Genetic Structure of the Mulberry Silkworm Population in Sri Lanka: I. Estimation of Combining Ability and Heritability

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Abstract

Genetic characterization of Sri Lankan silkworm bivoltine population has not been attempted so far, since its sporadic introduction of bivoltine strains into the island, starting from the 1950's. Genetic structure of Sri Lankan population of mulberry silkworm *Bombyx mori* was investigated through estimation of general (GCA) and specific combining ability (SCA) and heritability (h^2_B), on the economic quantitative characters from leading 8 inbreds and their 28 F1's in a half diallel cross, in an attempt to utilize the estimates in determination of future breeding methods and to predict the breeding value over the phenotypic value. It was found that the breeding population of the bivoltine silkworm in Sri Lanka has still maintained considerable amounts of additive gene action as well as nonadditive. For some time in the future, both breeding strategies of "selection without inbreeding" and also "inbreeding followed by crossing" should therefore be effective in genetic improvement of economic characters investigated. In addition, superior combiners in general and in specific F1's were identified for each of 6 economic characters, to be immediately utilized in selection and also in cross breeding programs in Sri Lanka.

Key words : Mulberry silkworm, *Bombyx mori*, half-diallel cross, combining ability, heritability

INTRODUCTION

Recent introduction of bivoltine silkworm stocks into the Sri Lankan Island was initiated by religious groups, starting from the 1950's. Those breeding stocks, whether inbred or hybrid varieties, were geologically originated mostly from China, India, Italy, Japan, Korea, Taiwan and Thailand. It is expected they have gone through more rapid inbreeding than in the originator countries, as long-term storage of bivoltine silkworm eggs is not practiced presently in Sri Lanka. Stocks are maintained in Sri Lanka by continuous rearing all the year round, 4~5 generations a year. Germplasm resources for the silkworm in Sri Lanka are presently contained in 10 genetic stocks and 49 inbred lines. Breeding programs for isolation of additional parental inbreds are now actively operational, utilizing the imported bivoltine hybrids.

Understanding genetic structure and gene composition of the base population is an important prerequisite for the proper decision of breeding schemes to be applied. Combining ability and heritability are two of important parameters for dissection of genetic backgrounds of an inter-breeding population (ESCAP, 1993). The values of both parameters can be estimated by analyzing variance components in such a serial crosses as diallel or

Table 1. *Performance of parental inbreds and their F1's in a half-diallel cross*

Parent/F1	CS	SW	CW	S%	PR	CY[a]
JE2 × JE2	102	33	171	19.3	96	16.4
JE4	84	42	206	20.5	96	18.4
JE13	82	41	198	20.5	84	15.7
JE15	81	39	207	19.0	88	17.7
JE16	76	41	210	19.6	83	14.5
CE6	74	41	210	19.6	84	15.9
CE10	74	43	205	20.8	90	16.6
CE12	77	42	214	19.8	84	16.2
JE4 × JE4	98	37	180	20.4	97	16.1
JE13	83	41	193	21.6	81	14.3
JE15	82	43	208	20.7	82	14.0
JE16	78	43	214	20.3	87	17.2
CE6	80	40	198	20.1	82	15.4
CE10	83	39	184	21.0	89	16.4
CE12	74	40	195	20.3	86	13.2
JE13 × JE13	89	36	174	20.7	95	17.0
JE15	85	37	181	20.2	89	17.9
JE16	80	37	190	19.1	84	15.3
CE6	82	35	174	20.0	91	15.4
CE10	87	34	171	20.1	96	16.5
CE12	76	38	194	19.6	93	18.2
JE15 × JE15	84	37	177	20.6	87	14.5
JE16	63	45	232	19.4	78	14.0
CE6	75	38	190	19.8	87	15.1
CE10	80	39	190	20.7	90	15.5
CE12	64	42	211	20.0	85	14.7
JE16 × JE16	82	35	183	19.3	91	15.3
CE6	71	48	205	18.3	63	10.7
CE10	83	37	187	19.7	90	16.7
CE12	76	37	190	19.7	88	15.4
CE6 × CE6	78	34	172	19.9	84	14.2
CE10	76	38	180	20.9	83	14.2
CE12	77	35	186	18.7	91	16.5
CE10 × CE10	77	39	174	22.4	91	14.3
CE12	72	42	194	21.3	86	17.1
CE12 × CE12	64	39	194	19.8	75	12.8
Overall mean	79	39	193	20.1	87	15.5
LSD/.05	5.0	2.4	9.9	0.6	9.1	2.3
LSD/.01	7.0	3.4	14.1	0.8	13.0	3.2
CV(%)	5.3	5.3	4.4	2.3	9.0	12.4

[a]CS; cocoon size (cocoon/*l*), SW; cocoon shell weight (cg), CW; single cocoon weight (cg), S%; cocoon shell percentage (%), PR; pupation rate (%), CY; cocoon yields (kg)/10,000 larvae.

top-crosses. Genetic improvement of quantitative characters can be achieved more efficiently and effectively when combining ability of each stock inbred lines and heritability of each economic characters under consideration are estimated (Sp-

rague and Tatum, 1942; Falconer, 1960).

MATERIALS AND METHODS

1. Parental purelines and cross combinations

Eight inbreds were selected generally for their promising average performance in economic characters during the last 4 years (1989~1993). The designationof them are JE2, JE4, JE13, JE15, CE6, CE10 AND CE12. Most of them were previously used as parental lines for hybrid eggs which were produced at the Silkworm Breeding and Grainage Station (SBGS), Silk and Allied Products Development Authority (SAPDA), Nillambe, Kandy, Sri Lanka and reared for cocoon production in Sri Lanka. Without reciprocals, they were crossed in a half-diallel combination, obtaining 28 F1 genotypes.

2. Rearing and characters examined

Standard methods and procedures for handling and treatment to egg stage, larval rearing, caring for pupae and moths were followed, in 4 replications for each of 36 genotypes, including 8 parents and 28 their F1's. Parental lines were chosen for their superiority mainly in cocoon shell percentage and cocoon yields. Crosses were made and the eggs were subjected to immediate acid treatment during the month of May 1993. In each replication were 200 individual larvae, as counted on the first day of fourth instar, and reared at SBGS, Nillambe during the months of May and June 1993. Average performance of parents and F1's is presented in Table 1. Quantitative data were taken for the major test items of cocoon size (CS, cocoon/liter), cocoon shell weight (SW, cg), single cocoon weight (CW, cg), cocoon shell percentage (S%, %), pupation rate (PR, %) and cocoon yields/10000 larvae (CY, kg). For simplicity in genetic interpretation, data for males and females were pooled together for each character investigated. Observation and examination were made according to the standard rules, methods and techniques as described in the reference (ESCAP, 1993).

3. Statistical applications

Table 2. *Analysis of variance for major economic characters and combining ability of parental inbreds, and heritability estimates as expressed in their F1's in a half-diallel cross*

Source	d.f.	Mean squares					
		CS	SW	CW	S%	PR	CY[a/]
Total	143						
Genotypes	35	252.6**	35.5**	884.7**	2.6**	175.4**	10.3**
GCA	7	654.5**	41.8**	1454.7**	8.9**	240.1**	13.3**
SCA	28	152.1**	34.0**	742.2**	1.1**	159.2**	9.5**
Blocks	3						
Error	105	17.9	4.2	71.6	0.2	60.7	3.7
h^2_B		0.77	0.64	0.74	0.73	0.65	0.33

[a/]CS; cocoon size (cocoon/*l*), SW; cocoon shell weight (cg), CW; single cocoon weight (cg), S%; cocoon shell percentage (%), PR; pupation rate (%), CY; cocoon yields (kg)/10,000 larvae. **; highly significant.

The observation values for each character were analyzed on a personal computer with the BASIC program for Griffing's (1954) diallel analyses, which were originally developed and kindly provided to us by Magari and Kang (1994). Genetic component of total phenotypic variation was obtained by a formula of $\sigma^2_G = \dfrac{(\sigma^2_E + \gamma\sigma^2_G) - \sigma^2_E}{\gamma}$, and the heritability in broad sense was calculated according to the formula $h^2_B = \dfrac{\sigma^2_G}{(\sigma^2_E + \sigma^2_G)}$ (Table 2).

Other statistical interpretations were made according to the concept of Steel and Torrie (1960).

RESULTS AND DISCUSSIONS

1. Average performance of parents and their hybrids

Cocoon size of parental inbreds ranged between the largest 64/*l* of CE12 and the smallest 102 of JE2, while for hybrids the largest 63 of JE15 × JE16 and the smallest 87 of JE13 × CE10, with overall mean value of 79/*l*. Cocoon shell weight ranged from 33 to 39 cg for parents and 34~48 for hybrids, overall mean 39 cg/cocoon. The heaviest single cocoon weight 194 cg/coon was obse-

rved from the parental line CE12 and the lightest 171 of JE2, while 171 for the hybrid JE13 × CE10 and 232 of JE15 × JE16, with overall 193 cg/cocoon. Cocoon shell percentage for parents was highest 22.4% in CE10 and lowest 19.3 in JE2 and JE16, and for hybrids highest 21.6 in JE4 × JE13 and lowest 18.3 in JE16 × CE6, with overall mean of 20.1%. Among parental lines, least pupae 75% survived in CE12 and most 97 in JE4, and among hybrid genotypes, least 63 in JE16 × JE6 and most 96 in JE2 × JE4 and JE13 × CE10, overall 87% of pupation rate. One of the parents JE13 yielded the most 17.0 kg/10000 larvae and CE12 the least 12.8, while a hybrid JE2 × JE4 the most 18.4 and the other JE4 × CE12 the least 13.2, with overall 15.5 kg/10000 larvae.

Sri Lankan averages for parents are comparable or higher in pupation rate to those of Korean averages (68~93%), comparable in cocoon yields to Korean's (11.8~17.4 kg/10000 larvae), lower in single cocoon weight than those of Korean parental lines (183~224 cg/cocoon), but far lower than those of Korean parental inbreds (23.3~25.9%) in cocoon shell percentage. For hybrids, the averages in all characters investigated are inferior to those of Korean's; pupation rate 94~97%, cocoon yields 19.0~23.6 kg/10000 larvae, single cocoon weight 208~248 cg/cocoon, and cocoon shell percentage 23.0~25.3% (SES, 1994). The observation indicates that heterotic effect among Sri Lankan inbred lines are meager, as compared with that among Korean inbreds, and also that the direction of future breeding programs in Sri Lanka should be pointed toward improvement and exploration of hybrid vigor phenomena in the silkworm, as it is revealed by this experiment that the potential to be improved exists.

2. Estimation of combining ability

Analysis of variance for quantitative characters investigated and combining ability of parental lines and heritability estimates are presented in Table 2. The difference between means of 36 genotypes and between combining ability are all highly significant in all the characters examined. Among components of genotypic variance, effect of general

combining ability (GCA) is more attributed to additive gene action and that of specific combining ability (SCA) more to nonadditive dominance and interaction between genes responsible for the phenotypic expression of a character (Falconer, 1960). Therefore, for this genetic population investigated, variation between parents is significantly contributed by both additive and nonadditive components, indicating that the population will respond significantly to the "mass" and "pedigree" selection in each parent and also that to the breeding methods of "cross-breeding" after certain degree of gene frequency fixation by inbreeding for those characters studied. Genetic structure of the population can thus be described as "Fixation of gene frequency is incomplete for those parental lines, however, between some loci there exists some degree of interaction."

Estimated values of GCA and SCA are presented in Table 3. For cocoon size, inbred JE4 showed the highest 4.8 GCA effect and CE12 the lowest -6.7 with LSD/.05$=1.57$. GCA for Cocoon shell weight ranged from CE6 -1.6 to JE4 1.2 with LSD/.05 $=0.76$. The range of GCA for single cocoon weight fell between -8.7 and 5.8 with LSD/.05$=3.13$. Cocoon shell percentage ranged from -0.64 to 0.84 in GCA effect with LSD/.5$=0.17$. Pupation rate can be improved better with the inbred JE13, while CE6 may not be good a parent for improvement of pupation rate, judging from the GCA effect of 2.7 by JE13 and that of -3.2 by CE6, LSD/.05 between means of which is 2.89. Cocoon yields can be increased more effectively when JE2 is used as parent than for CE6, since GCA effects for cocoon yields are highest 0.79 in JE2 and least -0.82 in CE6 with LSD/.05$=0.72$.

SCA effect for the character cocoon size was negatively prominent in the cross between JE15 $\times$JE16, that is, in this cross combination the average cocoon size was bigger than expected, as compared to the mean value of each parent, while in the crosses of JE16$\times$CE10 and CE6$\times$CE12 cocoon size of their F1's was smaller than the average of means of parents. For single cocoon weight, the highest SCA effect 29.2 was shown in the cross combination of JE15$\times$JE16, while the lowest -11.9

in JE16$\times$CE12. Cocoon shell percentage increased over parental mean value in the JE4$\times$JE13 and decreased in JE13$\times$CE10. SCA effect indicates that pupation rate collapsed far below the parental mean in the F1 population of JE16$\times$CE6, while inflated over the parental mean in the F1 progeny between CE6 and CE12. For the cocoon yields as calibrated for cocoon harvest from 10000 silkworm larvae, performance of F1 offspring between JE13 and CE12 exceeded the parental average and cocoon yields of F1 of JE16$\times$CE6 came short of the parental average. For those with higher effect of SCA, they could be utilized in further hybrid breeding programs for that specific character under consideration.

3. Heritability

As it is the case with GCA and SCA, each population should have its own estimates in heritability, for the purpose of predicting breeding value out of total phenotypic value for each economic character and in each different environmental circumstance. The extent of all the components of variance will affects the value of the heritability; population history and backgrounds, the character under investigation, genotypes used, design and accuracy/precision of experimental operation, etc. A small inbreeding population with variable environmental conditions should show lower heritability. A value for the heritability of a given character refers only to a particular population under that specific experimental conditions.

Heritability estimates in broad sense are presented in Table 2. Relative magnitude of genetic component was rather higher than earlier observations in other breeding populations (SES, 1983). This result was not expected, as it is contrary to the concept in that small populations maintained long enough for an appreciable amount of gene fixation to have taken place are expected to show lower heritabilities than large heterogeneous populations. However, high values of heritability estimates confirm the result in that variance contributed by additive gene action was highly significant between parental inbreds (Table 2). Higher reliability of the phenotypic value as a guide to the breeding value was observed in the characters of

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Table 3. *Estimated values of general (GCA) and specific combining ability (SCA) between parental inbreds*

Parent/F1		CS	SW	CW	S%	PR	CY[a]
GCA							
	JE2	4.1	0.7	5.6	−0.24	1.9	0.79
	JE4	4.8	1.2	2.2	0.45	1.5	0.14
	JE13	4.1	−1.4	−8.7	0.15	2.7	0.75
	JE15	−1.4	0.7	3.8	0.01	−0.9	−0.18
	JE16	−2.3	−0.2	5.8	−0.62	−2.8	−0.55
	CE6	−2.2	−1.6	−4.8	−0.38	−3.2	−0.82
	CE10	−0.3	0.0	−7.6	0.84	2.5	0.17
	CE12	−6.7	0.4	3.7	−0.20	−1.8	−0.31
SCA							
JE2 ×JE4		−3.7	1.6	5.2	0.19	5.4	1.94
	JE13	−5.3	2.7	8.6	0.46	−7.6	−1.39
	JE15	−0.5	−0.9	4.6	−0.85	0.5	1.56
	JE16	−5.3	2.0	6.1	0.35	−3.3	−1.30
	CE6	−7.2	3.4	16.5	0.16	−1.8	0.43
	CE10	−8.6	3.0	14.5	0.12	−1.6	0.06
	CE12	0.6	2.4	11.5	0.11	−2.5	0.16
JE4 × JE13		−5.0	2.8	6.8	0.87	−10.0	−2.11
	JE15	−0.2	1.9	9.5	0.16	−5.8	−1.46
	JE16	−4.0	3.0	12.7	0.39	1.0	2.08
	CE6	−1.3	1.5	8.1	−0.10	−3.0	0.50
	CE10	−0.5	−1.4	−3.8	−0.35	−1.8	0.54
	CE12	−3.1	−0.8	−3.6	−0.05	−0.2	−2.11
JE13 ×JE15		3.2	−1.5	−7.0	−0.07	0.7	1.83
	JE16	−0.8	−0.6	0.4	−0.49	−3.1	−0.45
	CE6	0.8	−0.9	−5.5	0.09	4.5	−0.08
	CE10	4.4	−3.1	−5.9	−1.03	4.3	0.06
	CE12	−0.9	0.3	5.8	−0.48	5.6	2.18
JE15 ×JE16		−12.8	5.7	29.2	−0.08	−5.0	−0.82
	CE6	−0.7	−0.1	−1.7	0.08	4.4	0.57
	CE10	2.7	−0.2	1.1	−0.26	1.1	−0.06
	CE12	−6.7	2.4	10.3	0.11	−0.5	−0.34
JE16 ×CE6		−4.0	0.6	10.8	−0.77	−18.0	−3.46
	CE10	6.4	−1.8	−4.4	−0.59	3.8	1.53
	CE12	6.0	−1.7	−11.9	0.38	5.4	0.70
CE6 × CE10		−1.0	0.6	−0.1	0.32	−2.8	−0.62
	CE12	6.4	−2.8	−5.8	−0.83	9.3	2.05
CE10 ×CE12		0.3	2.3	5.2	0.57	−1.9	1.67
G(i-j): LSD/.05		1.57	0.76	3.13	0.17	2.89	0.72
LSD/.01		2.23	1.08	4.46	0.25	4.11	1.02
S(ij-ik): LSD/.05		4.70	2.28	9.41	0.52	8.66	2.15
LSD/.01		6.68	3.24	13.38	0.74	12.32	3.05
S(ij-kl): LSD/.05		4.43	2.15	8.87	0.49	8.17	2.02
LSD/.01		6.30	3.06	12.62	0.70	11.62	2.88

[a]CS; cocoon size (cocoon/*l*), SW; cocoon shell weight (cg), CW; single cocoon weight (cg), S%; cocoon shell percentage (%), PR; pupation rate (%), CY; cocoon yields (kg)/10,000 larvae.

cocoon size (0.77), single cocoon weight (0.73), and cocoon shell percentage (0.73). The estimated he-ritability values were 0.65, 0.64 and 0.33 for pupation rate, cocoon shell weight and cocoon yields, respectively.

摘 要

스리랑카의 二化性 잠품종집단은 1950년대 이후로 이탈리아, 일본, 인도, 한국, 대만 및 타일란드로부터 수입된 원종 및 교잡종에서 분리된 60여개의 순수 계통으로 구성되어있다. 냉침사육이나 월년시키지 않고, 이화성 순종도 即浸에 의하여 연중 5-6회 연속계대사육으로 보존되어 오고 있다. 육종의 중점방향과 效果的이며 效率的인 육종방법을 채택하는데 지표로 활용할 목적으로, 실용형질에 대한 일반조합능력, 특수조합능력 및 유전력 推算의 방법으로 이들 가잠집단의 유전적구조를 糾明하고자 본 연구를 수행하였다. 최근 수년간 교잡종 생산에 쓰인 8개 원종과 이들의 半二面交雜에 의한 28개 교잡종을 대상으로 분산분석의 방법으로 얻은 결과에 의하면, 예상했던 바와는 달리, 이들 집단은 원종간에 아직도 유의할 만한 相加的 및 非相加的 유전자 작용효과를 유지하고 있는 것으로 판단되어, 개체 및 계통선발에 의한 육종방법 뿐만 아니라 순계분리와 교잡에 의한 육종법에도 앞으로 당분간은 效果的으로 반응할 수 있는 遺傳集團임이 판명되었다. 아울러, 현재 진행중인 교잡육종에 곧바로 이용될 수 있다고 보여지는, 특정 실용형질에 대한 조합능력이 상대적으로 높은 원종도 본 연구의 결과로 선별되었다. 表現型價에 대한 育種價의 상대비율 (유전력)은 조사된 실용형질 모두에서 비교적 높게 나타났는데, 이는 연중사육으로 각 遺傳子座位에서 同型接合型의 빈도가 높아졌을 때 예상되는 결과와는 정반대가 되는 것으로서, 이는 순계보존상에 사육현장의 관리상 기능적 문제로 인하여 異型接合인 좌위의 빈도가 비교적 높게 유지되었을 때 나타날 수 있는 현상으로 생각된다.

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