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SEX CONTROL WITH MUTANT GENES IN SILKWORM (*BOMBYX MORI* L.): A REVIEW

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SUMMARY

The silkworm (*Bombyx mori* L.) belongs to an important category of insects that have succeeded in their domestication around 5,000 years ago and utilization by humans for their specific needs. The vital studies discovered artificial sex control, radiation-induced mutagenesis, reinterpretation of the heterosis, and genetic principles of the quantitative traits in the silkworm. In quality traits, the cocoon quality depends on the genotypes and their hybrids in the silkworm. Less development and use of high-productivity breeds and hybrids with better indicators of silk quality caused less boost in raw silk output, silk yield, and cocoon silkiness in the sericulture industry. For developing such types of breeds and hybrids, one must know how the various qualitative and quantitative traits reached inheritance through various gene actions in silkworms. The productivity characteristics of different sexes in such types of organisms vary, and mostly, one sex contributes to key economic traits. It follows from this that a comprehensive assessment of sex determination, as well as the expansion of its practical application in industrial sericulture, will contribute to improving economic efficiency in the future. This is the basis for increasing the scale of production in leading countries that develop silk production.

Keywords: Silkworm (*B. mori* L.), *B. mandarina, B. mori*, sex-marking, eggs, lethal, mutation, larva, cocoon

Key findings: This review focused on various past studies conducted on the sex genetics in silkworms (*B. mori* L.), which transpired in leading sericulture countries, such as China, India, Japan, Korea, Bulgaria, and Uzbekistan. The present worldwide research data will serve as a key source and opportunity for advancing future research on silkworms.

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INTRODUCTION

Globally, in silkworm (*Bombyx mori* L.), the raw cocoon production has reached 917,650 tons. Among the cocoon-producing countries, China, India, and Uzbekistan hold the leading position and accounted for 97.16% of the world's total cocoon production. The increasing demand for 3A-, 4A-, and 5A-grade silk fibers by the textile and light industry has heightened the need for developing high-quality silk-producing silkworm breeds and hybrids (Kizi *et al*., 2021).

In nature, the wild species *B. mandarina* L. has also gained preservation (Deng *et al*., 2019). Given the continuous selective breeding, the silkworm has undergone significant variations in its characteristics, leading to the identification of over 500 mutations to date.

The silkworm's reproduction occurs sexually with a diploid chromosome set of 28 pairs (Bakloushinskaya, 2024). Among them, the Z and W chromosomes in the gametes are responsible for sex determination. In the zygote, the ZZ chromosome pair leads to the development of a male, while the WZ chromosome pair results in a female embryo.

Currently, in silkworm genetics, one of the most crucial issues is determining the causes of sex ratio variation and developing the genetically controlled methods to selectively obtain the desired sex. Such type of genetic control is particularly important for the targeted implementation of economically valuable characteristics in the sericulture industry (Hăbeanu *et al*., 2023).

Silkworms (*Bombyx mori*), such as the migratory locust (*Locusta migratoria*), have also become food alternatives in some countries due to their high alpha-linolenic acid content (Ochiai, 2024).

MATERIALS AND METHODS

The development of sex control and regulation methods has ongoing implementation with the silkworm, as one of the first organisms (Biason-Lauber, 2010). By subsequent research experiments, it has become possible to produce silkworm eggs of a specific sex in the desired quantity.

For the experimental study, the selection of breeds and lines of the silkworm (*B. mori* L.) took place for rearing as a young instar at a temperature of 26 °C–27 °C with 70%–75% relative humidity. The adult worms had a temperature of 24 °C–25 °C with relative humidity of 65%–70% in a special cocoonery, using 1000 kg of mulberry leaves for one box of worms.

The imaging method using a camera to determine the sex of silkworm pupae is becoming increasingly popular in sericulture. Images of the frontal sex glands serve to aid in the gender classification process. For this purpose, Guo *et al*. (2022) developed an image exposure method with a correction algorithm to eliminate the problems with underexposure and overexposure of the images. With this approach, an accuracy of 90.5% was successful, which was about 7% higher than using the original images of the sex glands. He *et al*. (2023) also presented a comprehensive approach for determining the type and sex of silkworm pupae using machine and deep-learning methods utilizing pupal images. The said methodology allowed for obtaining the accuracy of the gender classification at the 99% level. The cocoon images taken by the camera also aided in gender classification, which avoided cutting the cocoon. The features of the cocoon shape entailed studies in the gender classification process (Raj *et al*., 2019; Mahesh *et al*., 2017).

RESULTS AND DISCUSSION

Sex determination at the egg stage

Strunnikov (1987) reported the translocation of the *+w2* gene to the W chromosome from the $+w_1$, $+w_2$, $+w_3$, $+w_4$, $+w_{os}$, and $+w_{o}l$ genes on the 10th autosome of silkworm (*B. mori* L.) that provided pigmentation in the egg's serous layer with a complementary gene effect. With the new genetic system having the $+w_2$ gene on the W chromosome, the female eggs were colored gray, while males were pale yellow on the 10th autosome due to the presence of the w_2w_2 recessive homozygous genes.

At the Plovdiv Agricultural University, Bulgaria, the research commenced on the combinations of sex-limited breeds in both egg and larval stages and non-sex-limited silkworm new commercial F1 hybrids of silkworm (*B. mori* L.) with the participation of sex-limited lines. They studied the crosses between the different silkworm individuals, such as T15/4 and TBV2/24, XT215/38 and TV3/2, and XT215/38 and B2/6, as well as other crosses, and compared them with the control hybrid (Super1 × Hessa2) (Petkov *et al*., 2004).

At the Shandong Sericulture Research Institute, China, the backcross breeding proceeded in F_1-F_3 generations using silkworm breeds with sex-limited eggs. In this experiment, Romanian breeds entailed crossing with the local non-sex-limited Jinsong breed. In determining the genotypes of the different generations, they performed a statistical analysis for the ratio between light yellow and gray eggs. For the F_1 generation, all the eggs emerged gray. Their studies further revealed that the ratio in light yellow eggs was 1/8 (59), and in gray eggs, the ratio was 7/8 (392) in the F_2 generation (Li-xia *et al*., 2006).

However, the balanced genes linked to Z-linked recessive embryonic non-allelic lethals help with the development of embryos in silkworms (Xuan *et al*., 2010). Mutations affecting egg color showed an association with either the eggshell or the serosal membrane. Numerous egg color mutants have succeeded in their identification, including white, brown, red, purple, orange, and rust-colored in silkworms and other insects (Komoto *et al*., 2009; Tatematsu *et al*., 2011). Their exact classification was as follows (Fan *et al*., 2006; Osanai-Futahashi *et al*., 2012): red (re), brown (b-4), orange (ci), and rust-colored (*re*/*reci*/*ci*) egg mutants. However, this study classified the lethal mutation in silkworm eggs into two categories (Chen *et al*., 2012):

1) Mutations that result in abnormal egg shape occur due to incomplete eggshell structure formation. These mutations influence the integrity and morphology of the eggshell, leading to irregularly shaped eggs.

2) Embryonic developmental anomalies emerged from mutations in key genes that play a crucial role during embryonic development. These mutations can disrupt normal growth, leading to defective organ formation, halted development, and even lethality at various life stages.

Sakai *et al.* (2013) focused on the expression patterns of *Bmdsx* (a double-switching gene in the cascade of sex determination in *B. mori*) and *BmIMP* (a gene expressed specifically in males involved in male-specific Bmdsx splicing) to study the key stages of sex determination in this insect. Recessive homozygous lethal egg mutants, known as 'Ming' (*l-em*), lose moisture from the eggs after emerging as the butterfly, causing them to convert into a triangular shape within one hour (Chen *et al*., 2009, 2012). The Bulgarian scientists examined 15 new silkworm lines based on the 10 primary economic and quantitative traits. As expected, their research showed the sex-limited lines during the egg stage (XT215/38 and Vratza2001) and at the larval stage (Vratza2002, Vratza2003, TBV2/24, and TV3/2) were very productive and kept the sexes completely separate in silkworms (Panayotov *et al*., 2015).

The silkworm takes 48 hours for eight genes with close linkage to the *re* gene to show the effects of recessive lethal genes in the *Fuyin-lre* gene (Chen *et al*., 2015). Chen *et al*. (2015) also identified the Fuyin-lre (fuyin-lethal red egg) mutant in silkworm germplasm. This mutant produced the red eggs and caused the death of embryos before reaching their full development.

Furthermore, the studies have shown the *semaphorin-1*a*-like* gene affects the *Fuyin-lr*e gene during embryonic development, which makes eggs red (Chen *et al*., 2020). The deep learning algorithm combined with THz images of silkworm eggs successfully demonstrates rapid recognition of the stages of development of silkworm eggs with a recognition accuracy of 98.5%. By combining optical and terahertz imaging, Xiong *et al.* (2021) further improved the accuracy of AI recognition of the developmental stages of silkworm eggs to 99.2%. Uzbek sericulture research has also contributed to research on sex-limited

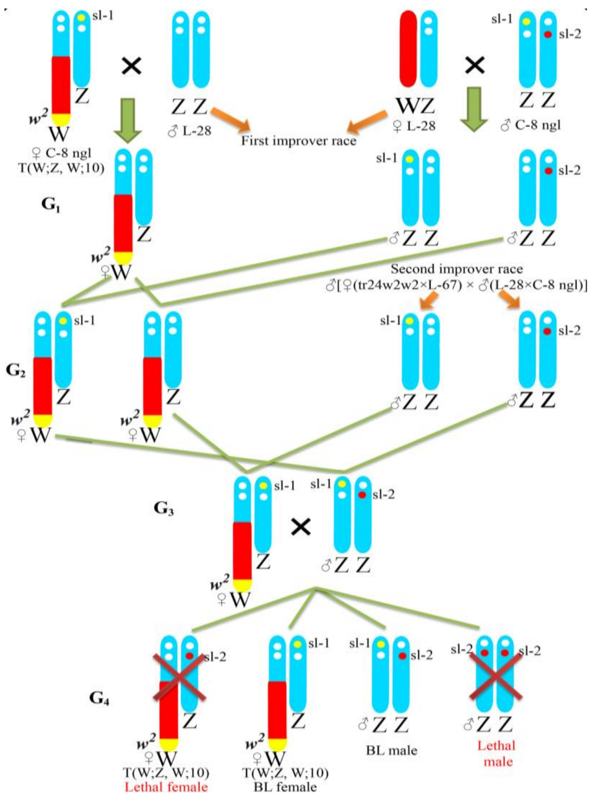

Figure 1. A scheme for improving the embryonic Z-lethal balanced line of mulberry silkworms that only provides male offspring (Nasirillaev and Abdikodirov, 2022).

silkworm breeds at the egg stage through various studies (Abdukadirov *et al*., 2024). Specifically, they have enhanced the sex-limited silkworm breeds to balance embryonic lethal genes (Figure 1) (Nasirillaev *et al*., 2023, 2025).

Sex determination at the larval stage

Strunnikov (1987) used the *os* gene as a marker to isolate Z-linked lethal genes in silkworms. Zhongyan *et al*. (2005) utilized the P3-4 secondary protein technology, which appeared associated with temperature-sensitive sex-linked 'reddening' in silkworms. Their study discovered the temperature-dependent *sch* gene-related sex-linked trait in silkworm embryos.

Petkov *et al*. (2005) studied how traits like cocoon weight and cocoon shell weight changed and incurred inheritance to interline combinations of Japanese and Chinese silkworm breeds that were sex-limited at the larval stage. Their findings showed that in the F_2 generation, positive transgression was evident for cocoon weight and cocoon shell weight. Using the sex-limited breed BL67 × CSR19, Raghavendra *et al*. (2006) determined the heterotic effects (59.78%) in relation to different economic traits, mainly the cocoon yield and cocoon weight in silkworms.

Marked silkworms during the larval stage using brown spots emerged from the combination of the general spot gene (+*p*) and the brown spot gene (+ℓ). In tests with brown-spot-marked breeds (C021 × LN010), the male hybrid cocoons had longer silk, faster reeling speed, finer silk, and more raw silk yield than the female hybrids (Guitian *et al*., 2006). Additionally, the researchers compared the Daepoongjam breed, which originated from Japanese lines and is sex-limited during the larval stage, with the Kumokjam breed, which came from Chinese lines (Kang *et al*., 2006).

Table 1. Marker genes used for identification of silkworm individuals with mutant genes (Kawaguchi *et al*., 2009).

Linkage group	Mutant gene	Marker gene (trait)
1	*Ge*	*os* (larval skin translucent)
		sch (newly hatched larvae reddish brown)
2	*gr-r*	*pM* (larval marking moricaud)
3	*sm* (and *smn*)	*Ze* (larval marking zebra)
5	*gap*	*oc* (larval skin translucent)
6	*ki*	*ECa* (larvae additional marking and legs)
	mgr	*ECa* (larvae additional marking and legs)
7	*sm-3*	*q* (larval marking with quail-like pattern)
12	*emi*	*C* (cocoon color yellow)
13	*sm-2*	*ch* (newly hatched larvae reddish brown)
15	*Se*	*bl* (larval marking solid black)
18	*gon*	*mln* (larval marking and moth color black)
19	*ki-2*	*nb* (larval breast narrow)
20	*vit*	*oh* (larval skin translucent)

According to Wang *et al*. (2007), developing new hybrid combinations was successful by continuously crossbreeding the sex-limited silkworm lines 1303 and 1302 during summer and autumn in Sichuan Province, China. An 18.39 kg cocoon yield resulted in a total silk length of 1180.5 m, a continuous reeling length of 968.8 m, an 82.04% reeling coefficient, and a 96.0 point silk purity score. The silkworm possesses several marker traits (Table 1), many of which are still widely applicable in experiments today. In fact, three extensively utilized gene markers surfaced as Z-linked in silkworms (Kawaguchi *et al*., 2009): *os* semi-transparent skin color, *sch* chocolate-colored body in newly hatched larvae, and *e* elongated-shaped larval body.

The mass production of male scallops and sex-restricted larvae as hosts reached confirmation for the development of *Isaria tenuipes* synnemata (Ji *et al*., 2012). Among the tested silkworm species, Hansaengjam males showed the highest pupation rate (98.7%). The use of Bulgarian silkworm breeds (19, 1013, Magi 2, and Lea 2) served to develop the new hybrids by crossing them directly, as well as with other hybrids. The hatching rates of these new hybrids were high; the 5th instar larvae were healthy, developed normally, and also proved resistant to diseases. Clear sex markings existed on the larvae and cocoons, the pupation rates were very high, and the raw cocoon yield per box of eggs was also leading (Panayotov *et al*., 2015). The development of two new silkworm hybrids led to the identification of the larvae by crossing silkworm breeds with limited sex and breeds with high endurance (Tzenov *et al*., 2022). Under the conditions of the provocative silkworm rearing regime, the silkworm hybrid HB2 × Nova-2 showed significantly higher viability (81.17%).

The Uzbek Research Institute of Sericulture has long been engaging in silkworm genetic studies (Nasirillaev *et al*., 2023). The World Collection of Mulberry Silkworms brings together the different breeds around the world, including 120 breeds from 12 ecological zones, becoming a unique gene pool of silkworms. The world's collection of mulberry silkworms served as a genetic basis and resource to solve various problems in sericulture. These problems comprised the development of high-quality silkworm hybrids, getting hybrids that guarantee 100% purity of genotypes, and sex identification of parthenoclone silkworms at the larval stage. Overall, the breeds were diverse and varied from each other in color, origin, structure, shape, and quality traits (Figure 2).

Sex determination at the cocoon stage

With the extra C locus (yellow cocoon shell) (Hirayama *et al*., 2006), the recessive locus (yellow), and its inhibitor (+I) locus, the gene *Sy* displayed a connection to the yellow color

Figure 2. Sex-limited larval-marking strains of silkworm (*B. mori* L.).

(Banno *et al*., 2005). Female silkworms carrying the *Sy* gene can be easily noticeable by their yellow hemolymph and yellow cocoons. The Y locus from the second autosome entailed joining to the W chromosome in *Sy* females, which means that the segment has been moved. The Y locus absorbs carotenoids from the midgut into the hemolymph (Sakudoh *et al*., 2007, 2010).

According to Liu *et al*.'s (2013) selection, the variety Shuhuang No. 1 was yellow-golden, and the males and females bore differentiation by the structure and color of the cocoon. In this silkworm breed, the cocoon filament length was about 1,115.0 m, and the non-broken filament was 882.95 mm long, with an estimate of 79.15% of the total length.

Zhu and Zhang (2014) used silk glands, blood, and the shells of six yellow-red cocoons as breeding material in their experiments. In studies of cocoon color, confirming the presence of tissue-specific delivery of certain carotenoids was by the genetic information about the silkworm (*B. mori* L.), and the identified mutant genes appeared responsible for cocoon color, such as yellow blood (y), yellow cocoon (C), and flesh cocoon (F) (Tsuchida and Sakudoh, 2015).

By screening the cocoons under 365 nm UV light, the cocoons displayed distinct fluorescence: male cocoons appeared yellow, while the female cocoons were white. The accuracy coefficient of the sex-marking method reached 98% (Zhang *et al*., 2016). Past studies conducted on the sex-limited silkworm breeds during the cocoon stage derived the biparental Hanbyeolnue breed from the Japanese Jam-319 and Chinese Jam-320 breeds (Kee-young *et al*., 2016). The Hanbyeolnue breed demonstrated a higher cocoon-spinning coefficient than the control breeds Hanseangjam and Hwangbojam. However, its cocoon shell weight was relatively low.

Visually distinguishing silkworms based on easily recognizable external traits is one of the traditional methods used in sericulture (Sahara *et al*., 2016). Using this method for sex control, the researchers have successfully developed a fluorescent, cocoon-colored hybrid generation named 'Yingguang × Chunyu' (Hu *et al*., 2020). The identification of bioactive peptides, as performed by *de* novo sequencing in a yellow cocoon, had seven candidate peptides identified with a high content of essential antioxidant amino acids (His, Phe, Trp, and Tyr vs. Arg) in the sequence. Moreover, the prediction of biological activity of some peptides succeeded in using bioinformatics databases (Yakul *et al*., 2020).

Fang *et al.* (2020) performed high-resolution quantitative feature locus (QTL) mapping for four cocoon yield features. Identified QTLs totaled 11, including one yield-enhancing QTL in wild silkworms. By integrating population genomics and transcriptomic analysis with QTLs, some favorable genes were notable, including 14 genes related to domestication and 71 genes with different expression (DEG) in the transcriptome of fifth-instar larval silk glands in *B. mori* and *B. mandarina*.

Molecular mechanisms in the formation of green silkworm cocoons have been progressing but have not received full studies before (Lu *et al*., 2023). Their results demonstrated that five out of seven genes emerged responsible for sugar transport and incurred specific duplication in the family Bombycidae. The WZ bivalent structure was evident in the *Sy* line, which is a radiation-induced mutant that showed sex marking during the cocoon stage (Kakihara *et al*., 2024). Chandrakanth *et al*. (2024) reported breeding silkworm mutants using various mutagens and gene editing tools and explored the future prospects through mutation breeding to improve sericulture.

CONCLUSIONS

In sericulture, raising male silkworms on a large scale considerably increases the raw silk production as compared with females. The artificial sex control methods in silkworms enable the absolute production of hybrid eggs in industrial silkworm breeding. Moreover, by solving the artificial sex control issue in silkworms, production could shift entirely to raising only male silkworms. As a result, the time-consuming and labor-intensive process of manually sorting cocoons by sex, currently with limited accuracy, would no longer be necessary.

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