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The effect of temperature on combining ability and genetic parameters of parental silkworm Lines(*Bombyx mori* L.)

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ABSTRACT

Every silkworm breeding center tries to add new silkworm lines to its germplasm. This study investigated the genetic differences between two parental lines in the silkworm breeding programs in response to high temperatures. Ten dumbbell-shape cocoons (DSC) genotypes (Japanese) and fifteen oval-shape cocoons (OSC) genotypes (Chinese) were reared under the two temperatures: high (37 ± 1 °C) (HT) and normal (24 ± 1 °C) (NT), separately. General combining ability (GCA), specific combining ability (SCA), Baker's ratio and MSGCA/MSSCA (additive to non-additive genetic effects) estimated for best cocoon weight (BCW), cocoon shell percentage (CSP), larval viability (LV) and pupal viability (PV) traits using second Griffing's method for partial diallel analysis. The GCA and SCA of viability traits (PV and LV) were much higher than cocoon traits (BCW and CSP) under HT conditions for both DSC and OSC groups, which caused the ranking of genotypes for GCA and SCA to change in each group. MSGCA/MSSCA ratio also increased significantly for PV than other traits under HT. The contribution of additive effects in controlling the CSP was more than BCW and viability traits in both temperature conditions and genetic groups. The comparison of MSGCA/MSSCA and Baker's ratio under NT and HT conditions showed that BCW and CSP had almost equal values in both DSC and OSC genotypes. But MSGCA/MSSCA and Baker's ratios of PV under HT were several times higher than NT condition with the superiority of GCA variance. Additionally, applied heat treatment may well discriminate between genotypes.

1. Introduction

Unlike silkworm breeds in tropical regions, temperate regions' silkworms are sensitive to heat [1,2]. The high sensitivity of silkworms to heat in the conditions we are facing with global warming will be one of the serious challenges of silkworm rearing in temperate regions in the future. In some countries such as India and Iran, parts of which have hot and dry weather, these climate changes significantly affect silk production [3]. Therefore, thermotolerance mainly in adverse silkworm-rearing zones should be considered in special breeding programs to produce silkworm hybrids with high genetic plasticity [1,4]. Thermotolerant parental lines will also be needed to introduce robust silkworm hybrids for hot environmental conditions in temperate areas. To develop selection criteria for improving thermotolerance in parental silkworms, seeking a basic understanding of gene action and the mode of inheritance for productive and viability traits (larval and pupal) is very important.

Single-cross hybrids are the most common commercial silkworm produced by two parents, including Chinese parents (oval-shaped cocoon) and Japanese parents (dumbbell-shaped cocoon). Therefore, in hybrid-based silkworm breeding systems, two genetically different lines are produced for at least 5–6 years [5]. Evaluation of the genetic capacities of parents based on genetic parameters of important traits, such as thermotolerance, may be of great help to the breeders to finalize the selection of parental silkworms. There are several methods to estimate the genetic parameters of silkworms. The Griffing methods [6] are a

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procedure to find the best parent and hybrid combinations from a diallel set of crosses in silkworm [7]. Extensive studies aimed at determining the combining ability of silkworm varieties and hybrids [7–10]. These parameters may help breeders to introduce the best parents for hybridization. If either or both parents are better, the performance of their offspring may be unacceptable; in such situations, the genetic parameters derived from diallel analysis play a critical role in the decision [9–11]. However, Chen et al. [12] asserted the accumulation of superior GCA and SCA alleles is an important contributor to heterosis and QTLs that greatly contributed to combining ability. This achievement may accelerate the identification of elite inbred lines and the breeding of super hybrids. In the future, SNP markers may significantly help in the selection of parents with superior performance for crossbreeding programs.

The mulberry silkworm which has been domesticated for a long time is not able to survive under environmental stress. This is due to the mechanism of adaptation, which is practically different from the other insects [13]. However, silkworms can grow at 7–40 °C, but physiologically 20–30 °C is better for silkworm growth, and economically 22–27 °C is the best for increasing rearing efficiency [14]. Thus, higher temperatures would reduce the important traits of the silkworm. Direct and long-term heat exposure influences tolerance and metabolic rate; consequently, viability and expected growth of silkworm larvae change [1,13].

Some traits like thermotolerance are vital for durable yield under thermal conditions. Usually, disease resistance and tolerance to environmental stress are negatively correlated with productive traits [15]; thus, improving thermotolerance will be a great challenge in the breeding program and choosing superior genotypes. First of all, it is necessary to evaluate thermotolerance in silkworm hybrids and parental lines [13,16]. Then, the productive (e.g cocoon weight and cocoon shell percentage) and viability traits (e.g larval and pupal mortality) should be improved simultaneously during the silkworm breeding program. Genetic improvement is successful only when the inheritance of productive and viability traits, gene function, and genetic parameters are clearly understood, especially in the challenge of environmental stresses [13,16,17]. For example, Zambrano-Gonzalez [17] estimated the heritability and genetic correlation of three important traits in three genotypes when the temperature changed slightly (+2 and + 4).

The present study is an attempt to compare some important genetic parameters for productive and viability traits in both Japanese and Chinese genotypes between two environmental conditions (normal and thermal). To achieve this objective, a partial diallel crossing was performed between the parental lines.

2. Materials and methods

2.1. Silkworm genotypes

The DSC genotypes consisted of four lines named 103, 151, 153, and 1524 with their crosses, and the OSC genotypes were five lines named 32, 104, 124, 154, and Y with their crosses. All parental lines belong to the Iranian silkworm germplasm, in the Iran Silk Research Centre located in Guilan province in the north of Iran. These parental lines were chosen based on stability in rearing and production.

2.2. Rearing and recording

Silkworm rearing was done in the Sefid Roud Agriculture and Livestock Company farm - Anzali branch. Silkworm larvae were fed by mulberry (Morus alba) leaves (Kenmochi variety) during the spring season in 2017. Two rooms with indoor environmental control equipment were used for NT and HT treatment (Fig. 1). Since nutrition and environmental factors affect silkworm performance [17,18], all the rearing condition was the same except the temperature.

All rearing procedures in this experiment were according to the standard silkworm rearing method [19]. The thermal exposure was started from the fifth instar. In the normal temperature (NT) room, the fifth instar larvae were constantly maintained at 24 °C with 75% humidity, but in the high temperature (HT) room, they were exposed to 37 °C with 65% humidity for 8 h (9 a.m.–5 p.m.) from the 2nd to 7th day. This process started one day after the fourth molting until one day before larval cocooning. In this interval, larval mortality percentage was regularly recorded for all experimental trays to record larval viability (LV).

After cocoon harvesting and visual assessments, the number of good, moderate, weak, and double cocoons were counted while their liveness and deadness were also measured. After sex determination, cocoon

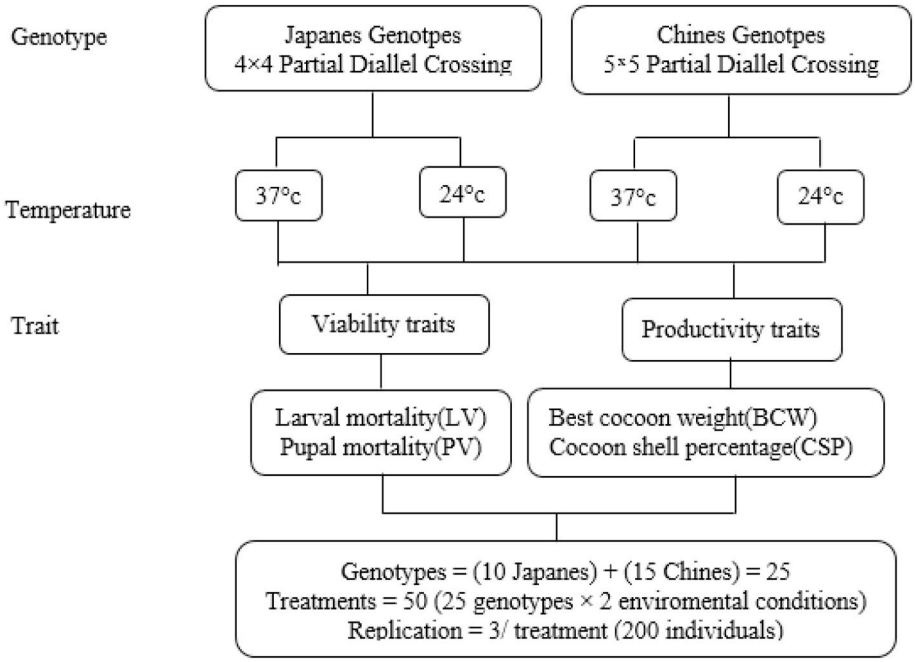

Fig. 1. Experimental plan to compare silkworm genetic parameters.

weight and cocoon shell weight traits were recorded for 25 males and 25 females. Two important productive traits, including BCW and CSP, and two important viability traits including LV and PV were measured based on the following formulas:

$$LV = \frac{(Number\ of\ Primary\ Larvae - Number\ of\ Dead\ Larvae)}{Number\ of\ Original\ Larva} \times 100 \quad (1)$$

$$PV = \frac{Number\ of\ Alive\ Pupa}{Total\ Number\ of\ Pupa\ (Alive\ and\ Dead)} \times 100 \quad (2)$$

$$CSP = \frac{Female\ Cocoon\ Shell\ Weight}{Female\ Cocoon\ \ Weigt} + \frac{Male\ Cocoon\ Shell\ Wight}{Male\ Cocoon\ Weight} \times \frac{1}{2} \times 100 \quad (3)$$

2.3. Experimental design

The silkworm genotypes derived from partial diallel crossing, including 10 Japanese (four parents and six crosses) and 15 Chinese (five parents and ten crosses), were reared in three replications (trays), each containing 200 larvae (Fig. 1). All trays in each room were designed based on a completely randomized design (CRD).

Diallel analysis was performed using the fixed model of the second method of Griffing [6] by applying of IML procedure of SAS software [20]. The statistical model was as follows:

$$X_{ij} = \mu + gca_i + gca_j + sca_{ij} + e_{ij} \quad (4)$$

X_{ij}: Observed value of the trait in the hybrid gained from cross i^{th} parent with j^{th} parent,
μ: Population mean,
gca_i: General combining ability of the i^{th} parent,
gca_j: General combining ability of j^{th} parent,
sca_{ij}: Specific combining ability of the ij^{th} cross,
e_{ij}: Test error of the ij^{th} observation.

2.4. Genetic parameters

In this study, the genetic parameters consisting of the proportion of additive to dominance effects, general combining ability (GCA) of the parents, and specific combining ability (SCA) of the crosses were evaluated under high (+13 °C) and normal temperature conditions.

The mean square ratio of GCA to SCA (MSGCA/MSSCA) was used to determine the proportion of additive or non-additive effects of genes in controlling each quantitative trait. Accordingly, if the ratio of MSGCA to MSSCA is closer to one, it shows an equal portion of the additive and non-additive effects of genes; more than one, indicates a greater portion of the additive gene effect, and for less than one, indicates the greater portion of the non-additive effects of the genes [21].

Baker's ratio determines the portion of the additive and non-additive effect of genes using the following equation:

$$\text{Baker's ratio} = \frac{2MSgca}{2MSgca + MSsca} \quad (7)$$

MSgca: Variance of general combining ability
MSsca: Variance of specific combining ability

Accordingly, a ratio geater than 0.5 represents the greater portion of the additive effect, less than 0.5 represents the greater portion of non-additive effects, and equal to 0.5 means that the portion of both additive and non-additive effects is the same.

3. Results

3.1. Analysis of variance

The mean square of the main effects of genotype and temperature as well as the interaction of genotype x temperature were highly significant ($p < 0.01$) for all traits and both DSC and OSC genotypes (Tables 1 and 2). Mean squares of GCA and SCA for Japanese and Chinese genotypes under both normal (NT) and high (HT) temperature conditions using second Griffing's method have been shown in Tables 1 and 2, respectively. The mean squares of GCA and SCA in both DSC and OSC genotypes were higher in HT than NT. The mean square of GCA and SCA of all traits in both Japanese and Chinese genotypes were significant ($p < 0.01$ or $p < 0.05$) under HT; also the mean square of SCA of all traits in both Japanese and Chinese genotypes were significant under NT ($p < 0.01$ or $p < 0.05$). It showed the significant differences between crosses, and consequently the presence of the non-additive effect of genes in controlling these traits.

3.2. Gene effect

MSGCA/MSSCA of BCW and CSP (cocoon traits) in DSC and CSP in OSC genotypes were more than one under both HT and NT conditions (Tables 1 and 2). MSGCA/MSSCA of viability traits (larval and pupal) for both DSC and OSC genotypes were less than one (except PV under HT) which indicates the superiority of SCA and non-additive genetic effects for these traits under HT and NT conditions (Tables 1 and 2).

A comparison of MSGCA/MSSCA and Baker's ratio showed that three traits BCW, CSP, and LV in both DSC and OSC, had almost equal values under HT and NT conditions. But MSGCA/MSSCA and Baker's ratios of PV trait under HT were several times more than NT condition with the superiority of GCA variance. Consequently, the additive effects of genes had more contribution in controlling this trait (Tables 1 and 2). Moreover, the higher temperature increased MSGCA/MSSCA and Baker's ratio in BCW and CSP, but the results were opposite for LV, indicating the environmental effects are high, and consequently, the portion of additive genetic variance decreased. While for CSP and PV, the additive genetic effects and for LV, the non-additive genetic effects played a significant role in both DSC and OSC genotypes; but, for BCW, the additive and non-additive genetic effects had different contributions in DSC and OSC genotypes.

3.3. General and specific combining ability

GCA and SCA of the studied traits under NT and HT conditions are presented in Table 3 for DSC genotypes and Table 4 for OSC genotypes. Among the Japanese lines, line 153 for BCW, LV, PV, and 1524 for PV showed positive and significant GCA under HT conditions. Line 1524 also had a significant GCA for CSP under both conditions; while, line 103 showed no significant GCA in terms of studied traits under both temperature conditions. Line 151 showed positive and significant GCA for BCW and LV under NT conditions. Among the crosses, 103 × 153 for BCW and PV, 103 × 1524 for CSP and 103 × 151 for PV had positive and significant SCA under HT (Table 3).

Among the Chinese lines, line 124 for all traits,104 for BCW and PV, and 154 for LV showed positive and significant GCA under HT. Among the crosses, 124 × 154 for all traits and 104 × 124 for all traits except for CSP showed the positive and significant SCA under HT conditions. Two crosses 124 × Y and 32 × 124 showed highly positive and significant SCA for LV. Line 124 had a major effect on the positive SCA (as a consequence of genes with non-additive effects). When one parent of the crosses was variety Y, it showed the nearly good capability of SCA for LV trait.

In summary, results indicated that none of the studied parents have significant and high GCA for all quantitative traits. However, among the DSC genotypes, lines 153 and 1524, and among OSC genotypes, lines

Table 1
Mean squares of the studied traits for DSC genotypes and some genetic parameters derived from the second Griffing's method under normal (NT) and high temperature (HT) conditions.

Source of Variation		df	Mean Squares							
			BCW		CSP		LV		PV	
Genotype (G)		**9**	581.36**		1.4**		126.48**		262.05**	
Temperature(T)		**1**	486388.88**		20.9**		14120.16**		46630.42**	
G × T		**9**	1027.91**		0.3**		148.46**		193.20**	
		NT	**HT**	**NT**	**HT**	**NT**	**HT**	**NT**	**HT**
GCA	**3**	592.02**	1430.75**	1.35**	2.16**	10.03**	185.66**	6.43 ns	628.88**
SCA	**6**	392.33*	733.93*	0.32*	0.49**	13.85**	333.06**	22.79*	260.75**
Diallel error	**18**	33.92	66.16	0.03	0.03	0.64	10.73	1.91	12.96
MS_{GCA}/MS_{SCA}		1.51	1.95	4.22	4.41	0.72	0.56	0.28	2.41
Baker ratio		0.75	0.80	0.89	0.90	0.59	0.53	0.36	0.83

ns, * and **: Not-significant and significant at 5% and 1% levels of probability, respectively.
GCA, general combining ability; SCA, specific combining ability; BWC, best cocoon weight; CSP, cocoon shell percentage; LV, larval viability; PV, pupal viability.

Table 2
Mean squares of the studied traits for OSC genotypes and some genetic parameters derived from the second Griffing's method under normal (NT) and high temperature (HT) conditions.

Source of Variation		df	Mean Squares							
			BCW		CSP		LV		PV	
Genotype (G)		**14**	3600.39**		2.16**		117.12**		267.36**	
Temperature(T)		**1**	709149.8**		40.71**		9435.14**		98347.55**	
G × T		**14**	1092.58**		0.77**		84.12**		91.02**	
		NT	HT	NT	HT	NT	HT	NT	HT	
GCA	**4**	811.07 ns	2553.84**	2.09**	2.49**	9.22**	99.96**	25.76 ns	461.89**	
SCA	**10**	1624.84**	3599.36**	1.13**	1.15**	11.98**	226.10**	111.00**	195.68**	
Diallel error	**28**	106.52	74.27	0.02	0.06	0.63	4.02	4.51	4.09	
MS_{GCA}/MS_{SCA}		0.50	0.71	1.85	2.17	0.77	0.44	0.23	2.36	
Baker ratio		0.50	0.59	0.79	0.81	0.61	0.47	0.32	0.83	

ns and **: Not-significant and significant at1% probability level, respectively.
GCA, general combining ability; SCA, specific combining ability; BWC, best cocoon weight; CSP, cocoon shell percentage; LV, larval viability; PV, pupal viability.

Table 3
General (GCA) and specific (SCA) combine ability of parents and hybrids for DSC genotypes under two temperature conditions (NT and HT).

	Parents and Crosses	BCW		CSP		LV		PV	
		NT	HT	NT	HT	NT	HT	NT	HT
GCA	**103**	3.42 ns	−3.83 ns	0.09 ns	−0.015 ns	−0.64*	−1.36 ns	−0.27 ns	−1.93 ns
	151	8.34 **	−9.22 **	−0. 40 **	−0.285**	0.94**	0.03 ns	−0.15 ns	−7.24**
	153	−0.83 ns	11.71 **	0.09 ns	−0.191**	−0.56 ns	4.44**	−0.46 ns	6.39**
	1524	−4.09 ns	1.34 ns	0.22 **	0.491**	0.25 ns	−3.06*	0.88 ns	2.78*
SCA	**103 × 151**	14.59 **	−19.08*	0.11 ns	0.048 ns	1.59*	−17.61**	3.72**	15.71**
	103 × 153	−1.39 ns	20.10 **	−0.32 ns	−0.412*	−1.07 ns	0.58 ns	1.28 ns	6.69*
	103 × 1524	−8.74 ns	−4.83 ns	−0.14 ns	0.402*	−0.21 ns	−5.75 ns	−2.35 ns	3.49 ns
	151 × 153	0.83 ns	12.86 ns	0.44 **	0.242 ns	−1.49*	5.08 ns	−3.70**	−2.95 ns
	151 × 1524	−7.68 ns	−8.91 ns	−0.36 *	−0.714**	−3.79**	5.58 ns	2.25 ns	−1.08 ns
	153 × 1524	18.29**	3.52 ns	−0.15 ns	0.122 ns	0.87 ns	−2.22 ns	−0.61 ns	−2.40 ns

ns, * and ** Not-significant and significant at 5% and 1% levels of probability, respectively.
BWC, best cocoon weight; CSP, cocoon shell percentage; LV, larval viability; PV, pupal viability.

104 and 124 had good combinatory under HT conditions. Additionally, the crosses 103 × 153 in the DSC group and 104 × 124 and 124 × 154 in the OSC group showed high specific combining ability for most of the studied traits, especially BCW and PV, under HT conditions.

4. Discussion

4.1. Comparison of GCA & SCA among genotypes

Introducing new varieties (lines) as superior parents are essential for producing commercial silkworm hybrids resulting from the crossing of Japanese and Chinese lines. In this research among the Japanese parents, lines 153 and 1524, with high GCA for BCW, CSP, and PV, may produce hybrids with positive and significant SCA. These traits not only are controlled by genes with additive effects but genes with non-additive effects also contribute to their controls. Ribeiro et al. [22] suggested that parents with higher GCA are better used in crossbreeding programs. Among the Chinese parents, line 124 had highly significant GCA for all studied traits under the HT condition. It means it has a high genetic capacity to transfer the additive genes to the future generation. Besides, this parent may be a specific combiner for the studied traits under HT. Virtually for all the crosses in which one of their parents was 124, the SCA was positive and significant. Considering SCA along with GCA may improve some of the silkworm traits. Hosseini Moghaddam and Etebari

Table 4
General and specific combine ability of parents and hybrids for OSC genotypes under two temperature conditions (NC and TC).

	Parents and Crosses	BCW		CSP		LV		PV	
		NT	HT	NT	HT	NT	HT	NT	HT
GCA	**32**	8.12*	−6.80*	0.004 ns	−0.006 ns	−0.52 ns	−1.82*	−0.65 ns	−3.12**
	104	0.85 ns	9.41**	−0.350**	−0.204*	−0.16 ns	0.87 ns	1.85*	5.74**
	124	−9.27*	8.97**	0.192**	0.597**	1.10**	2.06**	−0.13 ns	4.28**
	154	−0.77 ns	4.31 ns	−0.259**	−0.181*	−0.50 ns	1.70*	−0.06 ns	−2.20**
	Y	1.07 ns	−15.89**	0.414**	−0.206*	0.08 ns	−2.80**	−1.02 ns	−4.70**
SCA	**32 × 104**	4.36 ns	−8.69 ns	−0.779**	−0.817**	3.10**	2.86 ns	4.14*	−3.36 ns
	32 × 124	13.73 ns	1.92 ns	0.716**	−0.252 ns	1.34 ns	5.00**	3.62 ns	−3.15 ns
	32 × 154	−24.86*	−26.63**	0.520**	0.600*	−2.23**	−9.31**	−10.40**	−2.50 ns
	32 × Y	−2.08 ns	15.17 ns	0.257 ns	0.605**	−1.80*	5.02**	−2.72 ns	−3.66*
	104 × 124	35.19**	52.17**	−0.033 ns	−0.130 ns	1.15 ns	9.14**	4.27*	10.48**
	104 × 154	−35.81**	−37.02**	0.418**	0.738**	−1.09 ns	−0.83 ns	−6.30**	−10.41**
	104 × Y	−2.51 ns	24.16**	−0.836**	−0.627**	−2.33**	7.83**	1.82 ns	3.10 ns
	124 × 154	18.00 ns	40.48**	−0.100 ns	0.587*	−0.68 ns	3.64*	2.09 ns	13.29**
	124 × Y	−3.70 ns	4.31 ns	0.116 ns	0.172 ns	2.08**	7.31**	4.85*	3.42 ns
	154 × Y	−6.54 ns	−32.75**	0.543**	−0.576*	0.84 ns	−7.50**	−1.54 ns	−3.01 ns

ns, * and ** Not-significant and significant at 5% and 1% levels of probability, respectively.
BWC, best cocoon weight; CSP, cocoon shell percentage; LV, larval viability; PV, pupal viability.

[2] also reported high GCA for PV traits among Chinese genotypes, especially for line 110. They also confirmed that in a hybrid with high SCA, at least one of the parents had high gi (GCA effect). Farshadfar et al. [23] indicated that the parents with high GCA produce some hybrids with high SCA, leading to higher heterosis.

Sometimes two parents have no significant GCA, but their crosses may have significant and positive SCA. For example, under HT, lines 103 and 151 did not exhibit significant and positive GCA for either trait, but the cross 103 × 151 showed significant and positive SCA for the PV. Such a situation may be due to the interaction of non-additive effects of genes in their parents. Some genotypes showed a negative and significant GCA for one or more traits. Bayoumi [24] showed that crosses where the parents had a poor composition for grain yield with a negative GCA effect, but a high SCA effect, that could be due to the large genetic variation among the parents. Chen et al. [12] through a genome-wide association study of agronomic traits, indicated that the accumulation of superior GCA and SCA alleles is a crucial contributor to heterosis.

4.2. Gene action for studied traits

MSGCA/MSSCA and Baker's ratios are two parameters to show the type of gene action and show additive or non-additive gene effects of a trait [7,8]. The GCA and SCA also indicate the role of additive and non-additive (dominance and epistasis) gene effects, respectively [7, 21]. The ratio of additive to non-additive genes effects changed after exposure to temperatures, especially for viability traits (Tables 1 and 2).

A comparison between the two cocoon traits (BCW and CSP) indicated that the role of additive genes in the inheritance of CSP is more than in BCW which was consistent with the reports of Datta and Pershad [25], Singh et al. [26], and Sudhakara et al. [27]. Hosseini Moghaddam and Etebari [7] reported that the two Japanese silkworm lines, named 111 and 113, had significant GCA for BCW, cocoon shell weight, and CSP. Generally, parents with high positive GCA are suitable for a pedigree breeding program. The positive or negative values of GCAi indicate that parent i has a much higher or lower combining ability than other parents in the diallel scheme, hence a higher GCA means that the parent has a higher frequency of desirable alleles for the desired trait.

MSGCA/MSSCA and Baker's ratios for LV decreased at higher temperatures. The lower ratio of additive to non-additive genetic variance leads to lower efficiency of selection. However, it has a preference for crossbreeding based on the SCA values [12]. Due to the exothermic nature of insects, the metabolic rate of larvae depends on the temperature of silkworm rearing conditions. Therefore, many of their characteristics, particularly larval viability, change after exposure to high temperature for several days. This elevation above the normal physiological temperature leads to a profound alteration in gene expression, metabolism, respiration, and nervous and endocrine systems [28–30].

Pupal viability (PV) determined by pupation percentage is an important indicator of viability in silkworm. The pupation rate depends on the health of the larvae, as resistant and thermotolerant larvae usually progress to the pupal stage. The results of the PV data in this study showed that the role of additive genes in PV inheritance is greater than non-additive genes. This indicated that the selection of superior genotypes for PV leads to increased resistance or tolerance in the offspring of the parental moths. Consequently, it may apply to increase the thermotolerance of silkworms during a breeding program. Datta and Pershad [25], similar to the current study, observed that the additive genes have a vital role in the inheritance of pupation rate, while Ramesh Babu et al. [10] reported the role of both additive and non-additive gene effects in controlling this trait.

4.3. Gene-environment interaction

A comparative study of silkworm genetic parameters in both parental lines under normal and high-temperature conditions showed the importance of gene-environment interaction. The higher temperature changed the ranking of parents and crosses for both GCA and SCA in the DSC and OSC genotypes. This matter implies the importance of genetic × environment interactions in a silkworm breeding plan for improving thermotolerance. In other words, the interaction between genotypes and environmental temperature is effective in alterations of the combining ability and even the effect of genes. Based on GCA data, line 153 had a nearly good capability for both productivity and viability traits under HT, but had the lowest rank for these traits under NT condition. Moreover, line 153 did not have significant GCA under NT, but it had high and significant GCA for both viability traits and BCW under HT. In plant breeding, due to high interactions between the environment and genotype, especially under stress conditions, it is necessary to estimate the genetic parameters and even the combining ability of the cultivars and crosses under different environmental conditions [31].

5. Conclusion

The applied thermal treatment in this research showed that this could determine the genetic differences in thermotolerance among silkworm parental lines and combinations. Moreover, elevated temperature affected all the genetic parameters of viability traits more than productive traits. In this respect, there were no noticeable differences between the Japanese and Chinese genotypes. In the present study, the

nature of gene action was additive for CSP and PV, and non-additive for LV. Gene effects were the same in both the Japanese and Chinese genotypes. But, additive and non-additive genetic effects control BCW in the Japanese and Chinese genotypes, respectively. This indicated that the improvement of BCW in Chinese lines and LV in both Japanese and Chinese lines could not be managed by genetic selection procedures. This approach affirmed the benefit of genetic parameters in selecting superior silkworm parents; especially for those traits with a negative genetic correlation, such as tolerance (resistance) and productivity traits.

CRediT authorship contribution statement

Ahmad Asadpour Ardehjani: Investigation, Formal analysis, Writing – original draft. **Seyed Hossein Hosseini Moghaddam:** Supervision, Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Babak Rabiei:** Software, Verification. **Seyedeh Soheila Zarbafi:** Software, Formal analysis. **Seyed Ziaeddin Mirhoseini:** Methodology, Resources. **Shahla Nematollahian:** Investigation, Resources.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

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