Review

CROSSBREEDING AND HETEROSIS IN THE SILKWORM, *BOMBYX MORI*, A REVIEW

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Keywords: Crossbreeding, double cross, mid-parent.

INTRODUCTION

Crossbreeding is extensively used in silkworm improvement as a means of exploiting heterosis (Osawa and Harada, 1944; Harada, 1949, 1952, 1954, 1957, 1961; Yokoyama, 1957; Harada *et al.*, 1961; Krishnaswami *et al.*, 1964; Hirobe, 1985). The two big leaps in hybrid utilisation were the Japanese silkworm and American maize. In fact, the utilisation of hybrid vigour in the silkworm came slightly earlier than in the case of maize. The credit of introducing F_1 hybrids with a clear demonstration of their superiority over parental strains goes to Toyama (1906) of Japan. The hybrids which were crosses of Chinese and Japanese origin became so popular with the farmers there, that by 1919 over 90% of eggs produced were of hybrid origin, reaching 100% by 1928 (Yokoyama, 1973a). The average weight of cocoon shell, which had been brought by slow selection from a little below 20 cg in 1804 to a little over that weight in 1910, was increased rapidly to well over 40 cg by 1932 when the hybrids took over production in Japan (Hirobe, 1985). That was the power of hybrids and phenomenal contribution of hybrid vigour to silkworm improvement. However, unlike in many plant species like rice where highly inbred lines are used for commercial exploitation, in the silkworm, only the hybrids of highly inbred lines (Yokoyama, 1979; Chang *et al.*, 1981; Gamo and Hirabayashi, 1983) or of different breeds (Krishnaswami *et al.*, 1964) are used. The word "heterosis" was coined by Shull in 1914 (as cited by Shull, 1948) to describe the increased vigour of crossbreeds relative to their parents irrespective of the cause underlying such a phenomenon.

The domesticated silkworm, *Bombyx mori*, which enjoys the patronage of many countries in the world by virtue of its commercial value has wide distribution with well-defined geographical races (Hirobe, 1968). These races display genetic, physiological, ethological, morphological, biochemical and quantitative differences (Yokoyama, 1979; Gamo and Ohtsuka, 1980; Gamo, 1983). Besides, many intensive breeding efforts aiming at improving the productivity and quality of silk have yielded a number of inbred lines (Jolly, 1983; Datta, 1984). Many inbred lines which carry specific improvement for a particular character have also been developed (Miyahara, 1978; Maruyama, 1984). Relations between voltinism, moultinism and quantitative traits have been reasonably well defined (Nagatomo, 1942; Morohoshi, 1949; Nakada, 1970; Murakami, 1989; Murakami and Ohtsuki, 1989). The environmental influence on the manifestation of such characters has been elucidated (Morohoshi, 1949; Harada *et al.*, 1961; Singh and Hirobe, 1964; Tazima, 1988; Nagaraju, 1990).

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The objective of this paper is to review briefly the different forms of heterotic expression for different economic traits in the silkworm.

HYBRID VIGOUR FOR DIFFERENT CHARACTERS

During the different stages of silkworm development 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 which reveal intense manifestation of heterosis are as follows:

i) the duration of feeding in hybrids becomes shorter than that of the parents or the midparental values (MPV),
ii) the mortality rate is lower than that of the parents,
iii) the double cocoon rate is higher than that of the parents,
iv) the cocoon weight is higher than that of MPV,
v) the cocoon shell layers are heavier than that of MPV,
vi) the length of silk fibre is longer than that of MPV, and
vii) the cocoon fibre weight is heavier than that of MPV.

The earlier results of Osawa and Harada (1944) show the following values of hybrid vigour for different characters (Table I) considering the MPV as 100.

Table I. Heterosis for different characters in the silkworm.

Tableau I. Hétérosis pour différents caractères chez le ver à soie.

Characters ***Caractères***	**Heterosis*** ***Hétérosis****
Duration of feeding / *Durée du nourrissage*	97
Larval mortality / *Mortalité larvaire*	56
Double cocoon rate / *Taux de cocons doubles*	146
Silk filament size / *Titre de la bave de soie*	103
Cocoon shell weight / *Poids de la coque*	124
Egg number / *Nombre d'oeufs*	123

* Index value of 100 is taken for midparental values / *L'indice 100 correspond aux valeurs des parents moyens.*
(Osawa and Harada, 1944).

In the silkworm, the heterosis recorded by Harada (1957) was in the order of cocoon shell weight (27.8%), cocoon weight (25.9%), survival rate (23%), size of filament (20.7%), length of filament (19%) and growth rate (11%) (Fig. 1).

However, the level of heterosis recorded for different traits by different workers is not consistent. Subba Rao and Sahai (1990) using 30 bivoltine × bivoltine hybrids showed the highest significant level of heterosis for cocoon yield (14.25), which is a function of both survival rate and cocoon weight, followed by cocoon weight (3.89) and denier (3.08) as shown in Table II. Similar studies carried out for six multivoltine × bivoltine hybrids by Nagaraju (1990) showed the highest heterosis for larval weight (13.93%) followed by survival rate (12.7%) and single cocoon weight (8.7%) as shown in Table III.

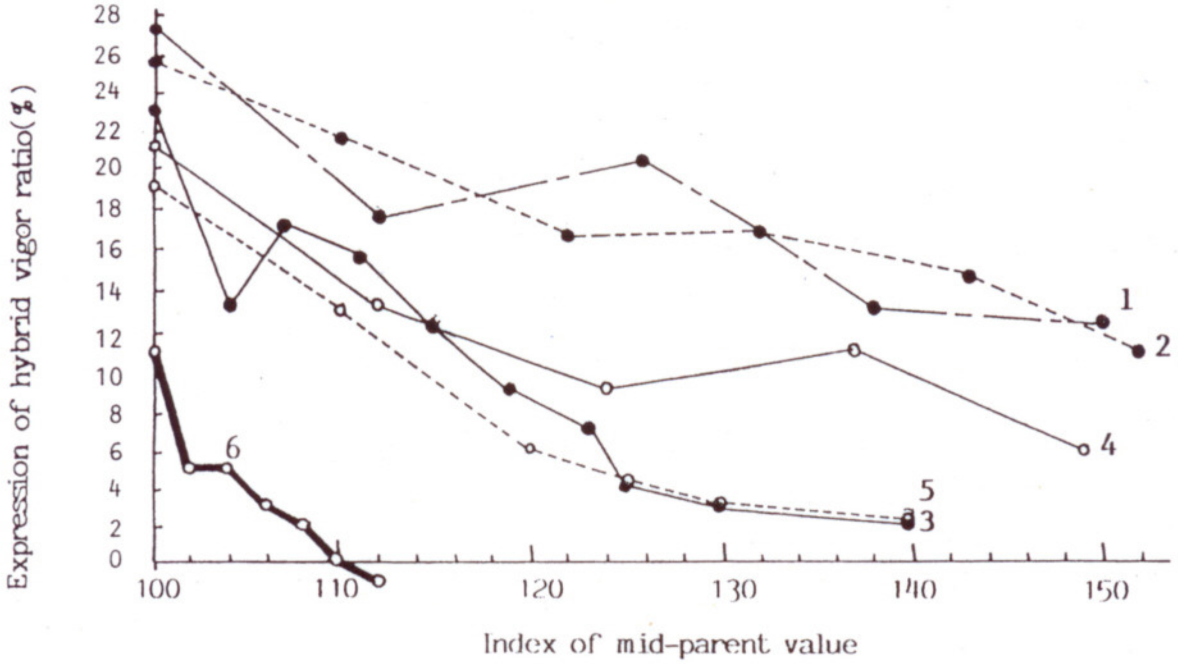

Fig. 1: A sample of expression of hybrid vigour for several characters in the silkworm.
(1) Cocoon layer weight 100 = 27.5 cg; **(2)** Single cocoon weight 100 = 1.4 g; **(3)** Survival rate 100 = 69.5 %; **(4)** Size of filament 100 = 2.5 d; **(5)** Length of filament 100 = 750 m; **(6)** Growth rate 100 = 32.5 d.

Fig. 1 : Exemple d'expression de la vigueur hybride pour plusieurs caractères du ver à soie.
(1) *Poids de la coque soyeuse 100 = 27,5 cg ;* ***(2)*** *Poids du cocon 100 = 1,4 g ;* ***(3)*** *Taux de survie 100 = 69,5 % ;* ***(4)*** *Titre de la bave 100 = 2,5 d ;* ***(5)*** *Longueur de la bave 100 = 750 m ;* ***(6)*** *Taux de croissance 100 = 32,5 d.*
Harada, 1957.

Table II. Heterosis for different characters in the silkworm (mean of 30 bivoltine × bivoltine hybrids).

Tableau II. Hétérosis pour différents caractères chez le ver à soie (moyenne de 30 hybrides bivoltins × bivoltins).

Characters / *Caractères*	$\frac{F_1 - MPV}{MPV} \times 100$
Cocoon yield / *Rendement en cocons*	14.25**
Single cocoon weight / *Poids d'un cocon*	3.89**
Single shell weight / *Poids de la coque*	3.29
Shell ratio / *Richesse soyeuse*	-0.558
Filament length / *Longueur de la bave*	-2.78
Denier	3.08
Larval duration / *Durée larvaire*	2.58
Survival rate / *Taux de survie*	0.87

* Significance at the 5% level / *Significatif au seuil de 5 %.*
** Significance at the 1% level / *Significatif au seuil de 1 %.*
(Subba Rao and Sahai, 1990).

Studies made by various workers show that the degree of heterosis varies steeply for different characters. Such wide differences in the manifestation of heterosis suggest that the parental strains involved in the hybrids differ in their genetic make-up, as reflected in their sharp differences in origin, voltinism and quantitative traits such as larval duration, single cocoon weight, cocoon shell weight, filament length, etc. (Harada, 1957; Yokoyama, 1957; Krishnaswami *et al.*, 1964; Chang *et al.*, 1981; Gamo and Hirabayashi, 1983; Tayade, 1987; Sathenahalli *et al.*, 1989).

Harada (1961) found a functional relationship between MPV and F_1 hybrid values. The degree of heterosis manifested is proportional to the quantity of MPV. The greater is the MPV, the less becomes the heterosis. According to Harada (1961), when the quantitative characters of the parents are improved through selection excessively, they become more homogenous for genic components, consequently the heterosis tends to become smaller, as found for weight of cocoon (Fig. 2) and length of silk filament (Fig. 3).

Table III. Heterosis for different characters in the silkworm (mean of 6 multivoltine × bivoltine hybrids).

Tableau III. Hétérosis pour différents caractères chez le ver à soie (moyenne de 6 hybrides polyvoltins × bivoltins).

Characters / *Caractères*	$\frac{F_1 - MPV}{MPV} \times 100$
Total larval duration / *Durée larvaire totale*	-5.30
5th instar larval duration / *Durée du 5e âge*	-1.40
Larval weight / *Poids larvaire*	13.93
Survival rate / *Taux de survie*	12.67
Single cocoon weight / *Poids d'un cocon*	8.65
Cocoon shell weight / *Poids de la coque*	6.17
Cocoon shell ratio / *Richesse soyeuse*	-0.22

(Nagaraju, 1990)

As a result, the characters of F_1 will gradually approximate to that of the parents themselves, as Hayes (1952) reported in maize. On this point, Smith (1936) has also found that the number of leaves of F_1 in *Nicotiana rustica* was consistently below the MPV. Such a result is interpreted as due to the preponderance of accumulated recessive genes for the characters favoured by selection.

HETEROSIS IN DIFFERENT CROSSING SYSTEMS

The hybrid vigour is at its best in the single cross of the genetically distinct populations, which decreases gradually like $F_1 > F_2 > F_3 > F_4$ ... and the phenomenon of heterosis disappears in about F_{14} generations in the silkworm (Hirobe, 1985).

Silkworm varieties could be crossed into single cross (A × B), three-way cross [(A × B) × C] and double cross patterns [(A × B) × (C × D)]. Generally, single cross hybrids manifest the highest rate of hybrid vigour as compared to three-way and double cross hybrids. Studies conducted on variation in quantitative characters in parental strains and hybrids of different crossing systems reveal that variability for quantitative traits is smaller in single cross hybrids than in parental strains, three-way and double cross hybrids (Watanabe, 1961; Sohn, 1983; Yokoyama, 1973b).

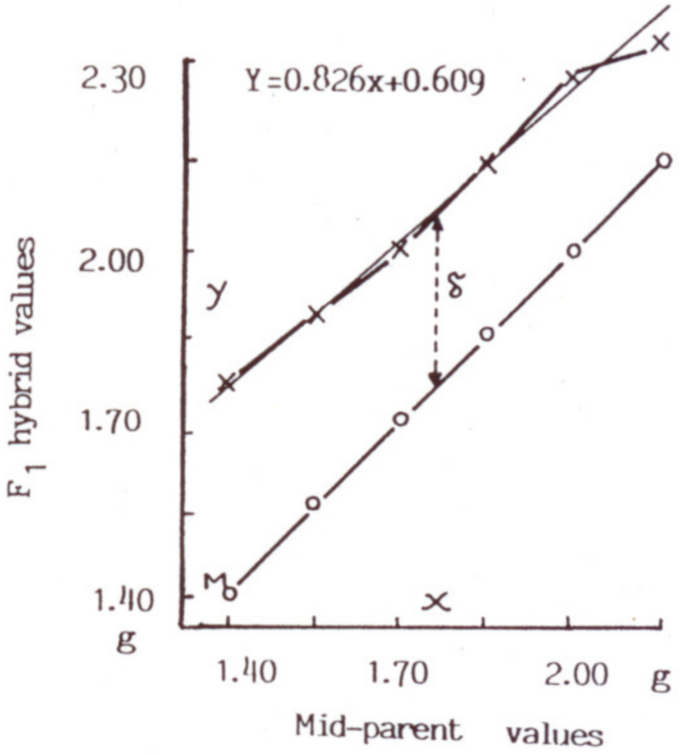

Fig. 2: Manifestation of heterosis in relation to midparental values in silkworm for cocoon weight.

x = midparent values, y = F1 hybrid values, effect of heterosis, x–y.

Fig. 2 : Manifestation de l'hétérosis en fonction des valeurs du parent moyen pour le poids du cocon chez le ver à soie.

x = valeurs du parent moyen, y = valeurs de l'hybride F1, effet de l'hétérosis, x–y.

Harada, 1961.

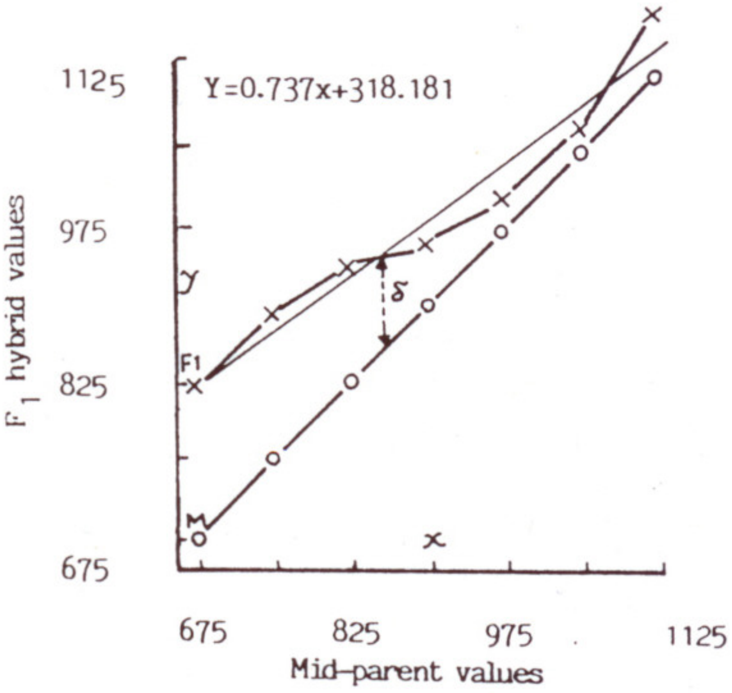

Fig. 3: Manifestation of heterosis in relation to midparental values in silkworm for length of silk filament.

x = midparent values, y = F1 hybrid values, effect of heterosis, x–y.

Fig. 3 : Manifestation de l'hétérosis en fonction des valeurs du parent moyen pour la longueur de la bave chez le ver à soie.

x = valeurs du parent moyen, y = valeurs de l'hybride F1, effet de l'hétérosis, x–y.

Harada, 1961.

Most of the studies recorded to date (Hirobe, 1985; Udupa and Gowda, 1988; Nagaraju, 1990) show that three-way and double cross hybrids are inferior to single cross hybrids. The results obtained by Nagaraju (1990) for three-way cross hybrids of (multivoltine × multivoltine) × bivoltine and (multivoltine × multivoltine) × bivoltine (Table IV) also corroborate these studies.

Such a difference between hybrids of single, three-way and double crosses could be interpreted considering the fact that one of the parents involved in three-way and both parents in the double cross hybrids are actually F_1 individuals. Furthermore, the population produced by three-way or double cross hybrids is a mixture of genotypes, all of which could in principle have been produced by single crosses, but differs from single cross hybrids in the following three ways (Falconer, 1981).

i) If the lines crossed have been selected, and if any of the consequent superiority of their single crosses is due to epistatic interactions, some of this superiority is lost in three-way and double crosses.

ii) There is genetic variation within the crosses and consequent loss of phenotypic uniformity.

iii) 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.

Donald *et al.* (1977) and Gaines *et al.* (1970) observed that the mean of three-way cross hybrids of cattle retains only approximately 40% of heterosis of the F_1 hybrids. Sheridon (1981) reviewing crossbreeding and heterosis in various animal species concludes that such results are best explained by parental epistasis model. Results obtained by various workers on heterosis in single, three-way and double cross hybrids in the silkworm tend to favour the parental epistasis model.

In the three-way crossing type it is difficult to make a choice between (Japanese × Japanese) × Chinese and (Chinese × Chinese) × Japanese hybrids. But considering the silk yarn quality the latter has been found to be better (Yokoyama, 1973b). The double crossing type (Japanese × Chinese) × (Japanese × Chinese) produces nonuniform cocoons with variable cocoon shapes and filament length, as compared to the (Japanese × Japanese) × (Chinese × Chinese) type, hence the latter is preferred (Table V) (Yokoyama, 1973b). The crossing effect is expressed in different ways in case of different crossing order according to the quantitative characters, especially cocoon shell weight in (Japanese × Japanese) × (Chinese × Chinese) crosses. The crossing effect has been found to be highest when the parental strains are crossed in the order of $(1 \times 2) \times (3 \times 4)$, with $4 > 3 > 2 > 1$ for cocoon shell weight.

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

HETEROSIS IN RECIPROCAL CROSSES

In the silkworm, many quantitative characters are closely associated with the nature of voltinism and maturity period which are known to be sex-linked (Nagatomo, 1942; Morohoshi, 1949; Nakada, 1970, 1972; Tazima, 1988). Hence, expression of heterosis varies in the reciprocal crosses of silkworm breeds which differ in voltinism and maturity period. In the reciprocal cross of polyvoltine × bivoltine, the male value is greater than the female one for cocoon shell weight, as demonstrated by Tazima (1988) (Table VIa). Besides, in the reciprocal cross of polyvoltine × bivoltine, cocoon weight, shell weight, filament length and filament weight are lower than those of direct crosses (Tazima, 1988) (Table VIb).

However, such reciprocal differences are not observed in the crosses which involve parental strains of the same voltinism. Nakada (1970) found the larval span of the females to be shorter than that of the males in the reciprocal cross hybrids. The fact that the females of the hybrids grow too quickly has an adverse effect on the cocoon shell weight (Morohoshi, 1949; Nakada, 1972). First, Nagatomo (1942) proposed that maturity genes linked to the Z chromosome play an important role in reciprocal hybrid differences since the larval maturity gene has a close correlation with body size, cocoon weight, cocoon shell weight and body weight. Later, Morohoshi (1949) proposed multiple allelism of maturity genes, i.e., early (lm), intermediate ($+^{lm}$) and late (Lm) maturity. In such a scheme, if one considers that polyvoltines possess the early maturity (lm) gene and the bivoltines carry the late

Table IV. Heterosis for different quantitative characters in single and three-way crosses.

Tableau IV. Hétérosis pour différents caractères quantitatifs chez des croisements simples et trois voies.

	Survival rate *Taux de survie*			Cocoon weight *Poids du cocon*			Cocoon shell weight *Poids de la coque*		
	MPV	F$_1$	Heterosis (%)	MPV	F$_1$	Heterosis (%)	MPV	F$_1$	Heterosis (%)
Single crosses / *Croisements simples* :									
polyvoltine × bivoltine / *polyvoltins × bivoltins*									
Pure Mysore × NB$_{18}$	86.20	98.20	13.92	1.46	1.55	6.16	.276	.267	-3.26
Hosa Mysore × NB$_{18}$	71.37	92.80	30.00	1.62	1.72	6.17	.306	.341	11.44
polyvoltine × polyvoltine / *polyvoltins × polyvoltins*									
Pure Mysore × Hosa Mysore	74.00	95.32	28.81	1.16	1.48	27.58	.190	.238	25.26
Three-way crosses / *Croisements trois voies* :									
(Pure Mysore × NB$_{18}$ × NB$_7$)	94.00	91.90	-2.23	1.66	1.60	-3.61	.321	.279	-13.08
Pure Mysore × Hosa Mysore × NB$_{18}$)	82.80	81.60	-1.45	1.67	1.64	-1.80	.312	.327	4.68

(Nagaraju, 1990)

maturity gene ($+^{lm}$) on Z chromosomes, in a cross between polyvoltine × bivoltine and its reciprocal hybrids, the reciprocal differences for maturity and related traits could be expected. Although this is an oversimplified version for explanation purpose, there seems to be an intricate, genetic mechanism which involves voltinism, maturity genes, temperature during silkworm rearing and hormonal interplay seem to operate on the manifestation of the traits (Oshiki, 1979).

Table V. Comparison of characters among parents and different crosses, spring 1972.

Tableau V. Comparaison des caractères entre les parents et différents croisements, printemps 1972.

Combination	**Pupation ratio (%)**	**Cocoon yield/ 10000 larvae (kg)**	**Single cocoon weight (g)**	**Cocoon shell weight (cg)**	**Cocoon shell ratio (%)**	**Filament length (m)**	**Denier**	**Raw silk**	**Neatness**
Combinaison	***Taux de nymphose (%)***	***Rendement en cocons/ 10000 larves (kg)***	***Poids du cocon (g)***	***Poids de la coque (cg)***	***Richesse soyeuse (%)***	***Longueur de la bave (m)***	***Denier***	***Soie grège***	***Netteté***
Rb (J)	90	17.2	1.81	40.8	22.5	1140	2.67	82.2	96.0
137 (C)	94	18.3	2.07	52.0	25.1	1343	2.96	84.4	94.0
Sfp (J)	91	19.3	2.17	50.4	23.2	1488	2.33	82.2	93.0
13a (C)	95	19.3	2.20	53.8	24.5	1530	2.57	88.5	96.5
Single cross / *Croisements simples*									
Sfp × rb	95	19.3	2.02	47.8	23.7	1370	2.67	84.5	95.5
13a × 137	95	18.5	2.00	50.8	25.4	1513	2.50	83.7	94.4
Sfp × 13a	97	21.6	2.26	54.4	24.1	1577	2.67	85.5	95.5
Three-way cross / *Croisement trois voies*									
(Rb × Sfp) × 13a	98	23.0	2.38	57.6	24.2	1438	3.03	85.0	92.5
Double cross / *Croisements doubles*									
(Sfp × rb) × (13a × 137)	97	22.9	2.38	56.2	23.6	1479	2.97	87.8	89.5
(Sfp × 137) × (Rb × 13a)	98	20.1	2.18	52.2	23.9	1420	2.78	85.9	92.5

J: Japanese / *Japonais*. **C:** Chinese / *Chinois*.
(Yokoyama, 1973b)

Table VI(A). Sexual differences in the quantitative characters in direct and reciprocal crosses of the silkworm.

Tableau VI(A). Différences entre les sexes pour les caractères quantitatifs chez des croisements directs et réciproques du ver à soie.

Cross	**Larval span (days:hr)**	**Single cocoon weight (g)**			**Cocoon shell weight (g)**		
		Male	**Female**	**Mean**	**Male**	**Female**	**Mean**
Croisement	***Durée larvaire (jours:h)***	***Poids du cocon (g)***			***Poids de la coque (g)***		
		Mâle	***Femelle***	***Moyenne***	***Mâle***	***Femelle***	***Moyenne***
Pure Mysore (F) × N_4 (M)	21:22	1.68	2.16	1.92	0.318	0.349	0.334
N_4(F) × Pure Mysore (M)	21:00	1.57	1.70	1.65	0.297	0.252	0.275

M: Male / *Mâle*. **F:** Female / *Femelle*.
(Tazima, 1988).

Table VI(B). Difference in the quantitative characters in direct and reciprocal crosses of the silkworm.

Tableau VI(B). Différences entre les caractères quantitatifs chez des croisements directs et réciproques du ver à soie.

	Single cocoon wt. (g)	**Shell weight (cg)**	**Shell ratio (%)**	**Filament length (m)**	**Filament weight (g)**
	Poids du cocon (g)	***Poids de la coque (cg)***	***Richesse soyeuse (%)***	***Longueur de la bave (m)***	***Poids de la bave (g)***
Pure Mysore	1.00	13.3	13.3	272	0.07
C134	1.83	48.5	26.8	1245	0.37
Pure Mysore × C134	1.87	32.4	17.3	841	0.25
C134 × Pure Mysore	1.59	27.0	17.0	729	0.20

(Tazima, 1988)

HETEROSIS AND ENVIRONMENT

According to the concept of genetic homeostasis (Lerner, 1954), heterozygotes are likely to be better buffered than homozygotes against environmental variations. Consequently, heterozygotes might be expected to display less variation both between and within environments as compared to their parental strains. Thus, the degree of manifestation of heterosis shown by a particular cross can be influenced by the environment (Barlow, 1981). This concept of genotype-environmental interactions influencing the level of heterosis has been dealt with by different authors for different animal species (Sang, 1964; Griffing and Zsiros, 1971; Knight, 1973; Orozco, 1976; Ruban *et al.*, 1988; Santiago *et al.*, 1989; Ehiobu and Goddard, 1989).

Generally, in a good environment (which includes optimum temperature of 25 °C, mulberry leaves of high nutritive value, optimum rearing space, germ-free conditions, air current and 70-75% relative humidity) silkworm parental strains register a higher silk yield and its attributes (Krishnaswami, 1978; Rapussas and Gabriel, 1976; Ueda, 1963; Ueda *et al.*, 1969). As a result, MPV is close to hybrid mean values with a little difference. In fact, when one of the parental strains is a high-yielding bivoltine strain and the other one is a polyvoltine strain in a cross, heterosis over the high-yielding strain will be negative when both parental strains and hybrids are raised in a good environment.

On the other hand, when both the parental strains and the hybrids are raised in an adverse environment (for example, high temperature > 31 °C), the mean of the hybrids will be much higher than the mean of the parental strains. In such cases, heterosis over both MPV and better parental values will be higher (Fig. 4). This condition is similar to the "Greek temple model" proposed by Cunningham (1987) for the traits exhibiting a greater degree of heterosis in a poor environment. The means of six single cross hybrids of polyvoltine and bivoltine strains raised in optimum (25 °C) and high (31 °C) reveal differences in heterosis for survival rate and cocoon characters (Table VII).

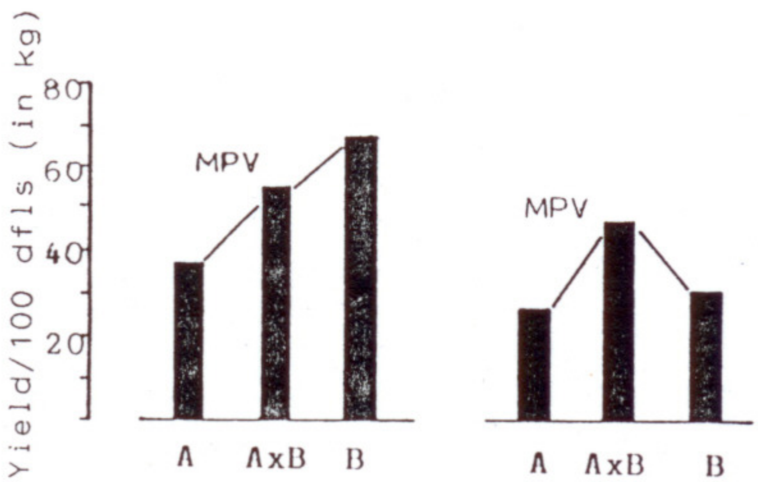

Fig. 4: Schematic representation of cocoon yield differences in parental strains and other hybrids under optimum and adverse rearing conditions.

A: Polyvoltine, **B:** Bivoltine, **A × B:** Hybrid.

Fig. 4: Représentation schématique des différences de rendement en cocons entre les souches parentales et d'autres hybrides dans des conditions d'élevage optimales et défavorables.

A: Polyvoltin, B: Bivoltin, A × B : Hybride.

The results obtained by Watanabe (1960) on heterosis for starvation resistance at three temperatures, 13 °C, 20 °C and 31 °C, corroborate this view. In his study, F_1 hybrids recorded overdominance for starvation resistance in each instar at all the three temperatures. In the early instars, which recorded higher growth at 30 °C, heterosis was larger at 13 °C (47.3%) than at 30 °C (24.8%) while heterosis was higher (37.26%) for fifth instar larvae at 30 °C than at 20 °C (30.4%). Harada *et al.* (1961) found distinct differences in heterosis for the characters concerning reeling in the hybrid population of Japanese (N501 and 3 other strains) and Chinese (C502 and 5 other strains) strains raised during different seasons and years (Table VIII).

Table VII. Midparental value (MPV), F_1 hybrid value and heterosis in polyvoltine × bivoltine hybrids raised at two temperatures.

Tableau VII. Valeur du parent moyen (MPV), des F_1 et de l'hétérosis chez des hybrides polyvoltins × bivoltins élevés à deux températures différentes.

Characters *Caractères*	25 °C			31 °C		
	MPV	F_1	Heterosis (%)	MPV	F_1	Heterosis (%)
Survival rate / *Taux de survie* (%)	86.05	96.80	12.49	81.95	94.70	15.5
Single cocoon wt. / *Poids du cocon* (g)	1.51	1.64	8.60	1.29	1.43	10.9
Cocoon shell wt. / *Poids de la coque* (g)	0.28	0.30	7.14	0.25	0.27	8.0

(Nagaraju, 1990)

Table VIII. Comparison of heterosis (%) over midparental value for post-reeling characters in Japanese × Chinese hybrids raised during spring and autumn.

Tableau VIII. Comparaison de l'hétérosis (%) par rapport à la valeur du parent moyen pour les caractères post-dévidage chez des hybrides japonais × chinois élevés au printemps et à l'automne.

	Raw silk percentage *Richesse soyeuse*			Silk filament length *Longueur de la bave*			Silk filament weight *Poids de la bave*			Silk filament size *Denier de la bave*		
	F_1	MPV	Heterosis (%)	F_1	MPV	Heterosis (%)	F_1	MPV	Heterosis (%)	F_1	MPV	Heterosis (%)
Spring *Printemps*	18.8	18.6	1.07	1211	1068	13.40	40.40	31.25	29.30	3.03	2.66	14.0
Autumn *Automne*	17	16.3	9.20	1020	831	22.70	29.90	19.95	49.90	2.63	2.19	20.1

(Harada *et al.*, 1961)

SEXUAL DIFFERENCES IN THE MANIFESTATION OF HETEROSIS

The degree of manifestation of heterosis does not seem to show marked differences between sexes in the hybrid progeny. Results obtained by Shimizu (1966) show that females recorded slightly higher heterosis than males both for cocoon and cocoon shell weights (Table IX).

Table IX. Sexual differences in the manifestation of heterosis of cocoon and cocoon shell weights.*

Tableau IX. Différences entre les sexes de la manifestation de l'hétérosis pour les poids du cocon et de la coque.*

Sexes	Cocoon weight (g) *Poids du cocon (g)*				Cocoon shell weight (cg) *Poids de la coque (cg)*			
	Parents		F_1	Heterosis (%)	Parents		F_1	Heterosis (%)
	N124	C122			N124	C122		
Female / *Femelle*	2.154	2.007	2.670	28.36	45.687	44.597	56.99	26.25
Male / *Mâle*	1.662	1.537	2.015	26.01	42.357	41.641	51.62	22.90

* Average of ten rearings from 1956-65 / *Moyenne de dix élevages de 1956 à 1965.*
(Shimizu, 1966)

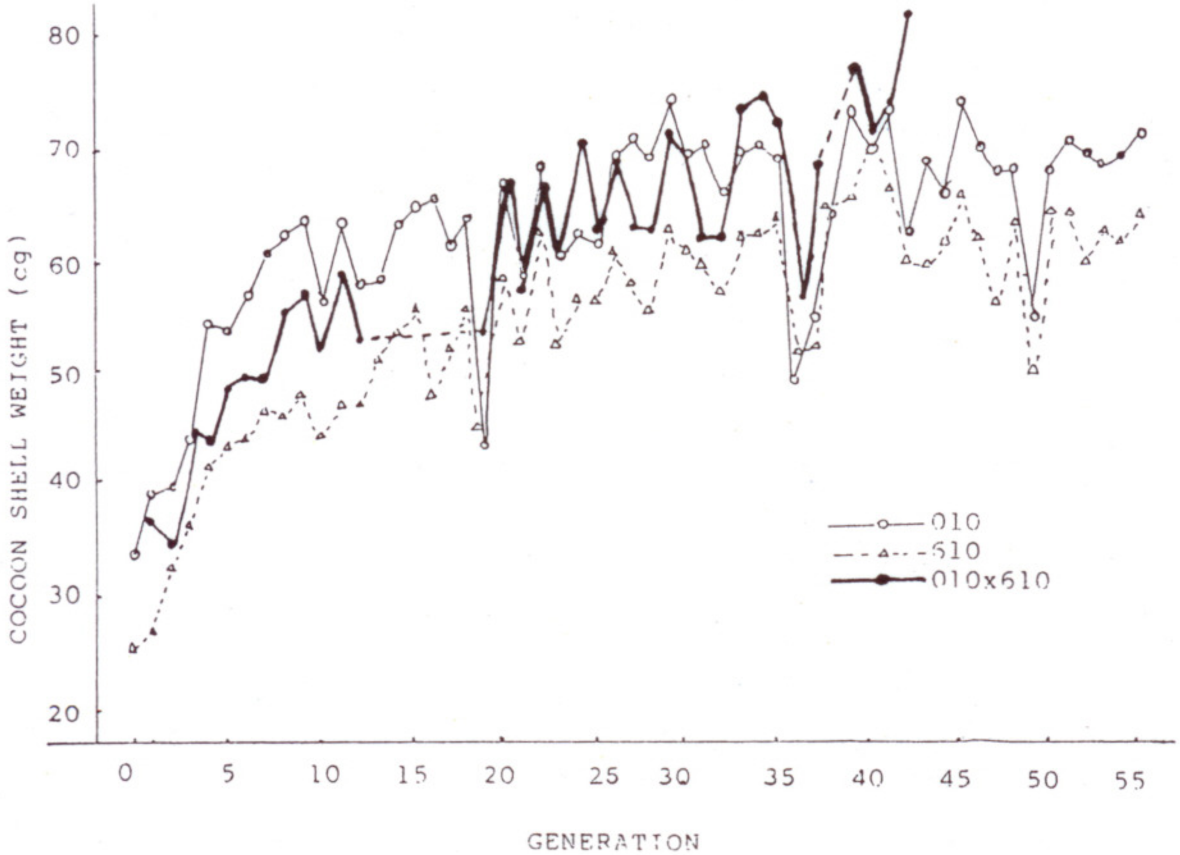

Fig. 5: Effect of selection for cocoon shell weight in 010 and 610 strains and their hybrid, 010 × 610.
Fig. 5 : Effet de la sélection du poids de la coque chez les souches 010 et 610 et chez leur hybride 010 × 610.
Maruyama, 1984.

HETEROSIS IN RELATION TO SELECTION FOR QUANTITATIVE TRAITS

The foregoing account shows that heterosis has been harnessed in the silkworm by crossing different breeds, inbred lines and geographical races. However, information is also available on how the amount of heterosis depends on the selection history of populations selected for different characters. The studies reported by Maruyama (1984) show that when the two lines, 010 and 610, selected for cocoon shell weight for 55 generations (from 1928 to 1982) were crossed, the hybrid mean for the selected trait (cocoon shell weight) was closer to the mean of the better parent (Fig. 5) and the heterotic values over MPV were not significant (Table X). On the other hand, mean values for cocoon weight, an unselected trait in the experiment, exhibited higher mean values which were outside the mean of both parental strains and also revealed a high level of heterosis specially from the ninth generation of selection (Table X). Consequent to the higher mean for cocoon weight, the cocoon shell ratio was found to be lower than that of both parents and heterosis over MPV for this character was found to be negative in almost all the generations (Table X, Fig. 6).

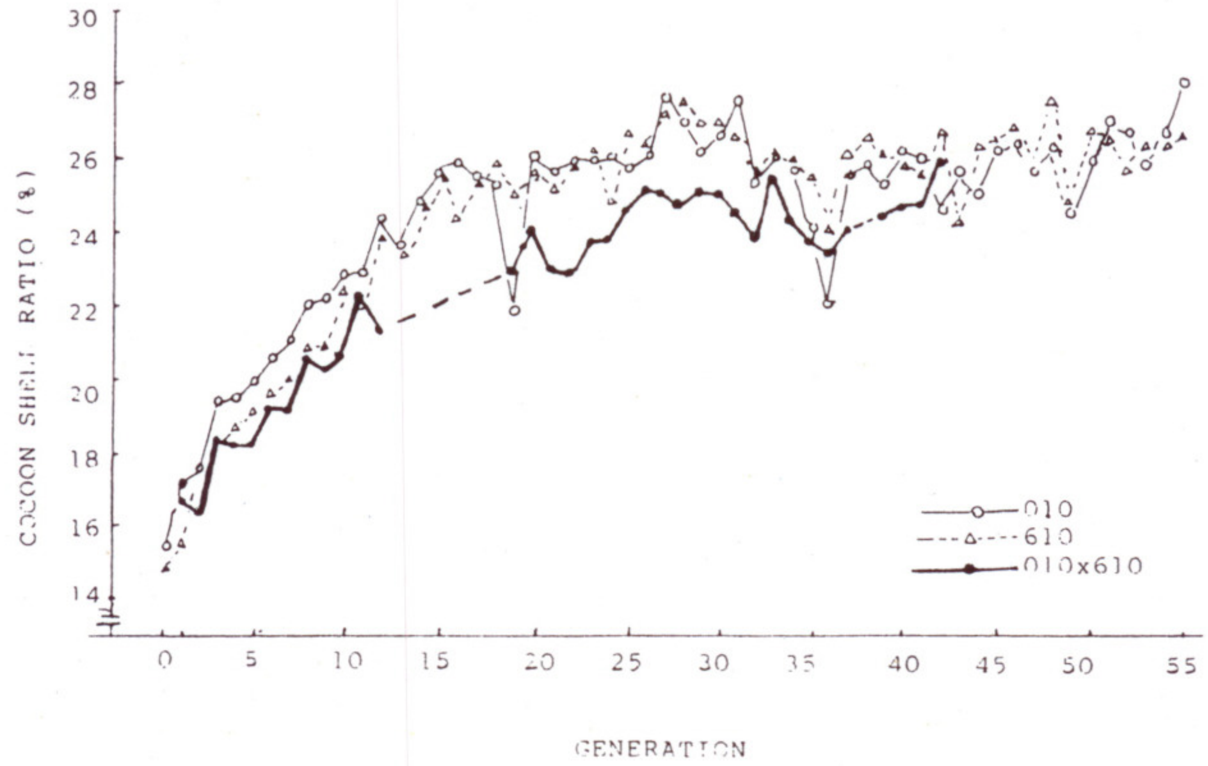

Fig. 6: Effect of selection for cocoon shell weight on cocoon shell ratio in 010 and 610 strains and their hybrid, 010 × 610.

Fig. 6 : Effet de la sélection du poids de la coque sur la richesse soyeuse chez les souches 010 et 610 et chez leur hybride 010 × 610.

Maruyama, 1984.

In another experiment, Suzuki and Miyahara (1961) crossed two different lines, namely 72 and MK, which were characterised by normal filament length and long filament length, respectively. The hybrid mean for filament length was nearer to the longer filament parent and the heterosis over MPV was substantial (Table XI). The mean values of the F_1 hybrid for filament length also showed a similar trend (Table XI). On the other hand, filament weight showed extensive heterosis over both MPV and better parent values (BPV) (Table XI).

Table X. Mean of characters and heterosis measured in 010 and 610 lines selected for cocoon shell weight and their hybrids.

Tableau X. Moyenne des caractères et de l'hétérosis mesurés chez les lignées 010 et 610 sélectionnées pour le poids de la coque et chez leurs hybrides.

Year *Année*	**G**	**Cocoon weight (g)** *Poids du cocon (g)*				**Cocoon shell weight (cg)** *Poids de la coque (cg)*				**Cocoon shell ratio (%)** *Richesse soyeuse (%)*			
		F_1	**010**	**610**	**H (%)**	**F_1**	**010**	**610**	**H (%)**	**F_1**	**010**	**610**	**H (%)**
1927	0	-	2.20	1.71		-	33.8	25.3		-	15.4	14.8	
1928	1	2.19	2.31	1.76	7.6	36.5	39.4	27.3	9.5	16.7	17.2	15.5	2.1
1929	2	2.09	2.26	1.89	0.7	34.3	39.8	32.5	-5.1	16.4	17.6	17.4	-6.3
1930	3	2.44	2.27	2.01	14.0	44.7	44.1	36.3	11.2	18.3	19.4	18.1	-2.4
1931	4	2.45	2.80	2.22	-2.4	44.3	54.9	41.5	-8.1	18.1	19.6	18.7	-5.5
1932	5	2.66	2.69	2.29	6.8	48.5	53.8	43.7	-0.5	18.2	20.0	19.1	-6.9
1933	6	2.58	2.76	2.26	2.8	49.6	56.8	44.2	-1.8	19.2	20.6	19.6	-4.8
1934	7	2.55	2.89	2.34	-2.5	49.0	60.9	46.7	-8.9	19.2	21.1	20.0	-6.6
1935	8	2.69	2.83	2.23	6.3	55.4	62.3	46.6	1.8	20.6	22.0	20.9	-4.0
1936	9	2.82	2.89	2.31	8.5	57.2	64.1	48.3	1.8	20.3	22.2	20.9	-5.8
1937	10	2.49	2.48	2.00	11.2	51.2	56.6	44.7	1.1	20.6	22.8	22.4	-8.9
1938	11	2.68	2.79	2.14	8.7	59.7	63.9	46.9	7.8	22.3	22.9	11.9	-0.5
1939	12	2.49	2.39	1.89	13.7	53.2	58.2	47.3	0.9	21.4	24.4	23.8	-11.2
1946	19	2.36	2.01	1.82	23.2	54.1	44.0	45.6	20.8	22.9	21.9	25.1	-2.6
1947	20	2.81	2.60	2.32	14.2	67.4	67.8	59.3	6.1	24.0	26.1	25.6	-7.2
1948	21	2.52	2.32	2.13	13.3	57.9	59.3	53.7	2.5	23.0	25.6	25.2	-9.5
1949	22	2.98	2.68	2.44	16.4	68.2	69.5	63.5	2.6	22.9	25.9	26.0	-11.8
1950	23	2.62	2.35	2.04	19.4	62.0	61.0	53.2	8.6	23.7	26.0	26.1	-9.0
1951	24	3.00	2.42	2.31	26.9	71.7	63.1	57.5	18.9	23.9	26.1	24.9	-6.3
1952	25	2.60	2.41	2.16	13.8	63.9	62.2	57.6	6.7	24.6	25.8	26.7	-6.3
1953	26	2.79	2.69	2.35	10.7	70.1	70.2	62.0	6.1	25.1	26.1	26.4	-4.4
1954	27	2.55	2.60	2.17	6.9	63.9	72.0	59.1	-2.5	25.1	27.7	27.2	-8.6
1955	28	2.56	2.60	2.06	9.9	63.6	70.2	56.8	0.2	24.8	27.0	27.6	-9.2
1956	29	2.88	2.88	2.47	7.7	72.2	75.5	64.1	3.4	25.1	26.2	26.0	-3.8
1957	30	2.81	2.64	2.30	13.8	70.5	70.6	62.1	6.3	25.1	26.7	27.0	-6.5
1958	31	2.56	2.60	2.29	4.7	63.1	71.7	61.2	-5.0	24.6	27.6	26.7	-9.4
1959	32	2.67	2.60	2.26	9.9	63.5	65.7	58.1	2.6	23.8	25.3	25.7	-6.7
1960	33	2.93	2.73	2.42	13.8	74.6	71.0	63.5	10.9	25.5	26.0	26.2	-2.3
1961	34	3.14	2.79	2.45	19.9	66.2	71.7	63.6	12.6	24.3	25.7	26.0	-6.0
1962	35	3.08	2.93	2.54	12.6	73.2	70.7	65.0	7.9	23.8	24.1	25.6	-4.2
1963	36	2.48	2.29	2.20	10.5	58.1	50.3	53.1	12.4	23.4	22.0	24.1	1.5
1964	37	2.77	2.13	2.06	31.9	66.4	54.8	53.8	22.3	24.0	25.6	26.1	-7.2
1966	39	3.24	2.96	2.57	17.2	78.8	74.8	67.0	11.1	24.3	25.3	26.1	-5.5
1967	40	2.92	2.72	2.80	5.8	72.2	71.2	72.6	0.4	24.7	26.2	25.9	-5.2
1968	41	3.05	2.89	2.59	15.3	75.4	75.0	66.4	6.7	24.7	26.0	25.6	-4.3
1969	42	2.24	2.59	2.31	32.3	83.9	64.0	61.9	33.2	25.9	24.7	26.8	0.6

G: Generation / *Génération*.
H: Heterosis / *Heterosis*.
(Maruyama, 1984)

Table XI. Mean of filament length, size and weight in parental lines, 72 and MK and their hybrids.

Tableau XI. Moyenne de la longueur, du titre et du poids de la bave chez les lignées parentales 72 et MK et chez leurs hybrides.

Line *Lignée*	Filament length (m) *Longueur de la bave (m)*	Filament size (d) *Titre de la bave (d)*	Filament weight (cg) *Poids de la bave (cg)*
Parents			
72	690	2.43	20.34
MK	1322	1.61	25.97
Hybrids / *Hybrides*			
72 × MK (F_1a)	1219	2.38	35.46
MK × 72 (F_1b)	1157	2.38	32.61
Heterosis % / *Hétérosis (%)*			
F_1a	21.17	17.82	53.10
F_1b	15.00	17.82	40.80

(Suzuki and Miyahara, 1961)

Table XII. Mean of characters and heterosis measured in LFL and SFL lines and their hybrids.

Tableau XII. Moyenne des caractères et de l'hétérosis mesurés chez les lignées LFL et SFL et chez leurs hybrides.

Characters *Caractères*	Lines *Lignées*		Interline matings *Croisements entre lignées*		Heterosis % *Hétérosis (%)*	
	LFL	SFL	LFL × SFL F_1a	SFL × LFL F_1b	F_1a	F_1b
Filament length / *Longeur de la bave (*m)	876	704	783	717	-0.89	-9.2
Denier	2.00	2.85	2.19	2.2	3.29	3.76
Single cocoon wt. / *Poids du cocon* (g)	1.375	1.345	1.416	1.349	4.17	0.80
Single shell wt. / *Poids de la coque* (g)	0.215	0.199	0.233	0.217	20.7	4.83
Cocoon shell ratio / *Richesse soyeuse* (%)						
Survival rate / *Taux de survie* (%)	56.25	68.06	73.12	74.97	17.64	20.06

SFL: Line selected for short filament / *Lignée sélectionnée pour une bave courte.*
LFL: Line selected for long filament / *Lignée sélectionnée pour une bave longue.*
(Nagaraju and Pavankumar, 1995)

Table XIII. Mean of characters and heterosis measured in LFL and SFL lines and their crosses with an unrelated tester line.

Tableau XIII. Moyenne des caractères et de l'hétérosis mesurés chez les lignées LFL et SFL et chez leurs croisements avec une lignée témoin non apparentée.

Characters *Caractères*	**Lines** *Lignées*		**Tester** *Témoin*	**Crosses** *Croisements*		**Heterosis (%)** *Hétérosis (%)*	
	LFL	**SFL**	**NB_{18}**	**HLF × NB_{18} F_1a**	**SFL × NB_{18} F_1b**	**F_1a**	**F_1b**
Filament length / *Longeur de la bave* (m)	876	704	870	1000	883	14.54	12.20
Denier	2.00	2.85	2.60	2.68	2.80	16.23	15.67
Single cocoon wt. / *Poids du cocon* (g)	1.375	1.345	1.668	1.723	1.679	12.93	11.48
Single shell wt. / *Poids de la coque* (g)	0.215	0.199	0.346	0.353	0.320	25.71	17.61
Cocoon shell ratio / *Richesse soyeuse* (%)							
Survival rate / *Taux de survie* (%)	56.25	68.06	47.50	66.40	72.08	23.81	25.14

SFL: Line selected for short filament / *Lignée sélectionnée pour une bave courte.*
LFL: Line selected for long filament / *Lignée sélectionnée pour une bave longue.*
(Nagaraju and Pavankumar, 1995)

The example is also available on how selection history of populations derived from the common genetic stock influences the manifestation of heterosis. Nagaraju and Pavakumar (1995) evaluated the crossing effects in the two lines selected divergently for long and short filament lengths for eleven generations from the same base population. The two lines selected for length of silk filament differed by 172 meters. The effect of accrued differences in filament length in the parental lines was seen in the hybrids of interline matings. The values of heterosis expressed as percentages of MPV are shown in Table XII. The hybrid mean was found to be below MPV for the selected trait, indicating the directional dominance of alleles from the line selected for shorter filament length (SFL). The effect of selection of length of filament was also evident in the selected lines when they were crossed with the common tester parent (Table XIII). the genetic differences observed in the line by virtue of selection corroborate the theoretical contention (Falconer, 1981) that subdivision of base population through inbreeding results in lines with different genic values. The directional dominance for the SFL probably reflects the history of past directional selection, towards increasing fitness as contended by Robertson (1955).

Table XIV. Manifestation of heterosis in trimoulter × tetramoulter and their reciprocal hybrids.

Tableau XIV. Manifestation de l'hétérosis chez un hybride trimuant × tétramuant et chez les hybrides réciproques.

Strains	**Voltinism**	**Larval span (days:hr)**	**Single cocoon wt. (g)**	**Cocoon shell wt. (g)**	**Shell ratio (%)**	**Filament length (m)**	**Denier**
Souches	***Voltinisme***	***Durée larvaire (jours:h)***	***Poids du cocon (g)***	***Poids de la coque (g)***	***Richesse soyeuse (%)***	***Longueur la bave (m)***	***Denier***
Parents							
NB_{18} (Tetra.)	Bivoltine	22:22	1.754	0.338	19.2	909	1.3
MHMP(W) (Tri.*)	Polyvoltine	17:01	0.727	0.110	15.1	614	2.6
Hybrids / *Hybrides*							
NB_{18} × MHMP (W)							
Trimoulters* / *Trimuants**		17:07	1.053	0.174	16.5	675	2.0
Heterosis (%) / *Hétérosis (%)*		-13.45	-15.11	-22.32	.379	-11.36	2.56
Tetramoulters / *Tétramuants*		21:07	1.490	0.283	18.9	933	2.6
Heterosis (%) / *Hétérosis (%)*		5.32	20.11	26.34	10.20	22.50	33.33
MHMP(W) × NB_{18}							
Tetramoulters / *Tétramuants*		22:02	1.555	0.288	18.5	901	2.1
Heterosis (%) / *Hétérosis (%)*		10.53	25.3	28.5	9.87	18.32	7.69

Tetra.: Tetramoulter / *Tétramuant*. **Tri.:** Trimoulter / *Trimuant*.

* Mean of only female individuals was taken since no male trimoulters were observed.

** Les moyennes concernent uniquement les individus femelles car aucun mâle trimuant n'a été observé.*

(Singh *et al.*, 1989)

HETEROSIS IN RELATION TO MOULTINISM

Manifestation of heterosis in the crosses of trimoulter and tetramoulter strains has been studied (Yamamoto *et al.*, 1986; Singh *et al.*, 1990). Singh *et al.* (1990) observed negative heterosis in trimoulter hybrid segregants for almost all the traits except denier (Table XIV). It is not surprising that negative heterosis was observed for all the traits, considering the fact that trimoulters have a shorter larval duration, spin smaller and lighter cocoons with a short filament length. On the other hand, tetramoulter segregant hybrids revealed a high degree of positive heterosis for all the traits except for filament length (Table XIV). In the reciprocal cross, i.e., trimoulter female × tetramoulter male, only tetramoulters of both sexes appeared (Table XIV). A high magnitude of heterosis for all the traits was observed in this hybrid. Similar results have also been reported by Morohoshi (1949) in univoltine × polyvoltine and bivoltine × bivoltine crosses. The appearance of only female trimoulters in the cross of tetramoulter × trimoulter is due to the sex-linked nature of the trimoulter gene and the non-appearance of trimoulters in the cross of trimoulter female (polyvoltine) × tetramoulter (bivoltine) is due to differences in the sex-linked maturity genes ($+^{lm}$, lm) in the parental strains which act in co-operation with moulting genes.

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