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Review

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An Analysis of Heterosis in the Silkworm, *Bombyx mori* (L.)

Tribhuwan Singh*, Beera Saratchandra and Geetha N. Murthy
Central Silk Board, B. T. M. Layout, Madivala, Bangalore-560 068, India.

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The introduction of hybrid and exploitation of heterosis has played a vital role in Indian sericulture industry, which clearly depicts a quantum jump in silk production during the last four decades. Since, the introduction of heterosis, progress in silkworm breeding has depended on success or failure in identifying better combiners. Systematic procedures developed have enabled the breeders to identify the best combiners by combining ability test, line x tester analysis or D^2 analysis for maximum expression of heterosis. The level of heterosis expressed in the crossbreed population is determined by the interaction between genotype and prevailing environmental factors. Except some of the pre and post cocoon parameters, heterosis is invariably higher in single crosses compared to three-way and double crosses. However, during hot and humid season, when rearing of F1 bivoltine hybrid is unsuccessful at field level and indigenous races results in very low and poor quality yield, three-way and double crosses can play an important role as an intermediary technology. The objective of this article is to review briefly the concept and causes of heterosis, utilization of different forms of heterosis in silk production and its significance in silkworm, *Bombyx mori* breeding.

Key words: Heterosis analysis, *Bombyx mori*

Introduction

The primary goal of silkworm breeding programme is to bring together the desirable genes in appropriate combinations in order to improve the genetic performance (Basavaraja *et al.*, 1998) for maximizing the yield and productivity per unit area. Silkworm breeding consists of two distinct strategies *viz.*, (a) establishment of inbred lines by selection of quantitative and qualitative traits at successive generations and (b) selection of suitable hybrids for commercial use. These two objectives will be achieved only when widely varied and distinctly divergent gene pools are created in the parent silkworm races, so that high degree of heterosis will be exhibited in the hybrid (Thangavelu, 1998).

In the field of biological sciences it is well established that hybrids become very strong, a fact mentioned by Darwin in his book "Origin of Species" in 1859. The term heterosis derived from the Greek word 'Heteros' and 'Osis' (heteros = different; osis = conditions) was coined by Shull in 1914 (as cited by Shull, 1948) to describe the superiority of cross breeds. This phenomenon was first studied by Koelreuter in 1763 (East and Hayes, 1912) and termed it hybrid vigour relative to their parents irrespective of the cause. Genetically, heterosis is the function of a hybrid over the parents resulted from crossing of unlike individuals differing in their one or more parameters. The silkworm set the earliest and best example in utilization of hybrid vigour like corn. The pioneering works of Toyama (1906), a Japanese silkworm-breeding expert, on hybridization and use of F1 hybrids for commercial rearing made an epoch in the history of sericulture. The hybrids, which were the crosses of Japanese and Chinese origin, became so popular with the farmers in Japan that by 1919 over 90% of eggs produced were of hybrid origin, reaching 100% by 1928 (Yokoyama, 1973). Enhanced heterotic expression in various economic traits have been reported in single, three-way and double crosses over their parents (Gamo, 1976; Datta, 1984; Singh *et al.*, 1994; Krishnaswamy, 1987; Das *et al.*, 1994; Singh, 2001)

In this review article, an attempt has been made to elucidate briefly the works carried out on basic concept of heterosis, causes of heterosis, utilization of heterosis by producing single, three-way and double cross hybrids, manifestation of heterosis and its significance in silkworm breeding.

* To whom correspondence should be addressed.
Central Silk Board (6th Floor), B. T. M. Layout, Madivala, Bangalore-560068, India. Tel: +91-080-6688704; Fax: +91-080-6681511; E-mail: tnspriya@yahoo.com

Characteristics of F1 hybrids of silkworm

- Usually stronger compared to the parent variety.
- Greater vigour, faster growth, development and productivity and can withstand unfavourable environmental conditions to a great extent.
- Better reproductive potential.
- Resistance to diseases and suitable for artificial diet.
- Uniform cocoon, higher cocoon weight, shell weight, shell ratio and cocoon yield.
- Better adoptability expressed in the form of stable cocoon crop.
- Uniform hatching, moulting and spinning.
- Comparatively shorter larval duration than that of parents or the mid-parent values.
- Better filament length, raw silk yield and reduced renditta.

Classification of heterosis

The various types of heterosis reviewed by Nittler (1978) are classified as individual, maternal and paternal heterosis. The heterosis caused by improvement in performance, vigour etc in an individual (relative to the mean of its parents) that is not attributable to either maternal, paternal or sex-linkage effects are called individual heterosis, while heterosis in a population attributable due to using of cross breed, instead of pure-breed is referred as maternal / paternal heterosis.

Chandrasekharaiah (1994) classified heterosis in silkworm as balanced, mutational and pseudo heterosis. The heterosis resulting from hybridization is referred as balanced or true heterosis, while that resulted from creation of mutation is called mutational heterosis. The heterosis resulting from more favourable environmental conditions is termed as pseudo-heterosis or false heterosis. Mostly, heterosis exploited in sericulture for the production of commercial silk is due to hybridization (true heterosis).

Sarkar (1998) stated that according to Mackey, heterosis might be classified based on direction [positive heterosis (+) (beneficial) or negative heterosis (–) (non-beneficial)] or function [luxuriant heterosis, adaptive heterosis, selective heterosis and reproductive heterosis].

Theoretical basis of heterosis

The several theories have been proposed to explain the manifestation of heterosis, which are reviewed by Bowman (1958). The theories are -

a) The dominance theory: The dominance theory postulates that the parental lines are homozygous dominant for different favourable loci. This theory is proposed on the basis of the superiority of dominant alleles over the recessive alleles. The dominance theory states that inbreeding in a particular line produces homogygosity for some recessive genes and when crosses are made between such inbred lines, the recessive genes of one line get masked by the dominant genes of the other line producing heterotic effect in F1 (Reddy and Raju, 1998). In such instances, it is the presence of dominant gene that produces heterosis rather than heterozygotic loci.

b) The over-dominance theory: The over-dominance theory postulates that the heterozygote is superior to homozygote. Various versions of this include "enheterosis theory" (super-dominance or over-dominance at the chromosomal level) and the "physiological balance theory" (Randal, 1953). Mostly, the theory of dominance and over-dominance leads to the same expectations. In both the cases, gain on out-breeding and loss (decrease) of vigour on inbreeding is established. Bowman (1958) pointed out that, the dominance theory is based on the homozygous dominant alleles for different characters present in the parental lines, while over-dominance is postulated on the basis of effect of allelic differences in heterozygotes.

c) The epistasis theory: It includes all types of inter locus interactions. Sheridon (1980) stated that epistatic theory is referred to as either 'F1-epistasis' or 'parental epistases'. However, contribution of epistasis to heterosis in cross breeds has generally been considered to be negligible (Falconer, 1981). Hayman and Mather (1955) reported generalized formulae for various types of genetic interactions including dominance modifications, dominant epistasis, recessive epistasis, duplicate genes, recessive suppressor and complementary genes. They further stated that heterosis is end product of either complementary or duplicate gene interactions.

d) Biochemical theory: Biochemical basis for heterosis accords with the assumption that the primary heterotic effect is concern with growth substances such as regulatory proteins and hormones, the predominant activity of which is registered in the early part of the developmental cycle of the silkworm. Greater metabolic efficiency in mitochondria of the heterotic hybrid was observed while no such changes occurred in those not exhibiting heterosis.

Initial arguments about the mechanism of heterotic effect supported the dominant gene hypothesis. But, there were several objections to the theory -

- Amassing all favourable alleles could possibly develop a completely homozygous superior line.
- If dominance was the major contributor to heterosis, the F2 frequency distribution should be skewed and be reflected in the binomial pattern of (3/4+1/4) n. How-

ever, the linkage between favourable and unfavourable genes would tend to reduce or eliminate such skewedness.

- Single gene loci could show an over-dominance effect. This thinking has arrived at a blend of both theories. There is no doubt that for some loci, dominance is the major factor contributing to the heterosis. However, as an explanation of the heterosis mechanism, there are enough inconsistencies to consider either of the alternatives.

Before starting hybridization between pure breeds, it is imperative for the breeders to adopt following strategies to obtain better heterosis leading to fruitful results:

i. Collection of endemic and exotic genotypes of both multivoltine and bivoltine silkworm strain.
ii. Evaluation and documentation of the collected genotypes and studies on their genotypic and phenotypic stability.
iii. Clustering / grouping of genotypes both genotypically and phenotypically through diallel analysis besides study on region, season and environmental stability.

Yokoyama (1957) while reviewing the literature on hybridization studies in silkworm by previous workers stated that it is economical for the farmers to rear F1 hybrids. In India, utilization of hybrid vigour started during 1920s. However, this did not contribute to the rapid progress in productivity. After few years, the male parental strain involved in the hybrid *viz.*, C. Nichi became polyvoltine (Reddy and Raju, 1998). During 1940 attempts was made to improve the indigenous multivoltine races *viz.*, Nistari and Chotopolu by hybridization with a few Italian races. Consequently Nismo, Ichhot and Iton were evolved from the hybrid population, which were reported to be better than indigenous multivoltine breed Nistari (Ghosh, 1949; Datta, 1984). Cross breeding of silkworm races which differed in voltinism and quantitative characters were initiated during 1960s by utilizing polyvoltine Pure Mysore and exotic bivoltine races such as J112, C108, J122 × C122, J124, Sanish, Azarbaizan and NN6D. Even though, these hybrids were found superior but the goal of achieving increased productivity could not be fully realized.

In India, first systematic hybridization following the diallel crossing method was reported by Krishnaswamy *et al.* (1964) involving 5 genetically pure multivoltine races. Since then various crossing systems like diallel, line × tester, three-way crosses and double crosses were attempted by various workers for the utilization of hybrid vigour at commercial level (Sengupta *et al.*, 1974; Narasimhanna *et al.*, 1976; Das *et al.*, 1997). Almost all the economic traits expressed hybrid vigour in the hybrids exhibiting superiority over inbred lines. The characters *viz.*, fecundity, larval weight, single cocoon and shell weight, cocoon-shell ratio, cocoon yield/100 Dfls, ERR by number and weight are found to improve substantially in F1 hybrids. In addition, reduced mortality in F1 hybrids, less renditta, better filament length adds to the advantage of silk reeling industry. The heterosis varies from season to season, crosses to crosses, characters to characters, and sexes to sexes besides voltinism to voltinism. If the parental genotypes posses high values for the characters, the degree of heterosis will be less for that particular trait in the hybrid. Heterosis is calculated either over checks parent value (CPV), mid-parent value (MPV) or better parent value (BPV) by using following formulae:

- Heterosis over CPV $= \frac{F1 - CPV}{CPV} \times 100$
- Heterosis over MPV $= \frac{F1 - MPV}{MPV} \times 100$
- Heterosis over BPV $= \frac{F1 - BPV}{BPV} \times 100$

If the value for a particular trait is high in F1, the calculated heterosis will be positive but if F1 value is less, then the heterosis will be negative and should not be exploited except for larval duration and renditta, as short larval duration and less renditta are the beneficial characters.

Hybrid vigour in different crossing systems

Hybrid vigour is at its bests in F1 hybrid which decreases gradually as F1 > F2 > F3 > F4 > F5 and so on and the phenomenon of hybrid vigour disappears in about 14 generations in silkworm (Hirobe, 1985). Silkworm strains can be crossed in different manners viz., single cross [A × B], three-way cross [(A × B) × C] and double cross [(A × B) × (C × D)].

The quantitative characters in silkworm (*B. mori*) are highly variable and have a greater economic value. F1 (single cross) hybrids are most commonly used for commercial cocoon production because they represent high heterosis for most of the economic characters (Harada, 1961). It has also been reported that F1 hybrids are less variable than parental lines, three-way and double crosses (Watanabe, 1960, 1961). Variability in cocoon shape has been used in identification of uniform strains and hybrids (Mano, 1994).

In the study of heterosis in the silkworm many characters have been found to have a relationship with the qualitative and quantitative aspects of silk yield (Ohi *et al.*, 1970). However, the characters in hybrids showing high manifestation of heterosis are:

- Shorter feeding duration and better larval weight.

Table 1. Heterosis for different characters in silkworm

Characters	Heterosis % *
Feeding duration	97
Larval mortality	56
Silk filament size	103
Shell weight	124
Egg number	123

*Index value of 100 is taken from mid-parental values.

Table 2. Heterosis for different characters in *Bombyx mori* (mean of 30 Bi × 30 Bivoltine hybrids) (after - Subba Rao and Sahai, 1990)

Characters	Heterosis %
Cocoon yield	14.25
Cocoon weight	3.89
Shell weight	3.29
Denier	3.08
Larval duration	2.58
Survival rate	0.87

Table 3. Heterosis for different characters in Bombyx *mori* (mean of 10 multi × 10 multivoltine hybrids) (after- Singh and Rao, 1996)

Characters	Heterosis %	
	Favourable	Unfavourable
E.R.R. (Number)	10.39	23.84
ERR weight	40.49	69.59
Single cocoon weight	25.54	50.43
Single shell weight	32.22	60.91
Cocoon-shell ratio	2.70	14.25
Yield/100 Dfls	73.37	119.83

Table 4. Comparative performance of three-way and conventional single cross for post cocoon parameters (after Krishnaswamy, 1987)

Characters	Three-way cross	Conventional cross
Filament length	714	694
Filament denier	2.71	2.55
Reelability %	81.0	72.0
Renditta	8.00	8.40
Size deviation	2.49	3.95
Tenacity (gm/d)	3.00	2.46
Elongation %	23.0	23.4
Neatness %	80.0	77.0
Evenness %	80.0	80.0
Cleanness %	96.0	95.0

- Low rate of mortality and better Effective Rate of Rearing (ERR).
- Higher cocoon and shell weight.
- Longer filament length and reduced renditta.
- Better pupation rate and raw silk percentage.

The earlier results of Osawa and Harada (1944) showed hybrid vigour for silk filament size, shell weight and egg number considering the mid-parent value as 100 (Table 1). However, the level of heterosis recorded for different strains by different workers are not consistent. Subba Rao and Sahai (1990) using 30 Bivoltine × 30 Bivoltine hybrids reported highest manifestation of heterosis for cocoon yield (14.25%), which is a function of both survival rate and cocoon weight (Table 2). While conducting studies on 10 multi × 10 multivoltine, Singh and Rao (1996) reported highest heterosis for cocoon yield/100 Dfls that differs from season to season with highest value in unfavourable season (119.83%) (Table 3). ERR by number and weight, single cocoon and shell weight along with cocoon-shell ratio have also been reported showing positive heterosis by these workers.

Nagaraju (1990) reported highest heterosis for survival rate in multivoltine × bivoltine crosses. Studies made by various workers reported that the degree of heterosis varies steeply for different characters. Such wide differences in the manifestation of heterosis suggests that the parental strains involved in the hybrid differs in their genetic make-up as reflected in their sharp differences in origin, voltinism and quantitative traits such as larval duration, single cocoon weight, single shell weight, filament length etc. (Yokoyama, 1957; Chang *et al.*, 1981; Gamo and Hirabayashi, 1983; Sathenahalli *et al.*, 1989). Harada (1961) stated that heterosis becomes lesser with the increase in mid-parental value. According to him, when the quantitative characters of the parents are improved through selection excessively, they become more homogenous for genetic components; consequently the heterosis tends to become smaller as found for weight of cocoon and length of silk filament.

Heterosis in three-way crosses: In India, the exploitation of using three-way crosses of the silkworm were demonstrated by Krishnaswami (1987), Rao *et al.* (1989), Das *et al.* (1994) etc. Most of the studies (Hirobe, 1985, Udupa and Gowda, 1988; Singh *et al.*, 1994) showed that three-way cross hybrids are inferior to single hybrids. Similar results was also reported by Nagaraju (1990) for three-way cross hybrids of (multi × multi) × Bi and multi × (Bi × Bi) crosses. Such a difference between hybrids of single, three-way and double crosses was interpreted considering the fact that one of the parents involved in three-way and both the parents in double cross hybrids are actually F1 individuals (Nagaraju *et al.*, 1996). Furthermore, the population produced by three-way or double cross hybrids is a mixture of genotypes, all of which could in principal have been produced by single crosses but differs from single crosses in the following three ways (Falconer, 1981):

- If the superiority of single cross is due to epistatic interactions, some of its superiority is lost in three-way and double crosses.
- There is genetic variation within the crosses and consequent loss of phenotypic uniformity.
- The variance between crosses is reduced and the best three-way and double cross hybrids are consequently not as good as the best single cross hybrids.

However, Krishnaswamy (1987) clearly demonstrated that three-way cross cocoons results in improved reelability, reduced renditta, lower size deviation and improved tenacity as compared to those of the conventional single

Table 5. Heterosis of different characters in three-way crosses (mean of 4 three-way cross involving multivoltine as female and bivoltine F1 hybrids as male parent) (after - Das *et al.* 1997)

Characters	June - July	Oct - Nov	Dec - Jan
Larval period	−6.52	−8.33	−4.62
Survival %	33.39	12.13	3.97
Single cocoon weight	27.18	19.66	19.18
Single shell weight	44.96	28.41	22.07
Filament length	39.70	18.06	20.95
Yield/100 Dfls	91.06	47.51	18.67

Table 6. Heterosis in three-way crosses during favourable and unfavourable seasons (after - Das *et al.*, 1994)

Combinations	Heterosis type	Survival %	Single shell weight	Yield/ 100 Dfls
June × July				
G (P5 × NB18)	MPV	24.58	27.96	87.41
	BPV	4.95	24.61	54.77
G (NB18 × P5)	MPV	29.13	33.45	98.06
	BPV	10.44	27.65	66.18
G (KB × NB7)	MPV	38.88	26.56	105.34
	BPV	4.36	20.86	49.26
G (NB7 × KB)	MPV	40.97	20.78	73.46
	BPV	0.98	14.71	23.74
October - November	MPV	8.03	2.68	30.73
G (P5 × NB18)	BPV	−2.01	4.76	−8.00
	MPV	2.21	14.64	36.09
G (NB18 × P5)	BPV	−7.26	−4.73	1.89
	MPV	22.21	27.86	72.31
G (KB × NB7)	BPV	20.49	13.23	33.28
	MPV	16.09	33.46	50.93
G (NB7 × KB)	BPV	9.45	17.14	18.14

hybrid cocoons (Table 4). During hot and humid season, when the rearing of bivoltine F1 hybrid is unsuccessful at field level and indigenous races gives very low and poor quality yield, three-way crosses can play an important role as an intermediary technology for commercial use (Das *et al.*, 1994). Three-way crosses showed highest heterosis for yield/100 Dfls followed by cocoon-shell weight during unfavourable season (Table 5). In another study, Das *et al.* (1997) observed that heterosis for different characters is higher during unfavourable season compared to favourable season (Table 5) and MPV over BPV (Table 6) in all the combinations tried.

Heterosis in double crosses: The primary objective of rearing double hybrids is to get the desired quantitative and qualitative traits into one combination (Datta and Basavaraja, 1998). It is well known that survival and fecundity are affected greatly with increase in quantitative traits beyond threshold level. Although survival could be maintained in single hybrids, they are handicapped by less number of eggs laid by inbred pure mother moths. Unless mother moth is a hybrid, the fecundity cannot be increased (Yokoyama, 1979). The increase in egg number is possible only with the foundation crosses, which are the parents of double hybrids. In addition, with clear advantage like easy rearing, superior to parental breeds in growth, vigour and other economic characters besides better in yield than single hybrids (Nirmal Kumar *et al.*, 1998), the double hybrids could be commercially exploited. Mukherjee (1998) stated that in general the heterotic manifestation is higher in case of three-way and double crosses for almost all the characters. Yokoyama (1979) observed that the double crosses invariably manifest greater heterosis for fecundity. Hirobe (1985) reported that double hybrids show 15 − 20% improvement in egg productivity compared to single hybrids. Nirmal Kumar *et al.* (1998) reported heterosis over mid-parent and better parent in double hybrids for pupation rate, cocoon weight, shell weight, filament length and raw silk % over foundation crosses (F1) with higher values in cocoon weight (Table 7). Further, the heterosis over MPV observed by them was invariably high compared to BPV.

Improved silkworm strains, which yield longer filament length, tend to lay fewer eggs (Ohi *et al.*, 1970). On the other hand, in double cross hybrids, the egg yield/female moth is 30% more than in single cross hybrids (Yokoyama, 1973). Hence, the usage of double cross hybrids was to an extent of more than 40% in Japan, while such a use is yet to gain initiative in India. A model proposed by Minagawa and Otsuka (1975) can predict the performance of three-way and double cross hybrids from the performance of single cross hybrids of the constituent lines. Ghosh *et al.* (1996) reported heterosis in fecundity

Table 7. Heterosis of different characters in double-crosses (Mean of three double crosses) (after - Nirmal Kumar *et al.*, 1997)

Characters	Heterosis %	
	Mid-parent	Better parent
Pupation rate	7.50	4.33
Cocoon weight	12.04	11.68
Shell ratio	2.56	0.90
Filament length	10.71	5.94
Raw silk	7.17	5.64

Table 8. Heterosis in fecundity over foundation crosses

Type of crosses	Favourable	Unfavourable	Average
Foundation crosses	479	399	439
Double crosses	509 (6.26%)	522 (30.82%)	516 (17.53%)

Table 9. Heterosis % in different crossing systems (after - Mukherjee, 1998)

Characters	Single crosses	Three-way crosses	Double crosses
Fecundity	14.13	2.03	9.62
Larval duration	0.33	–4.22	–4.26
Larval weight	5.85	25.00	31.82
Yield/10000 larvae	5.40	17.82	23.05
Single cocoon weight	18.63	26.98	25.99
Single shell weight	66.67	39.18	35.88
Shell ratio	52.98	21.62	19.48
Filament length	10.04	31.26	38.43
Denier	16.90	17.50	15.63

in double hybrids over foundation crosses (Table 8). They stated that if foundation crosses were used at P1 level, it would eventually increase the commercial seed production. This approach may be adopted to bridge the gap of commercial seed production and quality. Also the benefit by the use of double hybrids is -

- Increased crop reliability if foundation crosses are raised and reared at P1 level especially in unfavourable seed crop season.
- Increase in number of eggs up to an extent of 20% promoting an enhanced production.
- Seed crop rearers will not hesitate to accept the foundation crosses because of crop assurance.

Mukharjee (1998) reported that in general for shell weight and shell ratio, heterotic manifestation is higher in case of single crosses than the three-way and double crosses (Table 9) and concluded that results are in conformity with Minagawa and Otsuka (1975). Moreover, his results have not confirmed the findings of Yokoyama (1957) who had reported that double crosses manifest greater heterosis for almost all the characters. Sengupta *et al.* (1974), Narasimhanna (1976), Mukharjee (1998) reported lower degree of heterosis in multivoltine crosses. It is evident that the genetic background of Indian polyvoltine breeds is more or less similar in view of long inbreeding history. In the multi × Bi crosses, the cocoon characters have invariably failed to exceed the better parent value. The negative heterosis might be due to the superiority of bivoltine strains. Udupa and Gowda (1988) and Gowda *et al.* (1993) also reported instances of negative heterosis in cocoon characters when multivoltine female parents were crossed with bivoltine male parents.

Mukharjee (1998) reported that performance of heterosis on individual cross basis in different crossing system had good number of crosses, which failed to exhibit heterosis, and thereby showed negative heterosis. This trend of result could be attributed to the specific combination of parental lines. Negative heterosis has also been reported by Kantartankul *et al.* (1987); Sengupta *et al.* (1974) and Narasimhanna (1976) in silkworm.

Egg productivity is positively correlated with number of eggs laid and number of effective moths capable of laying reasonable number of eggs but this character is negatively correlated with cocoon shell and raw silk per centage. Therefore, selection of inbred lines for high egg productivity without reducing the cocoon-shell % is difficult task. Hence, breeders are hybridizing two or more inbred lines (Datta and Basavaraja, 1998) to get desired result. Nirmal Kumar *et al.* (1998) observed no differences for shell ratio and neatness between pure breeds, foundation crosses (F1) and double crosses. However, major differences noticed by them were with respect to pupation rate, cocoon weight, filament length and raw silk recovery (Table 10). The selection of suitable parents for foundation crosses is very important. If the foundation crosses with high degree of heterosis are used for double hybrid preparation, the hybrid vigour may decline (Basavaraja *et al.*, 1998). Therefore, the foundation cross which show low heterosis should be utilized to have more hybrid vigour in double hybrids.

Relatively recently, Central Silk Board, Govt. of India has authorized single, three-way and double cross hybrids for commercial exploitation in different regions and seasons of the country (Table 11) and besides India, there is also great demand for supply of these hybrids from other countries also.

Heterosis exploitation: The phenomenon of heterosis or hybrid vigour has been fully exploited in both animals as well as in plant production. The classical example of the application of this phenomenon is corn in agriculture and silkworm in sericulture. Systematic and planned hybrid-

Table 10. Mean performance of parents, foundation (F1) and double hybrids

Characters	Parents		Foundation crosses		Double crosses
	Oval	Dumbbell	Oval	Dumbbell	
Fecundity (No)	459	536	503	517	----
Pupation %	69.90	70.40	90.10	88.60	96.00
Cocoon weight	1.55	1.66	1.86	1.85	2.08
Cocoon-shell %	24.16	23.80	23.92	23.46	24.18
Filament length	1114	1134	1167	1165	1295
Raw silk %	20.70	19.80	19.50	19.70	21.30
Neatness (P)	92.80	93.50	92.80	93.50	93.80

Table 11. Authorized silkworm hybrids for commercial exploitation

Sl. No.	Hybrids	Combinations	Seasons	State / region
1	P2D1 × NB18	MV × BV	Winter	Andhra Pradesh
			Spring	West Bengal, Assam, Bihar, Orissa, M. P.
			Summer / Early autumn	Uttar Pradesh
2	MY1 × NB18	MV × BV	Spring / autumn	West Bengal, Assam, Bihar, Orissa, M. P.
3	N × (NB18 × P5)	MV × BV	Autumn	West Bengal
			Summer / autumn	Assam, Bihar, Orissa, M. P.
4	PM × NB18	MV × BV	Summer	Assam, Bihar, Orissa, M. P.
5	RD1 × NB18	MV × BV	Summer / early winter	Uttar Pradesh
6	BL23 × NB18	MV × BV	Spring / autumn	Rianfed areas
7	BL34 × NB18	MV × BV	Spring / autumn	Irrigated areas
8	SH6 × KA	BV × BV	Spring / autumn / winter	West Bengal, Assam, Bihar, Orissa, M. P.
9	SH6 × NB4D2	BV × BV	Spring	Uttar Pradesh, J & K
10	CA2 × NB4D2	BV × BV	Spring	West Bengal, Assam, Bihar
			Spring, autumn / early winter	Orissa, M.P., Uttar Pradesh, J & K
11	NB18 × P5	BV × BV	Winter	Assam, Bihar, Orissa, M. P.
12	YS3 × SF19	BV × BV	Spring	J & K, Uttar Pradesh
13	PAM101 × NB4D2	BV × BV	Autumn / early winter	J & K, Uttar Pradesh
14	CC1 × NB4D2	BV × BV	Autumn / early winter	J & K, Uttar Pradesh
15	PAM111 × SF19	BV × BV	Autumn / early winter	J & K, Uttar Pradesh
16	CSR12 × CSR6	BV × BV	Spring / autumn	Temperate & tropical zones
17	CSR18 × CSR19	BV × BV	Autumn	Temperate & tropical zones
18	CSR16 × CSR17	BV × BV	Spring / autumn	Temperate & tropical zones
19	CSR3 × CSR6	BV × BV	Spring / autumn	Temperate & tropical zones
20	CSR2 × CSR4	BV × BV	Spring / autumn	Temperate & sub- tropical zones
21	CSR 2 × CSR5	BV × BV	Spring / autumn	Temperate & sub- tropical zones
22	KSO1 × SP2	BV × BV	Spring	Temperate & tropical zones
23	SKUAST-1 × SKAUST-6	BV × BV	Spring	J & K
24	APM1 × APS8	MV × BV	Spring & Autumn	South India
25	BL-43 × NB4D2	MV × BV	Spring & Autumn	South India
26	APS5 × APS4	BV × BV	Spring & Autumn	North India

ization together with improved farming and rearing practices has helped a great deal to increase the productivity of corn and silk by many folds. In fact Japanese silkworm and American maize are two big stars of hybrid utiliza-

Table 12. Heterosis in MV × BV hybrids raised at two different temperatures (after - Nagaraju *et al.*, 1996)

Characters	25°C			31°C		
	MPV	F1	Heterosis %	MPV	F1	Heterosis %
Survival rate	86.05	96.80	12.49	81.95	94.70	15.50
Single cocoon wt.	1.51	1.64	8.60	1.29	1.43	10.90
Single shell wt.	0.28	0.30	7.14	0.25	0.27	8.00

tion. The exploitation of hybrid vigour in silkworm came to being slightly earlier than in the American maize.

Crossing of inbred lines has made a major contribution of today's high productive silkworm races; ever since the phenomenon of hybrid vigour was discovered and adopted for cocoon production. In this case the purpose of crossing is to produce a heterotic effect rather than to provide genetic variation for selection. Another purpose of crossing inbred line is to produce superior crossbreed or F1 hybrid. Therefore, heterosis depends on selection as well as on inbreeding and crossing.

Since the introduction of heterosis, progress in silkworm breeding has depended on success or failure in identifying better combiners for a cross or a hybrid. One of the most important research activities for development of better hybrid varieties is the identification of inbred lines for specific cross combinations. Good combiners are distinguished by means of the combining ability test / line × tester analysis or D^2 analysis.

Heterosis and environment: Environmental factors known to influence growth and development of silkworm play very important role in the expression of heterosis. The level of heterosis expressed in a crossbreed population is determined by interaction between the genotype and environmental factors prevailing at that time. Lerner (1954) proposed the concept of genetic homeostasis in which heterozygous populations are expected to be less influenced by environmental factors in comparison to homozygous populations. Sang (1956), Griffing and Zsiros (1971), Knight (1973) and Orozoco (1976) reported that the heterozygous populations are found to possess the required genetic architecture to withstand the adverse environmental factors better than the homozygotes. Harada (1961) observed high degree of heterosis for various quantitative traits during spring compared to autumn season and stated that the difference in the expression of heterosis was due to the influence of environmental factors. Generally, in a good environment (optimum temperature, relative humidity, air current, rearing space, germ-free conditions and mulberry leaves of high nutritive value) silkworm parental strains register a high yield (Krishnaswamy, 1978). On the other hand, when both the parental lines and hybrids are reared in an adverse environment, the mean of hybrids will be higher than the mean of the parental strains. In such cases, heterosis over both MPV and BPV will be higher. This condition is similar to the 'Greek temple model' proposed by Cunningham (1987) for the traits exhibiting greater degree of heterosis in a poor environment (Table 12).

The degree of heterosis over mid-parental value will mostly be less under favourable environmental conditions. Further, when one of the parents involved in hybrid is high yielding bivoltine strain, the heterosis over the exotic parent will be negative if both, exotic parent and hybrids are raised under similar favourable conditions. On the other hand, when both parental strains and hybrids are raised in unfavourable environmental conditions, performance of hybrids will be much superior to both the parental strains. Under such conditions the heterosis will be higher over both mid-parental and better parental values.

Heterosis and silkworm breeding: Hybridization followed by appropriate selection bringing together the economic characters of choice from defined sources and to synthesize genotypes of desirable constitution and expression is the main aim of breeding. By utilizing the known and established breeding material, the objective of synthesizing new breeds can easily be realized by the application of appropriate selection pressure for desirable combinations of genes. The reciprocal crossing of two breeds which are good in some characters and poor for some other characters, to lead to the segregation of characters at indefinitely large number of loci in F2 generation (Lerner, 1954) and thus enabling the breeder to select the desirable combination of characters and reject the individual with undesirable characters.

Evolution of improved races through inbreeding of hybrids is well documented (Hirobe, 1968; Gamo, 1976; Yokoyama, 1979). The distinct genotypic and phenotypic differences between the races utilized in the hybridization produce high degree of phenotypic variability enabling the breeder to step up selection for different characters in the polygenic system (Gamo and Ichiba, 1971; Gamo, 1976) can be exploited by the application of systematic selection and bringing together some advantageous features of the parental races.

Exploitation of heterosis has played a vital role in increasing the silk production to a great extent. Continuous efforts are still being made to develop new hybrid combination for effective exploitation of heterosis and to increase productivity.

References

Basavaraja, H. K., N. Suresh Kumar, N. Mal Reddy and R. K. Datta (1998) New approaches to bivoltine silkworm breeding; in *Silkworm Breeding*. Sreerama Reddy, G. (ed.), pp.131-139, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

Bowman, J. C. (1958) Selection for heterosis. *Anim. Breed. Abst.* **27**, 261-273.

Chandrasekharaiah (1994) Silkworm breeding; in *Lectures on Sericulture*. Boraiah, G. (ed.), pp.70-78, Surmya Publication, Bangalore.

Chang, K. Y., K. S. Han and B. Y. Min (1981) Genetic studies on silkworm characters by diallel cross. II. Analysis of heterosis and combining abilities. *Korean J. Seric. Sci.* **22**, 1-7.

Cunnigham, E. P. (1987) Present and future prospective in animal breeding research. Proc. XV Intl. Cong. Genet. New Delhi, India.

Das, S. K., B. Ghosh, S. Pattanaik, N. K. Das, T. Singh, S. K. Sen and G. S. Rao (1997) Hybrid vigour in three-way crosses of mulberry silkworm, *Bombyx mori* L. *Indian J. Genet.* **57**, 447-453.

Das, S. K., S. Patnaik, B. Ghosh, T. Singh, B. P. Nair, S. K. Sen and Rao, G. S. (1994) Heterosis analysis in some three-way crosses of *Bombyx mori* (L). *Sericologia* **34**, 51-61.

Datta, R. K. (1984) Improvement of silkworm races (*Bombyx mori* L.) in India. *Sericologia* **24**, 393-415.

Datta, R. K. and H. K. Basavaraja (1998) Silkworm breeding in Japan, China and India; in *Silkworm Breeding*. Sreerama Reddy, G. (ed.), pp.18-38, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

East, E. M. and H. K. Hayes (1912) Heterozygosis in evolution and plant breeding. USDA. *Bur. Plant Ind. Bull.* **243**, 1-58.

Falconer, D. S. (1981) Introduction to Quantitative Genetics. 2nd Edition, Longman London and New York, pp. 340.

Gamo, T. (1976) On the recent concept and trends in silkworm breeding. *Farming Japan* **10**, 11-12.

Gamo, T. and T. Hirabayashi (1983) Genetic analysis of growth rate, pupation rate and some quantitative characters by diallel cross in the silkworm, *Bombyx mori*. *Jap. J. Breed.* **33**, 178-190.

Gamo, T. and S. Ichiba (1971) Selection experiment on fibroin hydrolyzing ratio in silkworm cocoons, its effects on the environmental characters. *Jap. J. Breed.* **21**, 87-92.

Ghosh, B., P. R. T. Rao, A. K. Sengupta, S. K. Sen and B. Saratchandra (1996) Utilization of hybrid vigor ñ An approach. *Indian Silk* **34**, 9-12.

Ghosh, C. C. (1949) Silk production and weaving in India. Govt. Printing Press, Calcutta.

Gowda, R. R., M. Gopalan, S. Jayaraj and N. Natarajan (1993) Heterosis in selected single cross hybrids of silkworm, *Bombyx mori* L. *J. Seric.* **1**, 50-55.

Griffing, B. and E. Ziros (1971) Heterosis associated with genotype environment interactions. *Genetics* **68**, 443-455.

Harada, C. (1961) On the heterosis of quantitative characters in the silkworm. *Bull. Sericult. Expt. Stn.* **17**, 50-52.

Hayman, B. L. and K. Mather (1955) The description of genetic interactions in continuous variations. *Biometrics* **11**, 69-82.

Hirobe, T. (1968) Evolution, differentiation and breeding of the silkworm ñ The Silk Road, past and present. Genetics in Asian Countries. XII Intl. Cong. Genet. Tokyo, pp. 25-36.

Hirobe, T. (1985) On the recent advancement of silkworm breeding in Japan. A Technical Report.

Kantaratanakul, S., C. Tharvornanukkulkit, S. Wongthong, S. Chareonying, A. Campiranon and P. Saksoong (1987) Diallel cross with polyvoltine strains of Thai silkworm (*Bombyx mori* L.). *Sericologia* **27**, 279-286.

Knight, R. (1973) The relation between hybrid vigour and genotype and environment interaction. *Theor. Appl. Genet.* **43**, 311-318.

Krishnaswamy, S. (1978) New technology of silkworm rearing. CSRTI, *Bull Central Silk Board* **2**, 1-23.

Krishnaswamy, S. (1987) A new concept of a three-way crosses in place of conventional Mysore x Bivoltine hybrids. *Indian Silk* **27**, 21-26.

Krishnaswamy, S., M. S. Jolly and S. Subba Rao (1964) Diallel analysis of quantitative characters in multivoltine races of silkworm. *Indian J. Genetics* **24**, 213-222.

Lerner, I. M. (1954) The Genetic Basis of Selection. John Wiley & Sons, Inc. New York.

Mano, Y. (1994) Comprehensive report on silkworm breeding. Central Silk Board, India, pp. 180.

Minagawa, I. and Y. Otsuka (1975) Relationships of actual performance of double cross hybrids and predicted value based on the mean value of the single crosses concerned in the silkworm, *Bombyx mori* L. *Jap. J. Breed.* **25**, 251-257.

Mukherjee, P. (1998) Hybrid vigour in different crossing system in silkworm, *Bombyx mori*; in *Silkworm Breeding*. Sreerama Reddy, G. (ed.), pp. 197-208, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

Nagaraju, J. (1990) Studies on some genetic aspects of quantitative characters in tropical silkworm, *Bombyx mori*. Ph.D. Thesis, University of Mysore, India.

Nagaraju, J., Urs Raje and R. K. Datta (1996) crossbreeding and heterosis in the silkworm, *Bombyx mori*. *Sericologia* **36**, 1-20.

Narasimhanna, M. N. (1976) Contribution to the genetics of silkworm. Ph. D. Thesis, University of Mysore, India.

Narasimhanna, M. N., Chandrasekharaiah, R. G. Geetadevi, N. Muneera and G. Prabha (1976) Ecogenetic attributes of the newly evolved bivoltine hybrid 'Nandi' in *Bombyx mori* L. Proc. Dunn-Dobzh. Symp. Genet. pp. 379-386.

Nirmal Kumar, S., M. Ramesh Babu, H. K. Basawaraja, N.

Mal Reddy and Datta, R. K. (1998) Double hybrids for improvement of silk production in silkworm, *Bombyx mori* L.; in *Silkworm Breeding*. Sreerama Reddy, G. (ed.), pp. 209-217, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

Nittler, G. (1978) Breed utilization for meat production in sheep. *Anim. Breed. Abst.* **46**, 131-143.

Ohi, H., T. Miyahara and A. Yamashita (1970) Analysis of practically important characteristics in the silkworm in early breeding generations of hybrids. Analysis of variations among strains, correlation between parents and offspring as well as relation between each character. *Tech. Bull. Sericult. Expt. Stn. Japan* **93**, 39-49.

Osawa, K. and C. Harada (1944) Studies on the F1 hybrid of the silkworm. III. On the effect of heterosis. *Bull. Sericult. Expt. Stn.* **12**, 183-211.

Orozoco, F. (1976) Heterosis and genotype environment interaction. Theoretical and experimental aspects. *Bull. Tech. Dept. de Genetique Anim. Inst. Nat. de flacher. Agronom.* **24**, 43-52.

Randal, J. M. (1953) Heterosis. *American Naturalist* **87**, 129-138.

Rao, G. S., S. K. Das and B. Ghosh (1989) Heterosis effect on some new silkworm hybrids evolved by three-way cross. *Pros. Cyto. Genet.* **6**, 373-378.

Reddy, G. S. and P. J. Raju (1998) Exploitation of heterosis in silkworm, *Bombyx mori*; in *Silkworm Breeding*. Sreerama Reddy, G. (ed.), pp.186-196, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

Sang, J. H. (1956) Hybrid vigor and animal production. *Anim. Breed. Abst.* **24**, 1-6.

Sarkar, Dilip De (1998) The silkworm Biology, Genetics and Breeding. Vikas Publising House, Pvt. Ltd., New Delhi, pp. 338.

Sathenahalli, S. B., R. Govindan, J. V. Goud and S. B. Magdum (1989) Genetic parameters and correlation coefficient analysis in silkworm, *Bombyx mori. Mysore J. Agric. Sci.* **24**, 491-495.

Sengupta, K., M. R. Yusuf and S. P. Grover (1974) Hybrid vigor and genetic analysis of quantitative traits in silkworm. *Indian J. Genetics* **34**, 249-256.

Sheridon, A. K. (1980) Cross breeding and heterosis. *Anim. Breed. Abst.* **49**, 131-144.

Shull, G. H. (1948) What is heterosis? *Genetics* **33**, 439-446.

Singh, T. (2001) Studies on the evaluation of some three-way cross hybrids of silkworm, *Bombyx mori* L. *Int. J. Indust. Entomol.* **3**, 153-155.

Singh, T., G. S. Rao and M. D. Senapati (1994) Studies on the heterotic expression in silk productivity in some hybrids of *Bombyx mori. Bull. Seric. Res.* **5**, 81-83.

Singh, T. and G. S. Rao (1996) Heterosis effect on economic traits in new hybrids of silkworm, *Bombyx mori* (L). *Canye Kexue* **22**, 42-46.

Subba Rao, G. and V. Sahai (1990) Combining ability and heterosis studies in bivoltine strains of silkworm, *Bombyx mori* L. *Uttar Pradesh J. Zool.* **9**, 150-164.

Thangavelu, K. (1998) Silkworm breeding in India × at cross road; in *Silkworm Breeding*. Sreerama Reddy, G. (ed.), pp. 498-59, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

Toyama, K. (1906) Studies on hybridology of some silkworm crosses with special reference to Mendelís law of heredity. *Bull. Coll. Agric., Tokyo Univ.* **7**, 259-293.

Udupa, S. M. and B. L. V. Gowda (1988) Heterotic expression in silk productivity of different crosses of silkworm, *Bombyx mori. Sericologia* **28**, 395-400.

Watanabe, H. (1960) Temperature effects on the heterosis of starvation resistance in the silkworm, *Bombyx mori. J. Seric. Sci. Jpn.* **29**, 59-62.

Watanabe, H. (1961) Studies on the differences in the variability of larval body and cocoon weights between single cross and three-way cross or double cross hybrids in the silkworm, *Bombyx mori. J. Seric. Sci. Jpn.* **30**, 463-467.

Yokoyama, T. (1957) On the application of heterosis in Japanese sericulture. *Proc. Intl. Genet. Symp. (*Suppl. Vol.) *Cytologia* 527-531.

Yokoyama, T. (1973) The history of sericultural science in relation to industry; in *History of Entomology.* Smith, R. F. and T. E. Miller (eds.), pp. 267-284, Animal Reviews, Palo. Alto. Calif.

Yokoyama, T. (1979) Silkworm selection and hybridization; in *Genetics in relation to insect management.* Working papers, The Rockfeller Foundation Management, pp. 71-83.