

Studies on Sex-linked Inheritance of Quantitative Characters in Direct and Reciprocal Crosses of Silkworm *Bombyx mori* L.

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The present investigation was carried out to study the possible cause for reciprocal difference in silkworm hybrids. By utilising the polyvoltine race Pure Mysore (PM) and newly evolved breeds (CSR2, CSR5, CSR16 and CSR17), the direct and reciprocal crosses of polyvoltine \times bivoltine and also bivoltine hybrids were studied. The hybrids of polyvoltine \times bivoltine (direct) are superior to their reciprocal crosses in respect of cocoon yield, cocoon weight and filament length. The reciprocal crosses of polyvoltine \times bivoltine are superior to their direct crosses in respect of fecundity and short larval duration. No significant differences were observed in the characters like cocoon shell ratio, raw silk percentage, denier, reelability and neatness in both polyvoltine \times bivoltine direct crosses and their reciprocals. The expression of cocoon characters as a function of sex revealed that direct crosses (polyvoltine \times bivoltine) showed higher cocoon weight, pupal weight, shell weight and longer filament length in females than the reciprocal crosses (bivoltine \times polyvoltine), where as these characters in males were almost the same in both direct and reciprocal crosses, indicating that the sex-linked genetic factor played a more important role. It was clear that difference in cocoon yield observed in reciprocal crosses of polyvoltine \times bivoltine was due to the low cocoon and shell weight in females which was turn due to presence of early maturity genes (Lme) linked with sex-chromosome (X) which effect on larvae period of the silkworm. In bivoltine hybrids, *i.e.*, both direct and their reciprocals crosses, all the characters *viz.*, hatching percentage, larval duration, survival, cocoon weight, cocoon shell weight, cocoon shell

ratio, raw silk percentage, filament length, denier, reelability and neatness did not show any significant difference (except number of eggs laid by moth) which could account for presence of same maturity genes (Lm) in both direct and reciprocal crosses. It was clear that reciprocal differences occur when the hybrids are prepared from the parental strains with different voltinism.

Key words: *Bombyx mori* L., Direct and reciprocal crosses, Quantitative characters, Sex-linked inheritance

Introduction

Hybrid vigour in silkworm has received a considerable attention because of marked effect of the yield components. It is well documented that F_1 hybrids are superior to their parents in many qualitative and quantitative characters (Toyama, 1906). In India, the polyvoltine as female and bivoltine as male components are being used for preparation of polyvoltine \times bivoltine (PM \times NB₄D₂/NB18) hybrids for commercial use. The polyvoltine males and bivoltine females are rejected while preparing the hybrid seed. The reciprocal crosses of bivoltine \times polyvoltine (NB₄D₂/NB18 \times PM) are not popularised. Differences in reciprocal crosses of PM with bivoltine breeds *viz.*, NB7 and NB18 and also with Japanese bivoltine breeds N4 and C146 was reported (Benjamin *et al.*, 1988; Tazima 1988). Although much data on reciprocal effect in bivoltine hybrids is probably available in many silkworm research institutes, but it is rarely published.

Hence the present study was under taken to assess the effect of reciprocal crosses of both polyvoltine \times bivoltine and bivoltine \times bivoltine hybrids and also to study the possible reasons for the manifestation of reciprocal differences, involving the polyvoltine breed PM and newly evolved productive bivoltine breeds.

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Materials and Methods

In the present study one polyvoltine race PM and four bivoltine breeds *viz.*, CSR2 (Oval type), CSR5 (Dumbbell type), CSR16 (Dumbbell type) and CSR17 (Oval type) were utilised for preparation of polyvoltine × bivoltine and bivoltine hybrids and also their reciprocal crosses as follows.

Polyvoltine × bivoltine		Bivoltine × bivoltine	
Direct crosses	Reciprocal crosses	Direct crosses	Reciprocal crosses
PM × CSR2	CSR2 × PM	CSR2 × CSR5	CSR5 × CSR2
PM × CSR5	CSR5 × PM	CSR16 × CSR17	CSR17 × CS

Three composite layings were prepared for each parental breed and hybrid and each composite laying consists of about 500 eggs taken from 10 disease free layings and brushed. After III moult, three hundred larvae out of each

composite brushing were retained and rearing was conducted as per standard rearing techniques (Krishnaswami, 1978). The rearing was conducted in conditioned temperature and humidity rearing house. The important characters that govern silk quality and quantity such as fecundity, larval duration, survival, cocoon yield, cocoon weight, shell weight, cocoon shell ratio, raw silk percentage, filament length, denier, reelability and neatness were studied. The characters such as cocoon weight, shell weight, cocoon shell ratio, raw silk percentage, filament length and denier were also recorded as a function of sex (female and male wise) to study the inheritance pattern of cocoon characters.

Results

The performance of the parental breeds was given in Table

Table 1. Performance of parental breeds (Season Dec. - Jan. 2000 - 2001)

Breed	Fecundity (No.)	Hatching (%)	Larval Period (hrs)		Survival (%)	Cocoon yield (kg)	Cocoon weight (g)	Shell weight (cg.)	Shell ratio (%)	Raw silk (%)	Filament length (m)	Denier (d)	Reelability (%)	Neatness (p)
			Total	5th instar										
Pure Mysore (PM)	469	95.7	672	240	94.8	9.29	0.98	12.7	13.0	7.5	243	2.36	-	-
CSR2	613	95.3	576	168	96.5	18.74	1.94	47.1	24.3	19.3	1094	3.10	83	94.0
CSR5	533	95.0	600	192	88.0	15.96	1.82	43.5	23.9	18.9	968	3.18	82	93.2
CSR16	453	94.7	586	176	92.8	15.35	1.65	37.1	22.5	18.2	984	2.92	81	93.7
CSR17	502	95.3	590	180	94.0	16.90	1.78	44.9	25.2	19.1	1017	2.83	84	94.0
CD at 5%	67.1	NS	16.3	8.20	4.9	2.6	0.12	2.1	0.4	NS	51.2	0.12	NS	NS

NS = Non-significant.

Table 2. Performance of direct and reciprocal crosses of polyvoltine × bivoltine hybrids (Season: January, 2001)

Hybrids	Fecundity (No.)	Hatching (%)	Larval Period (hrs)		Survival (%)	Cocoon yield (kg)	Cocoon weight (g)	Shell weight (cg.)	Shell ratio (%)	Raw silk (%)	Filament length (m)	Denier (d)	Reelability (%)	Neatness (p)
			Total	5th instar										
PM × CSR2	464	96.7	552	168	96.1	18.68	1.95	37.6	19.3	14.6	813	2.86	82	91
CSR2 × PM	620	95.9	528	156	95.3	17.16	1.85	35.5	19.2	13.5	774	2.74	83	92
PM × CSR5	474	96.3	573	188	96.0	19.89	2.05	41.4	20.3	14.8	875	3.07	81	92
CSR5 × PM	575	95.4	552	176	94.8	18.42	1.95	38.5	19.7	14.2	815	2.91	81	91
CD at 5%	35.62	NS	14.01	6.52	NS	1.14	0.04	0.89	NS	NS	34.2	0.21	NS	NS

NS = Non-significant.

Table 3. Performance of direct and reciprocal crosses of bivoltine hybrids (Season: January, 2001)

Hybrids	Fecundity (No.)	Hatching (%)	Larval		Survival (%)	Cocoon yield (kg)	Cocoon weight (g)	Shell weight (cg.)	Shell ratio (%)	Raw silk (%)	Filament length (m)	Denier (d)	Reela- bility (%)	Neat- ness (p)
			Period (hrs)											
			Total	5th instar										
CSR2× CSR5	605	95.8	548	168	95.2	20.05	2.09	49.8	23.8	19.6	1277	2.93	84	94
CSR5× CSR2	573	95.7	558	168	94.9	20.07	2.12	50.2	23.7	20.3	1202	3.02	86	93
CSR16× CSR17	492	95.3	542	166	95.6	19.87	2.11	49.3	23.4	20.3	1244	3.02	84	94
CSR17× CSR16	518	95.9	546	166	94.5	20.12	2.12	49.6	23.4	19.9	1220	3.04	85	94
CD at 5%	37.3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS = Non-significant.

1. It is evident from the data that the polyvoltine race (PM) was qualitatively and quantitatively inferior to the bivoltine breeds. Generally in tropical polyvoltine races the larval period is shorter than bivoltine breeds and there by the cocoon yield is also less. But in PM, the larval duration was longer than other polyvoltine and bivoltine breeds which is unique. The performance of direct (PM×CSR2 and PM×CSR5) and reciprocal (CSR2×PM and CSR5×PM) crosses of polyvoltine×bivoltine was given in Table 2, while the cocoon characters of these crosses as a function of sex (female and male wise) was given in Table 3.

Fecundity

Significance differences ($P < 0.01$) in fecundity was observed between direct and reciprocal crosses. Maximum fecundity was observed when bivoltine breeds were used as female parent *i.e.*, bivoltine×polyvoltine over the polyvoltine×bivoltine hybrids. The direct crosses PM×CSR2 and PM×CSR5 recorded fecundity of 464 and 474 respectively while reciprocal crosses CSR2×PM and CSR5×PM recorded the fecundity of 620 and 575 respectively.

Larval duration

The total larval duration and 5th age larval duration of reciprocal crosses (CSR2×PM and CSR5×PM) was shorter than the direct crosses (PM×CSR2 and PM×CSR5) by 24 hrs and 12 hrs respectively ($P < 0.05$).

Survival (Pupation)

Since the rearing was conducted in ideal environmental conditions, there was not much difference in survival of both direct crosses and reciprocal crosses. It is ranging from 94.8 to 96.1%.

Cocoon yield

Significant difference ($P < 0.05$) in cocoon yield was recorded between direct and reciprocal crosses. The direct

crosses PM×CSR2 and PM×CSR5 recorded cocoon yield of 18.68 kg and 19.89 kg respectively, as against 17.16 kg and 18.42 kg in reciprocal crosses of CSR2×PM and CSR5×PM, respectively.

Cocoon weight

The cocoon weight was significantly ($P < 0.01$) higher in direct crosses *i.e.*, PM×CSR2 (1.95 g) and PM×CSR5 (2.05 g) than reciprocal crosses *i.e.*, CSR2×PM (1.85 g) and CSR5×PM (1.95 g). As could be seen in Table 3, the female cocoon weight is more in direct crosses than in reciprocal crosses. However, the male cocoon weight was almost similar in both in direct and reciprocal crosses. The most striking character recorded in the present study was the higher cocoon weigh in cross between PM×CSR5 than in the cross of PM×CSR2. More, the pupal weight also follows the same trend as cocoon weight.

Cocoon shell weight

The shell weight was significantly higher ($P < 0.01$) in direct crosses *i.e.*, PM×CSR2 (37.6 cg) and PM×CSR5 (41.4 cg) than in reciprocal crosses *i.e.*, CSR2×PM (35.5 cg) and CSR5×PM (38.5 cg). The direct crosses yielded higher shell weight in females than in male, where as reciprocal crosses recorded higher shell weight in male than female.

Cocoon shell ratio and raw silk percentage

Both shell ratio and raw silk percentage did not differ significantly in both direct and reciprocal crosses of polyvoltine×bivoltine hybrids.

Filament length

The filament length was significantly higher ($P < 0.05$) in direct crosses *i.e.*, PM×CSR2 (845 m) and PM×CSR5 (900 m) than in reciprocal crosses *i.e.*, CSR2×PM (748 m) and CSR5×PM (797 m). The direct crosses recorded longer filament length in females, where as reciprocal crosses recorded longer filament length in males.

Table 4. Cocoon characters in direct and reciprocal crosses of polyvoltine \times bivoltine hybrids as a function of sex (Season: January, 2001)

Hybrids	Cocoon weight (g)		Pupal weight (g)		Shell weight (cg)		Shell ratio (%)		Raw silk %		Filament length (m)		Denier (d)	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
PM \times CSR2	2.20	1.69	1.82	1.32	38.0	37.1	17.3	21.9	13.6	15.7	845	781	2.90	2.81
CSR2 \times PM	2.01	1.69	1.69	1.31	33.8	36.6	16.7	21.8	11.9	15.1	748	798	2.76	2.69
PM \times CSR5	2.25	1.84	1.81	1.44	42.0	40.9	18.7	22.2	12.9	16.6	900	883	3.08	3.07
CSR5 \times PM	2.08	1.83	1.71	1.42	37.1	40.1	17.9	22.0	13.3	15.1	797	832	3.01	2.82
CD at 5%	0.13	0.06	0.09	0.05	1.68	1.30	NS	NS	NS	NS	69.9	NS	0.27	0.2

NS=Non-significant; F, female; and M, male.

Table 5. Cocoon characters in direct and reciprocal crosses of bivoltine hybrids as a function of sex (Season: January, 2001)

Hybrids	Cocoon weight (g)		Pupal weight (g)		Shell weight (cg)		Shell ratio (%)		Raw silk %		Filament length (m)		Denier (d)	
	F	M	F	M	F	M	F	M	F	M	F	M	F	M
CSR2 \times CSR5	2.31	1.85	1.80	1.36	50.6	49.0	21.9	26.5	18.8	20	1235	1317	3.08	2.78
CSR5 \times CSR2	2.37	1.85	1.85	1.37	51.9	48.4	21.9	26.2	18.0	22	1168	1235	3.19	2.85
CSR16 \times CSR17	2.33	1.88	1.83	1.40	50.2	48.4	21.5	25.7	19.3	21	1214	1273	3.14	2.89
CSR17 \times CSR16	2.32	1.89	1.82	1.40	50.2	48.9	21.4	25.9	18.2	22	1178	1262	3.18	2.89
CD at 5%	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS=Non-significant; F, female; and M, male.

Table 6. Inheritance pattern of quantitative traits in direct and reciprocal crosses as a function of sex

Hybrid combination	Genotype		Cocoon weight		Pupal weight		Shell weight		Filament length	
	F	M	F	M	F	M	F	M	F	M
Direct cross (A)	Z ^{Lm} W	Z ^{Lm} Z ^{Lme}	A > B	A = B	A > B	A = B	A > B	A = B	A > B	A = B
Reciprocal cross (B)	Z ^{Lme} W	Z ^{Lme} Z ^{Lm}								

A > B = Direct cross value is more than reciprocal cross.

A = B = Direct cross and reciprocal value is equal.

F, female; and M, male.

Denier, reelability and neatness

These characters did not differ significantly in direct and reciprocal crosses. The performance of direct (CSR2 \times CSR5 and CSR16 \times CSR17) and reciprocal (CSR5 \times CSR2 and CSR17 \times CSR16) crosses of bivoltine hybrids and cocoon characters as a function of sex were presented in Tables 4 and 5. All the characters *i.e.*, fecundity, hatching percentage, larval duration, survival, cocoon yield, cocoon weight, cocoon shell weight, raw silk percentage, filament length, denier and neatness did not show any significant difference in both direct and reciprocal crosses.

Discussion

Polyvoltine \times bivoltine and its reciprocal crosses

Data clearly showed that the crosses using bivoltine as

female parent (reciprocal crosses) are at disadvantage with significant reduction in cocoon yield, cocoon weight, cocoon shell weight and filament length. This corroborates with earlier work of Tazima (1988) and Benchamin *et al.* (1988). However, the clear advantages in reciprocal crosses were higher fecundity and short larval duration. Since, these hybrids of both direct and reciprocal crosses are reared in optimum environmental conditions, the survival of larvae is almost the same. The cocoon weight, cocoon shell weight and filament length are found to be greater in direct crosses in comparison with the reciprocal crosses. The most striking character recorded in the present study was the higher cocoon weight and shell weight in crosses between polyvoltine \times Japanese type bivoltine (PM \times CSR5 and CSR5 \times PM) than in the crosses with Chinese bivoltine (PM \times CSR2 and CSR2 \times PM). However, there was no significant difference in respect of

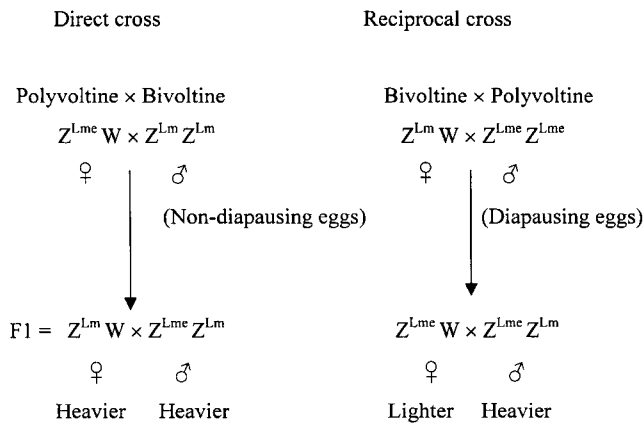


Fig. 1. Genotypic constitution of direct and reciprocal crosses of polyvoltine × bivoltine hybrids.

cocoon shell ratio, raw silk percentage, denier, reelability and neatness in both direct and reciprocal crosses.

The expression of cocoon characters as a function of sex revealed that direct crosses (PM × CSR2 or PM × CSR5) showed higher cocoon weight and pupal weight in females than the reciprocal crosses (CSR2 × PM or CSR5 × PM), whereas, the cocoon weight and pupal weight in males was almost the same in both direct and reciprocal crosses. The presence of Lm or Lme maturation genes, which are located on the sex chromosomes have been reported to make cocoon heavier or lighter respectively (Murakami and Ohtsuki, 1989). The genotype constitution of females was $Z^{Lm}W$ and $Z^{Lme}W$ in direct and reciprocal crosses respectively. Therefore it appears that the presence of Lm allele (gene) in the females can account for the heavier cocoon weight in direct than the reciprocal crosses (Fig. 1). On the other hand the genotype constitution of the males was ($Z^{Lm}Z^{Lme}$ and $Z^{Lme}Z^{Lm}$) same in both the crosses which could be an observation that the cocoon weight and shell weight was almost the same. This indicates that sex linked genetic factor played a more important role on cocoon and shell weight.

The direct crosses recorded heavier shell weight and longer filament in females than in males, whereas reciprocal crosses recorded higher shell weight and longer filament in males than in females. This is corroborated with the finding of Tazima (1988). Morohoshi (1949) reported that presence of multiple allelism of maturity genes of early maturity (Lme) and late maturity (Lm) and which are linked to Z chromosomes. He also demonstrated that the females in the reciprocal crosses grow too fast and this has adverse effect on cocoon traits. This was proved by Nakada (1970), who demonstrated that larval span of females is shorter than that of males in reciprocal crosses. In the present study, it was clear that difference in cocoon yield observed in reciprocal crosses of polyvoltine ×

bivoltine was due to the low cocoon and shell weight in females which was turn due to presence of early maturity genes (Lme) which are present on sex chromosome (Z). The cocoon shell ratio, raw silk percentage and denier did not show any significant change in direct and reciprocal crosses as a function of sex (sex wise) indicating common inheritance for these characters.

The reciprocal crosses of polyvoltine × bivoltine are quantitatively inferior as evidenced by lower cocoon weight and cocoon shell weight thereby difference in the yield. The differences reported here between direct and reciprocal crosses confirm the involvement of sex-linked genes which have previously been observed to cause differences in quantitative characters in the silkworm (Nagamoto, 1942; Morohoshi, 1949; Murakami and Ohtsuki, 1989).

Bivoltine hybrids

The data presented in Tables 4 and 5, clearly indicates that there is no difference between direct and reciprocal crosses of bivoltine hybrids, (CSR2 × CSR5, CSR5 × CSR2, CSR16 × CSR17 and CSR17 × CSR16) and also as a function of sex (sex wise).

It was clear that bivoltine strains possess late maturity gene (Lm), which is not involved in sex-linked inheritance of quantitative characters. The genetic constitution of female and male ($Z^{Lm}W$ & $Z^{Lm}Z^{Lm}$) is same in respect of maturity genes in both direct and reciprocal crosses, which could account for the observation that there was non-significant difference in qualitative and quantitative characters, except the number of eggs per disease free laying which is caused by maternal effect. It was clear reciprocal differences are not observed in the crosses which involve parental strains of the same voltinism.

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