

ORIGINAL ARTICLE

Genetic parameters in traits of productive importance in lines of *Bombyx mori* L.

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Abstract

In the textile industry, complex cocoon traits are closely related to silk production. The aim of the present study was to estimate genetic parameters of economic importance traits—cocoon length (CL), cocoon weight (CW) and shell weight (SW)—in three *B. mori* lines—Chinese (C6), Japanese (J7) and Indian (C. Nichi)—reared under different temperature and photoperiod conditions. For each of these lines, data were collected from several generations with a full-sib family structure and variance-covariance component were obtained via restricted maximum likelihood (REML) estimates based on a bi-trait animal model analysed through the multiple-trait derivative-free restricted maximum likelihood (MTDFREML) software. Genetic parameters of the traits varied between the silkworm lines were evaluated. Heritabilities were highest in J7 line (0.71, 0.89 and 0.93 for CL, CW and SW, respectively) followed by C6 (0.48, 0.54 and 0.50 for CL, CW and SW, respectively) and C. Nichi (0.36, 0.43 and 0.40 for CL, CW and SW, respectively). Phenotypic correlations among these lines were positive, with values ranging between 0.36 and 0.767. Similarly, genetic correlations between the analysed silkworm lines were observed to be positive, with high values ranging from 0.86 to 0.94. The evidence for environmental correlation in these lines was found only between CW-SW traits with moderate to high values ranging from 0.600 to 0.940. The magnitude of heritability and genetic correlations implies that phenotypic variations of the CL, CW and SW traits depend mainly on genotypic variation within the J7, C6 and C. Nichi lines, and that simultaneous genetic gains are possible by implementing selection processes for any of the evaluated traits.

KEYWORDS

Bombyx mori, genetic parameters, productive traits

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1 | INTRODUCTION

The silkworm, *Bombyx mori*, is a domesticated insect native to Northern Asia that is fully adapted for commercial breeding. Its development and productivity depend on biotic factors such as competition, predation and pathogens and abiotic factors such as temperature and photoperiod (Kumar et al., 2003). The success of silkworm farming is important to the textile industry, which relies on the productive efficiency of quantitative and qualitative traits associated with cocoon production and the optimization of by-products resulting from sericulture activity (Neshagaran et al., 2016).

B. mori has more than 3,000 improved lines and approximately 400 heritable mutants, for an estimated 4,310 geographic races, lines and mutants, which are distributed in different gene banks around the world (Doira et al., 1992; Goldsmith et al., 2005). The principles of silkworm breeding and the genetics of qualitative and quantitative traits have been previously documented by Singh et al. (2011). Traits contributing to silk performance are controlled by numerous genes influenced by environmental factors, making it difficult to judge whether the observed phenotypic variability is inherited or influenced by the environment (Reza & Rahman, 2005; Zhao et al., 2007). Genetic and environmental contribution to the phenotypic expression can be evaluated through quantitative genetic methods that generate useful information for genetic improvement programmes.

The genetic parameters of complex traits associated with silk production are essential for establishing effective genetic improvement programmes. Heritability, for instance, is a useful precision parameter for identifying the genetic potential of individuals from its phenotypic expression (Singh et al., 1994) and the magnitude of the selection response for a trait (Nyquist, 1991). Similarly, phenotypic and genetic correlations provide additional information on the degree of association between the observed and genetic values of two quantitative traits (Searle, 1961). Special attention is placed on genetic correlations because they make it possible to maintain the genetic gain within populations through the selection process with fewer traits, low heritability traits or even traits that are difficult to measure (Falconer, 1981). The heritability and correlations of quantitative traits have considerable impact on the observed genetic progress of any breeding program; hence, their knowledge is fundamental to the creation, evaluation, improvement or development of highly productive pure or hybrid breeds (Hemmatabadi et al., 2016).

Genetic studies conducted on *B. mori* silkworms have focussed mainly on silk production traits, such as cocoon weight, bark weight and bark percentage (Zamani

et al., 2019). Based on these traits, breeders have selected parents within and between different silkworm populations and environments (Bharat & Shunmugan, 2014). This has resulted in geographically differentiated races with a particular source of genes useful in breeding programmes for conservation purposes or hybridization to identify genotypes with superior genetic performance (Jolly et al., 1989). The objective of the present study was to estimate genetic parameters (heritability and genetic, phenotypic and environmental correlations) of economic importance traits in three lines of silkworm reared under different temperature and photoperiod conditions.

2 | MATERIALS AND METHODS

2.1 | Silkworm lines

Three silkworm *B. mori* lines were used in the present study: Chinese 6 (C6), Japanese 7 (J7) and Indian (C. Nichi). These were chosen according to their productive performance and voltinism (number of generations per year). The C6 and J7 lines are bivoltine and were selected for their high yield in important productive characters, while C. Nichi line is polyvoltine and is characterized by its rapid growth rate and tolerance to tropical conditions (Rao et al., 2006). These silkworm genetic lines were imported from the Experimental Station of Sericulture and Agriculture (SAES) in Vratsa, Bulgaria (National Environmental Licensing Authority [ANLA] Resolution 00431 of March 2018), specifically from the Department of Genetics Research for *B. mori* improvement.

2.2 | Rearing conditions

The experimental research was carried out at La Rejoia Plant Studies Center, attached to the Agrarian Sciences Faculty of the University of Cauca, located at Popayán in Northeast Colombia. The La Rejoia village is located in Cauca at 1,800 meters above sea level, has an average temperature of 18°C, and receives an average rainfall of 1,750 mm annually (Vivas & Morales, 2005). The experimental phase was conducted from July 2018 to April 2020. The lines were kept in optimal feeding and sanitary conditions in accordance with the protocols of Cifuentes and Sohn (1998) and Pescio et al. (2008). They were reared in incubators under controlled environmental conditions from egg stage to complete pupation stage, according to the modified protocols of Kumar et al. (2002) and Lakshminarayana et al. (2002), and during the number of generations required to estimate the lines voltinism—two generations for J7 and three for C6 and C. Nichi. The

incubators used for silkworm rearing were locally designed according to the technical characteristics described in Duque-T et al. (2018) and were equipped with instruments to control and monitor temperature, humidity, light, air speed, and CO₂ concentration.

The data used to estimate silkworm genetic parameters are part of a research project dedicated to analysing the effects of variables such as temperature and photoperiod conditions on the changes in voltinism recorded for the evaluated lines (Figure 1). The effects of these variables, as environmental factors, were chosen since they are recognized for influencing different development stages of *B. mori* and their voltinism expression (Kamili & Masoodi, 2004; Takamiya, 1974). Similarly, the evaluated levels of each environmental variable were chosen considering the maximum and minimum values reported to influence the silkworms' behaviour (Rahmathulla, 2012; Vermana et al., 2003). Other environmental factors, such as relative humidity (75 ± 5%), feeding (fresh mulberry), CO₂ concentration (<2%) and air speed (0.5–1 m/s), remained constant at levels considered optimal for *B. mori* rearing (Rahmathulla, 2012).

2.3 | Experimental design

The experimental rearing conditions are depicted in Figure 1. Briefly, three temperatures (24 ± 1°C, 26 ± 1°C and 28 ± 1°C) and photoperiod conditions (8–16, 12–12 and 16–8 of photophase or scotophase, respectively) were evaluated per generation (two generations for J7 and three for C6 and C. Nichi) and sex. The measurement of productive important traits, such as cocoon length (CL), cocoon weight (CW) and shell weight (SW), were recorded for each individual (Seidavi, 2010). In total, nine treatments

(factorial combination of temperature * photoperiod) with three repetitions were evaluated per generation. On each repetition, a group of approximately 100 individuals was observed, and seven to ten females and males were randomly taken for phenotypic measurements. Within each group, next generation parents were also randomly selected and mated. No selection process for the evaluated traits was exercised on the individuals chosen as parents of each generation. A total of 3,566 individuals were used, divided into 163 full-sibling families—61, 32 and 70 for C6, J7 and C. Nichi, respectively. The lengths and weights were measured individually in millimetres and grams, respectively. The shell weight was measured after removing the pupa, and this process was repeated throughout the different generations.

2.4 | Genetic analysis

Heritability and genetic, phenotypic and environmental correlations were estimated for CL, CW and SW variables in C6, J7 and C. Nichi lines. The variance-covariance components were obtained by the restricted maximum likelihood (REML) based on information of full-sibling family structure. A bi-trait animal model was used through the multiple-trait derivative-free restricted maximum likelihood (MTDFREML) software (Boldman et al., 1995). The evaluated models took into consideration the fixed effects of temperature, photoperiod, generations and sex. Meanwhile, the random effects were the direct additive-genetic component and error term. The relationship matrix included 1,337, 775 and 1,355 animals in C6, J7 and C. Nichi lines, respectively. The convergence criterion for variance-covariance estimation was 10⁻⁸, with a maximum of 500 iterations.

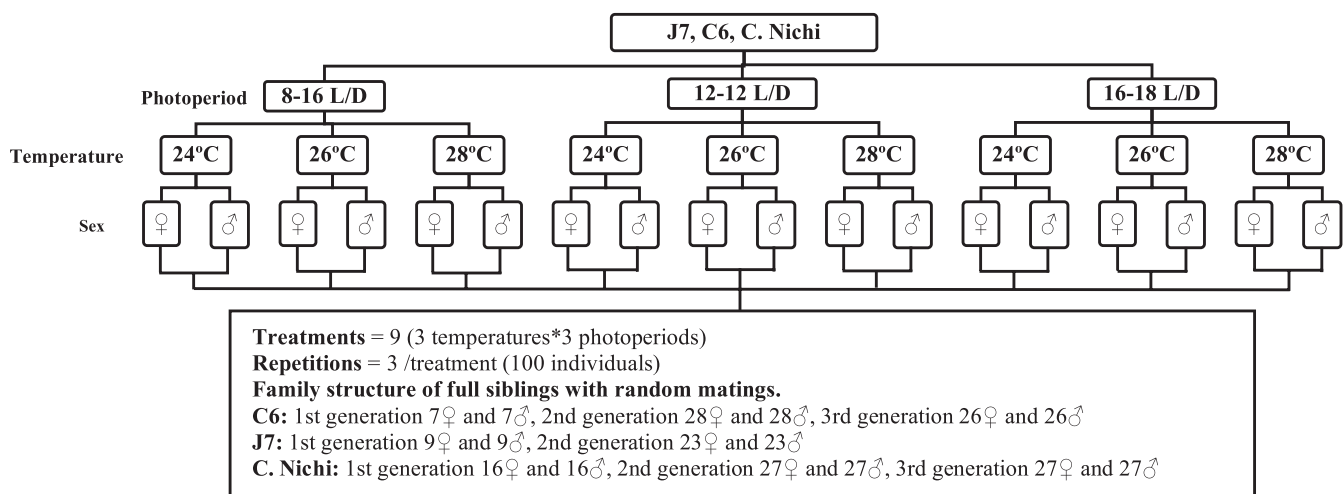


FIGURE 1 Rearing experimental conditions of the evaluated silkworm lines per generation

TABLE 1 Descriptive statistics of the general performance of each line through the combination of fixed effects

Line	Trait	Mean	SE	CV (%)
C6 (<i>n</i> = 1,220)	CL (mm)	28.98	2.52	8.70
	CW (g)	1.24	0.31	25.17
	SW (g)	0.23	0.07	32.80
J7 (<i>n</i> = 711)	CL (mm)	35.24	2.75	7.80
	CW (g)	1.34	0.31	23.41
	SW (g)	0.27	0.07	25.43
C. Nichi (<i>n</i> = 1,259)	CL (mm)	28.34	2.10	7.42
	CW (g)	1.14	0.24	20.95
	SW (g)	0.18	0.04	25.05

Abbreviations: CL, Cocoon length; CV, coefficient of variation; CW, cocoon weight; SE, standard error; SW, shell weight.

3 | RESULTS AND DISCUSSION

Table 1 presents the descriptive statistics of the evaluated traits on each line, obtained through the combination of fixed effects. In general, the highest average values of CL, CW and SW productive traits were found in line J7, while C6 and C. Nichi lines behaved similarly. The CL values ranged between 28.34–35.24 mm, the CW values ranged between 1.14–1.34 g, and the SW values ranged between 0.18–0.27 g. The CW and SW values obtained here are low compared to those obtained by Kumar and Kumar (2011) (1.476–1.890 g for CW and 0.241–0.351 g for SW). According to coefficient of variation among lines, CL was the trait with the least variation (7.42%–8.7%), while CW and SW presented the greatest values (20.95–25.17 and 25.05%–32.8%, respectively). The variability observed between lines and traits could be a direct reflection of environmental rearing conditions. It should be noted that highest coefficients of variation was found in the C6 line, which is in line with Kinoshita et al. (1982), who claimed that Chinese lines show greater susceptibility to environmental changes.

Table 2 shows the variance–covariance components and estimated heritability for the three evaluated traits. Phenotypic variance was highest in the CL trait (7.530, 5.072 and 3.525 for J7, C6 y C. Nichi, respectively), while the CW and SW traits ranged between 0.001 and 0.088 among the lines. The greater phenotypic variance observed in the CL character suggests that deeper phenotypic plasticity exists among individuals within each family group (Geber & Griffen, 2003).

Additive variance was highest in the CL trait with values of 5.346, 2.411 and 1.269 for J7, C6 and C. Nichi, respectively, meanwhile the lowest values were observed in SW (0.001–0.004). Low additive-genetic variance is

TABLE 2 Variance–covariance components and heritability values of economic important traits in C6, J7 and C. Nichi silkworm lines

Line	Trait	Additive			Phenotypic			Environmental			h^2 (SE)
		CL	CW	SW	CL	CW	SW	CL	CW	SW	
C6	CL	2.411	0.254	0.069	5.072	0.254	0.069	2.661	0.000	0.000	0.48 ± 0.033
	CW	0.254	0.035	0.008	0.254	0.066	0.128	0.000	0.031	0.005	0.54 ± 0.030
	SW	0.069	0.008	0.002	0.069	0.128	0.004	0.000	0.005	0.002	0.50 ± 0.031
J7	CL	5.346	0.561	0.133	7.530	0.561	0.133	2.184	0.000	0.000	0.71 ± 0.055
	CW	0.561	0.078	0.016	0.561	0.088	0.015	0.000	0.010	−0.001	0.89 ± 0.082
	SW	0.133	0.016	0.004	0.133	0.015	0.005	0.000	−0.001	0.001	0.93 ± 0.081
C. Nichi	CL	1.269	0.125	0.026	3.525	0.125	0.026	2.255	0.000	0.000	0.36 ± 0.035
	CW	0.125	0.014	0.002	0.125	0.034	0.005	0.000	0.019	0.003	0.43 ± 0.032
	SW	0.026	0.002	0.001	0.026	0.005	0.001	0.000	0.003	0.001	0.40 ± 0.033

Abbreviations: CL, Cocoon length; CW, cocoon weight; SE, standard error; SW, shell weight.

TABLE 3 Phenotypic (r_p), genetic (r_g) and environmental correlation (r_e) among the evaluated productive traits

Line	Parameter	CL - CW	CW - SW	SW - CL
C6	r_p	0.438	0.767	0.457
	r_g	0.860	0.940	0.890
	r_e	0.000	0.600	0.000
J7	r_p	0.695	0.736	0.721
	r_g	0.890	0.860	0.900
	r_e	0.000	0.940	0.000
C. Nichi	r_p	0.360	0.759	0.366
	r_g	0.890	0.880	0.900
	r_e	0.000	0.690	0.000

Abbreviations: CL, Cocoon length; CW, cocoon weight; SW, shell weight.

expected in traits exposed to a strong directional selection and are closely related to biological adequacy, where alleles have been fixed over time within the populations. In contrast, traits exposed to a weak selection process tend to present high levels of additive-genetic variation (Teplitsky et al., 2009). It is possible that the SW trait is less variable because it has been a manipulated character for centuries due to its economic importance (Trochez-Solarte et al., 2019).

Environmental variance ranged from 0.001 to 2.661 among the lines, with the highest values associated with the CL trait. Environmental variance is part of the phenotypic variance and reflects the phenotypic differences of individuals managed under similar environments, where the differences occur due to small variations found within that environment (Falconer, 1981; Molina, 1992; Schou et al., 2020). In general, environmental variance in the present study was low among the traits and lines, indicating that the environmental conditions associated with the treatments—temperature and photoperiod—were handled correctly during the experimental period.

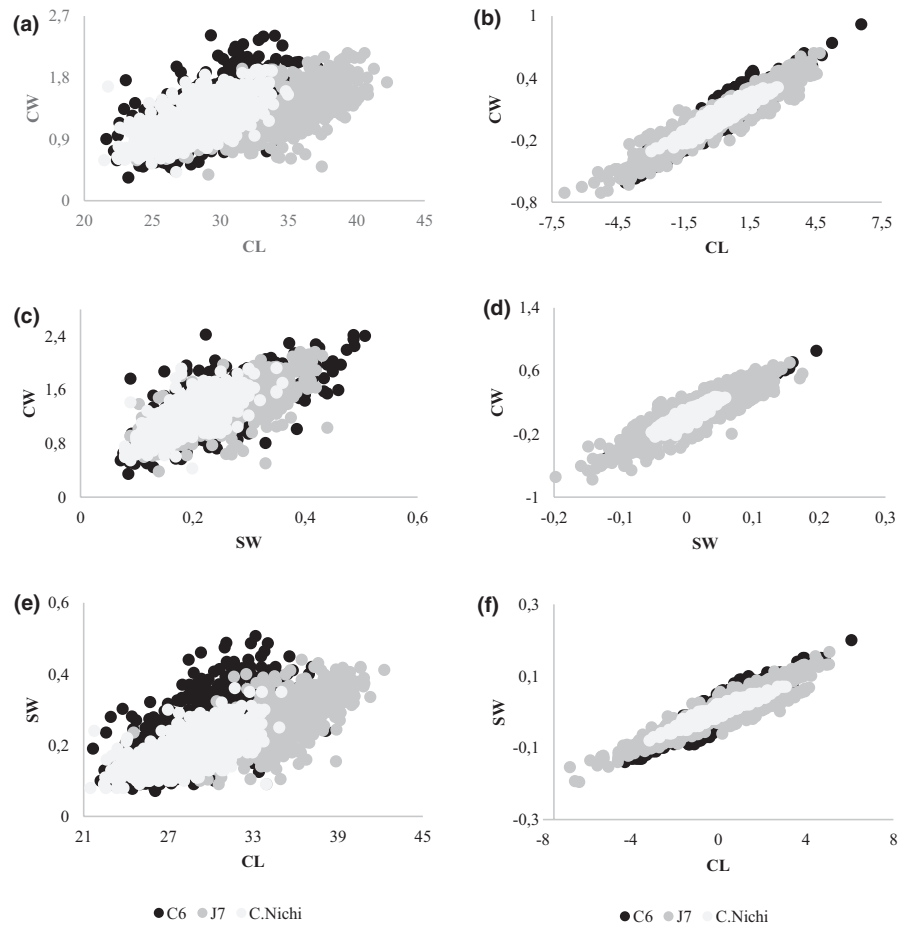
Heritability varied between silkworm lines (Table 2); the highest values were obtained in J7 line (0.71, 0.89 and 0.93 for CL, CW and SW, respectively) followed by C6 (0.48, 0.54 and 0.50 for CL, CW and SW, respectively) and C. Nichi (0.36, 0.43 and 0.40 for CL, CW and SW, respectively). The CW heritability obtained between lines (0.89, 0.54 and 0.43 for J7, C6 and C. Nichi, respectively) are within the 0.21–0.97 range reported for races of Chinese, Indian, and Iranian origin (Hassan et al., 2011; Kumaresan et al., 2007; Seidavi et al., 2008; Talebi et al., 2001). The estimated heritability of SW trait (0.93, 0.50 and 0.40 for J7, C6 and C. Nichi, respectively) also agreed with the 0.35–0.80 values reported in other studies (Bashir et al., 2015; Govindan et al., 1991; Seidavi, 2010; Singh et al., 2011). The heritability values

associated with the CL trait were 0.71 for J7, 0.48 for C6 and 0.36 for C. Nichi. Reports of CL heritability are scarce in literature, possibly because silkworm studies on genetic parameters focus mainly on other traits that are easy to measure and also fundamental for sericulture economy (Ghanipour et al., 2007). According to the scale proposed by Bavera (2000), the estimated heritability in the present study was high, suggesting that phenotypic variations of traits depend mainly on genetic variation with scarce influence from the environment (Ramírez et al., 2020). These results indicate that CL, CW and SW traits can be improved through selection processes within the evaluated populations (Quijano & Echeverri, 2015; Sabhat et al., 2009). Some studies indicate that high heritability in economic importance traits can be commonly found in domesticated varieties of *B. mori* (Kumaresan et al., 2000; Mirhosseini et al., 2005; Mu et al., 1995), especially those populations that have been subjected to the effects of genetic improvement programmes (Maqbool et al., 2005; Petkov & Nguyenvan, 1987).

The wide range of estimated heritability values is due to the fact that this parameter is particular to each trait and specific to each population (Nyquist, 1991). Based on the observations recorded under the particular rearing conditions of the present study, the contribution of genetic and environmental components to the phenotypic expression of a trait (CL, CW or SW) varies between the lines. The highest heritability values were found in the J7 line, indicating that CL, CW and SW can be rapidly improved in genetic terms through selection processes. However, a slower response is expected in the C6 and C. Nichi lines. The differences between the Japanese, Chinese and tropical lines may be the result of reproductive isolation and significant genetic differentiation among lines, especially the Japanese breed (Yukuhiro et al., 2011).

Phenotypic, genetic and environmental covariance are also reported in Table 2. Phenotypic covariance among lines was highest for CL-CW traits, with values ranging between 0.125 and 0.561. Meanwhile the lowest values were found in SW-CL traits (0.069) in C6 line, and CW-SW traits (0.005–0.015) for J7 and C. Nichi lines. Phenotypic covariance is further divided into genetic and environmental covariance. The former represents the part of phenotypic covariance attributed to common genetic factors, while the latter corresponds to the phenotypic covariance due to common environmental factors (Gao et al., 2021). The results showed that genetic covariance presented a similar tendency between lines, with greater values between CL-CW, followed by SW-CL and CW-SW traits. Environmental covariance was found in CW-SW traits, with values ranging from –0.001 to 0.005. Meanwhile,

FIGURE 2 Phenotypic (a, c, e) and additive genetic values (b, d, f) relationships between CW, CL and SW traits obtained with the evaluated silkworm lines



in CL-CW and SW-CL traits, a zero value was observed, indicating that the contribution of common environmental factors to the phenotypic covariance was negligible in these cases.

Phenotypic, genetic and environmental correlations are shown in Table 3. Between lines and traits, the phenotypic correlations were lower than genetic correlations, suggesting that the phenotypic expression of CL, CW, and SW traits is likely to be determined by genotype \times environment interaction ($G \times E$) (Irvine-Lopez et al., 2020; Rahman, 1984).

Phenotypic associations between traits and lines are shown in Figure 2. Linear tendencies were observed corresponding to positive phenotypic correlations in all cases. CW-SW correlation was similar among the lines, with values ranging between 0.736 and 0.767. CL-CW and SW-CL correlations were highest for J7 line (0.695 and 0.721, respectively), followed by C6 (0.438 and 0.457, respectively) and C. Nichi (0.36 and 0.366, respectively). These positive phenotypic associations are expected since SW is part of CW, and the latter was greater when CL increased. Kumar et al. (1995) and Grekov (1989) also identified significant and positive phenotypic correlation between CL, CW and SW traits (0.55–0.659).

The genetic correlations of CL-CW, CW-SW and SW-CL presented positive and high values between the analysed silkworm lines (0.86–0.94). These values are within the 0.709–0.989 range presented by Nagaraja et al. (1996) and Mirhosseini et al. (2007), Mirhosseini et al. (2002). These results suggest that the observed correlated response among traits are determined by the same or linked genes (Molina, 1992). The positive and high genetic correlations between CL, CW and SW traits indicate that selecting one of them would lead to the improvement of the others, resulting in simultaneous genetic progress (Seidavi, 2010). The genetic correlation results are illustrated in Figure 2, where the additive-genetic value relationship among the traits and lines are plotted. An evident linear and positive association is depicted in all cases. CW and SW are important traits in the sericulture chain for silkworm breeders and researchers, as well as those involved in the silk thread industry. According to the genetic parameters estimated in this research, any of these two traits are potential candidates for the establishment of selection processes in breeding programmes within the J7, C6 and C. Nichi lines.

The environmental correlation for CW-SW traits was positive, with moderate to high values between the lines (0.600–0.940), suggesting that the evaluated

rearing environmental conditions influenced both traits in a similar manner. These values are higher to the average 0.666 environmental correlation obtained in pure lines (Seidavi, 2010). On the other hand, environmental correlations between CL-CW and SW-CL were zero, as expected, since their environmental covariance was also zero. Such null environmental correlations suggest that factors like those evaluated in the present study—temperature, photoperiod and other breeding conditions—do not contribute to the possible causal relationship between CL-CW and SW-CL traits (Gao et al., 2021).

The implementation of genetic improvement strategies is successful only when the inheritance patterns of economic importance traits and genotype \times environment interactions are clearly understood (Murthy & Subramanya, 2007). The estimations of genetic parameters in silkworm farming are critical for understanding phenotypic changes in the population as a response to domestication, which would enable the improvement of economically valuable traits useful for increasing the profits of the sericulture industry (Darmand et al., 2011; Hemmatabadi et al., 2016). With regard to the J7, C6 and C. Nichi silkworm lines, selection is one of the best approaches that can be applied in their genetic improvement programmes, and in particular, individual selection of parental lines could provide better results (Hemmatabadi et al., 2016).

4 | CONCLUSIONS

The genetic parameters of CL, CW and SW traits showed differences within the J7, C6, and C. Nichi silkworm lines. However, both heritability and genetic correlations were high in all cases, indicating the possibility of obtaining genetic gains in economic importance traits through the implementation of selection processes for any of the evaluated traits within the genetic improvement programmes for the silkworm lines that were evaluated.

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CONFLICT OF INTERESTS


Authors declare no Conflict of Interests for this article.


AUTHOR CONTRIBUTIONS

Giselle Zambrano-Gonzalez: conceptualization, formal analysis, data collection, preparation of the original draft, methodology, writing, revision and editing. **Martha I. Almanza-Pinzon:** formal analysis, methodology, writing and revision. **Mauricio Vélez-T:** methodology, statistical analysis, writing and review.

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