several workers (Rajalakshmi *et al.*, 1997; Malik *et al.*, 1999; Ravindra Singh *et al.*, 2000). Contradictory results regarding relative importance of additive and non-additive gene actions may be due to genetic variability of different silkworm breeds utilised in the above studies.

In silkworm, most of the economic characters including cocoon yield, cocoon weight, cocoon shell weight and cocoon shell ratio, non-additive gene action was found predominant rather than additive gene action (Table 1). In one of the studies, for cocoon breadth, preponderance of non-additive genetic variance was observed in favourable season whereas additive genetic variance was important during unfavourable season (Rahman and Jahan, 1997). During the recent years, Line \times Tester analysis suggested by Kemthorne (1957), has been extensively employed in mulberry silkworm (Rajalakshmi *et al.*, 1997; Chauhan *et al.*, 2000; Ravindra Singh *et al.*, 2000, 2001a, b; Datta *et al.*, 2001; Raghavendra Rao *et al.*, 2002).

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