Genetic analysis of quantitative trait loci for cocoon and silk production quantity in *Bombyx mori* (Lepidoptera: Bombycidae)

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Key words. Lepidoptera, Bombycidae, *Bombyx mori*, cocoon and silk production quantity, genetic linkage map, QTL mapping

Abstract. Silk production quantity is the most economically important characteristic of the domesticated silkworm moth, *Bombyx mori*. It is controlled by multiple loci. The cocoon and silk production quantity of silkworm strains Jingsong and Lan10 have significantly diverged. A backcross population (BC) was bred using Jingsong and Lan10 as parents to identify quantitative trait loci (QTLs) for silk quality. In this research, a genetic linkage map of the silkworm was constructed using the BC mapping population. The map contained 85 sequence-tagged site markers, 80 simple sequence repeat markers, and 16 single nucleotide polymorphisms. A linkage map was constructed from the data, which consisted of 181 markers distributed over 28 expected linkage groups and spans 2147.1 cM in total length. Fourteen QTLs were detected for cocoon filament length, whole cocoon weight, pupae weight, filament weight, and cocoon shell weight. The 14 QTLs were distributed in 5 linkage groups (linkage groups 1, 14, 18, 23 and 25) based on the constructed linkage map. In addition, five QTLs, which had the highest logarithm (base 10) of odds (LOD) values, were located on the first chromosome, three of which located at the same region in linkage group 1. These results represent an important foundation for the map-based cloning of QTLs and marker-assisted selection for improving the silk quality of economically important silkworm strains.

INTRODUCTION

The silkworm moth, *Bombyx mori* L., has been domesticated over the past 5,000 years from the wild progenitor, *Bombyx mandarina* (Moore) (Xiang, 1991). The silkworm is important for genetic research as well as an economically important insect. More than 400 mutations have been identified in silkworms, and more than 1,000 silkworm strains are maintained as genetic resources (Ito et al., 2009; Meng et al., 2009). It is also a key model species of the order Lepidoptera, the second largest group of holometabolous insects, which includes many beneficial species and the most destructive agricultural pests.

Cocoon quality is very important because it influences sericulture yield and the selection of silkworm lines for silk production. Currently, modern techniques such as transgenesis and marker-assisted selection are the most effective ways of improving silk properties and they are applied widely in silk production (Lu et al., 2004). Molecular markers are powerful tools for genome analysis; they are applied comprehensively in the mapping functional genes and the molecular breeding of *B. mori* (Li et al., 2005b; Sreekumar et al., 2011). The construction of linkage maps is a fundamental aspect of gene analysis. It provides guidelines for marker-assisted selection and map-based cloning. An accurate linkage map is also necessary for further genetic analysis. In recent years, several linkage maps for *B. mori* have been constructed based on various molecular marker techniques, including restriction fragment length polymorphism (RFLP) linkage mapping (Shi et al., 1995), random amplification of polymorphic DNA (RAPD) linkage grouping (Promboon et al., 1995; Yasukochi, 1998), amplified fragment length polymorphism (AFLP) frame mapping (Tan et al., 2001; Lu et al., 2004), simple sequence repeat (SSR = microsatellite) linkage mapping (Miao et al., 2005), and single nucleotide polymorphism (SNP) (Yamamoto et al., 2006; Sreekumar et al., 2011). In many cases, maps from different parental populations and species have been integrated (Yasukohi et al., 2005; Zhan et al., 2009). However, some maps have relatively low density and could not be used effectively as guides for breeding *B. mori*.

In the present study, STS (sequence-tagged sites), SSRs, and SNPs were adopted to construct a linkage map of silkworm to map quantitative trait loci (QTLs) for silk quality because of their good transferability, high reproducibility, and co-dominant inheritance. These markers are particularly suitable for high-throughput genotyping, which allows the rapid analysis of hereditary monogenetic traits and QTLs (Maddox et al., 2001; Ihara et al., 2004; Lee et al., 2005; Huang et al., 2006). A linkage group was constructed and the QTLs were localized based on the cocoon filament length, cocoon shell weight, whole cocoon weight, pupae weight, cocoon filament weight, and cocoon shell ratio.

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MATERIAL AND METHODS

Silkworm strains

Significant hereditary and ecological divergence occurred in the genes responsible for the silk quality of silkworm strains Jingsong (JS) and Lan10 (L10), which are preserved in the Sericultural Research Institute, Chinese Academy of Agricultural Sciences. The JS strain is used widely in various applications and its silk properties are advantageous for silk production. In contrast, L10 has high stress resistance, but produces smaller cocoons and has poor silk-producing properties. Additional crosses between strains from different origins may increase the mapping efficiency of markers because of the increased potential for genetic diversity (Zhan et al., 2009). A backcross population (BC1) was bred from JS and L10 parents. The 93 male individuals were selected randomly from the resulting BC1 population.

Silk quality collection

The fresh cocoons were weighed before dipping in 0.6% sodium silicate solution (Na2SiO3) for 60 min at 24°C. The cocoons were transferred in pure water and then the silk fibers were reeled. The length of the cocoon filament was measured during reeling. The silk fibers were washed and dried after measurement. The cocoon filament weight and pupal weight of each cocoon were also determined. The cocoon shell weight was calculated using the following formula:

Cocoon shell weight = whole cocoon weight – pupal weight – weight of castoff skin inside the cocoon.

DNA preparation and PCR amplification

DNA was extracted from the parent moths, and pupae of the F1 progeny, and the 93 BC1 progeny as described by Xia et al. (1998). The purity and concentration of the prepared DNA were determined with a BioPhotometer Plus (Eppendorf, Hamburg, Germany) and diluted with 1× TE buffer (10 mM Tris-HCl, 1 mM EDTA), pH 8.0.

A total of 1120 pairs of STS/SNP primers were designed based on the silkworm genome database (The International Silkworm Genome Consortium, 2008), and 428 pairs of SSR primers were selected from the established SSR linkage groups.
The 93 DNA samples were diluted to a final volume of 10 ng/µl with sterilized double-distilled water and stored at 4°C prior to amplification using the polymerase chain reaction (PCR). The PCRs and the amplification using the SSR markers were performed according to Miao et al. (2005). The PCRs were performed via STS markers with an initial 3 min period at 94°C (denaturation), followed by 35 cycles of denaturation at 94°C in 30 s, 30 s of annealing at 56°C, 70 s of extension at 72°C; and a final extension time of 5 min at 72°C. The PCR products were electrophoresed using 2% agarose gel to determine their lengths. PCR products of the SNP markers were purified and then sequenced using an ABI 3130xl sequencer to detect SNPs.

Linkage map construction and data analysis

A genetic linkage map was constructed using MapMaker/Exp V3.0 (Lincoln et al., 1992). The QTLs for silk length, whole cocoon weight, pupal weight, silk weight, and cocoon shell weight were scanned using MapMaker/QTL v1.1b. Whole chromosomes were scanned every 2 cM for the presence of QTLs. Positions with LOD ≥ 2 were considered QTLs (Basten et al., 1994).

RESULTS

Phenotypic variations of five characteristics in the BC1 population

Whole cocoon weight, cocoon filament length, cocoon shell weight, cocoon filament weight, and pupal weight showed patterns of continuous and normal distributions, which indicate the quantitative inheritance of these characteristics (Fig. 1).

Genetic relationship among different characters of cocoon and silk production quantity

The genetic relationships among cocoon and silk qualities were analyzed. All characteristics were positively...
correlated (Table 1). The genetic correlations between silk weight and cocoon shell weight, as well as between whole cocoon weight and pupal weight, were extremely high (0.999 and 0.996, respectively). The lowest correlation was between cocoon filament length and pupal weight (0.699). These results suggest that the QTLs for some characteristics are linked.

**Construction of molecular linkage maps**

A total of 182 markers were polymorphic between the two parents JS and L10. The DNA polymorphisms from the 93 individuals of the BC1 population were amplified. The genotyping results of the 181 polymorphic primers (Supplement 1), including 85 STS markers, 80 SSR markers, and 16 SNPs accorded with the 1 : 1 ratio of the population. These markers were analyzed using Mapmaker/Exp (Version 3.0) and assigned into 28 linkage groups (Fig. 2). The total genetic distance was 2147.1 cM. The mean distance between adjacent markers was 8.5 cM.

**QTL analyses for cocoon and silk production quantity**

A total of 14 QTLs were detected for cocoon filament length, whole cocoon weight, pupal weight, cocoon fila-
ment weight, and cocoon shell weight using Mapmaker/QTL (Version 1.1b) (Table 2). The QTLs were distributed in 5 linkage groups (linkage groups 1, 14, 18, 23 and 25). Interestingly, the 5 QTLs located on the first chromosome had the greatest logarithm (base 10) of odds (LOD) values, which meant they were highly reliable, 3 of which located at the same region in linkage group 1 (232S1 and S0106). These findings indicate that some silk traits are significantly correlated with each other.

The clustered distribution of the QTLs is in accordance with the genetic relationship among these traits, which in turn is consistent with the relationships among whole cocoon weight, cocoon shell weight, and pupal weight. These findings highlight the significant relationship between the traits for cocoon production quantity, and explain why the highest QTLs were mainly detected in the same linkage group.

**DISCUSSION**

The two parent silkworm strains used to construct the linkage map have numerous genetic differences, which facilitated the expression of numerous extensive polymorphism markers leading to the construction of a molecular linkage map. The silkworm is one of the lepidopteran species in which no genetic exchange occurs in females (the heterogametic sex) during the formation of female gametes. Using the BC1 population as the mapping population circumvented this problem and allowed analysis using mapping software. In our research, the silk fibers were reeled from the cocoons while the pupae were still alive. Data, including the cocoon filament length data and cocoon filament weight, were recorded to utilize live pupae to extract DNA for linkage and QTL analysis. In addition, JS is one of most economically important strains and it has been used in silk production for nearly 30 years. Therefore, the study has a more direct applied importance to sericulture and the production of silk-related products.

The silkworm has attracted increasing attention as an important genetic and biomaterial resource. China has a long history of sericultural research and an accumulation of genetic data on silkworms. Xia et al. (2004) reported whole-genome shotgun sequencing and provided public access to the assembled silkworm genome data. In 2008, The International Silkworm Genome Consortium published the fine scale genome sequence of the silkworm, which is necessary for molecular genetics research in this insect. Cocoon quality is an important characteristic of silkworms; however, the genes of this insect are more difficult to map than single Mendelian factors (Zhan et al., 2009).

A total of 14 QTLs for the silk quality characteristics were identified. Cocoon filament length, cocoon shell weight, whole cocoon weight, pupal weight, and cocoon filament weight, which are controlled by multiple genes, are the economically significant characteristics of importance to the silk industry. The present investigation pro-

<table>
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<th>Trait</th>
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<th>Linkage group</th>
<th>Mark interval</th>
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**TABLE 1. Comparative genetic correlations of cocoon quality in Bombyx mori.**

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<td>Cocoon filament length</td>
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<tr>
<td>Pupal weight</td>
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<td>Cocoon filament weight</td>
<td>0.896</td>
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<td>Cocoon shell weight</td>
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**TABLE 2. Information of QTLs detected from BC1 in Bombyx mori.**
vides an excellent foundation for the map-based cloning of major genes that control silk production. Compared with previous research on QTLs for cocoon quality (Lu et al., 2004; Li et al., 2005a; Sima et al., 2005), the locations of the QTLs in the chromosomes were not identified because of the difficulties involved in duplicating both the AFLP or RAPD results. In research, the exact location of the STS, SSR, and SNP markers were determined from the silkworm fine scale genome sequence, and these markers can be duplicated in other silkworm strains. Our results are thus consistent with those by Zhan et al. (2009). Firstly, the detected QTLs were distributed mainly in groups 1 and 23. Secondly, the LODs of the QTLs in group 1 are extremely high. These results indicate that the data are accurate and repeatable. Both results show that one or more QTLs on chromosome 1 affect silk and cocoon quality. Our results also show that all of the QTLs on chromosome 1 are located at a region of 290 kb, and there were 12 predicted genes in that region. We are now trying to clone all the genes and compare them between Jingsong and Lan10. The findings by Zhan et al. (2009) indicate two QTLs for cocoon shell ratio in groups 18 and 19; however, we only detected two QTLs at the same locus and which controlled whole cocoon weight and cocoon shell weight on chromosome 18, but did not contribute to cocoon shell ratio, and no other QTLs were detected for cocoon shell ratio either. This result could be attributed to the fewer markers available in those groups, which were insufficient for detecting QTLs. Although we constructed a linkage map that covers all 28 chromosomes of the silkworm, the marker density was still low, and many QTLs that control cocoon and silk production quantity characters were not detected. More SSR and STS/SNP markers will be designed in future studies to finely map the QTLs and allow map-based cloning thereby leading to a better understanding of the mechanism of silk production in silkworm).

ACKNOWLEDGEMENTS. This project was supported by National Natural Science Foundation of China (grant No. 30972145, 30825007), and National Science Foundation of Jiangsu Province (BK2009220). We thank H. Loxdale for his helpful editorial comments on the manuscript.

REFERENCES


Received August 17, 2012; revised and accepted November 28, 2012

**Supplement 1. The Primer Sequences in the Linkage Groups.**

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SSR – Simple Sequence Repeat, PCR products size polymorphism; STS – Sequence tag site, PCR products size polymorphism; SNP – Single nucleotide polymorphism.

**Table:**

| SNP | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS | SSR | STS |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| T28214 | T28213 | S2816 | T27207 | S2714 | T27204 | T26305 | S2624 | T2505 | T2501 | S2529 | C2501 | T2419 | T2415 | T2407 | T2320 | T2318 | S2323 | T2301 | C2218 | S2002 | T2020 | T1905 | T1904 |
| TACCGATACACGACTCGCATA | TGTTTGCTGTGGCGGTAGTG | GGCAAAGACTGGATGTGAGATGTAA | TGCCTCTGTAGTTGTTACTTGTGA | CCAGCGAACGTAGGGGACA | AAACATCAAACAGTTAGGTGGGC | TCCTTCAGACCACAGCATTCATT | CGGGGACGGTGCTCCTTAC | CAGGACATACGCACGGAGTC | GTAGCCACTCACAGCCAGAC | TGAAGGTCTTGCCGAAGTTATGA | CACGGTCACGGCATTCTCTT | TTTAGTCATTCACAAAACAAACAAG | ACTGTCGATACATCGTCGCCAACAA | ACATCATGAGAATCGAAATAGT | TATAAGGTTTTGGTATTGTTGGAAG | TGCCTTCAACACACACACTTACT | SCP6 | TSC5 | TSC4 | TSC3 | TSC2 | TSC1 | TSC0 | TSC-1 |
| nscaf2797 | nscaf2797 | nscaf3071 | nscaf3098 | nscaf3071 | nscaf3097 | nscaf2330 | nscaf1071 | nscaf2815 | nscaf2823 | nscaf2822 | nscaf2822 | nscaf2822 | nscaf2822 | nscaf2823 | nscaf2962 | nscaf3026 | nscaf3027 | nscaf1962 | nscaf3089 | nscaf2795 | nscaf2789 | nscaf2789 | nscaf2768 | nscaf2768 |
| 1101kb | 582kb | 86kb | 442kb | 4032kb | 3204kb | 935kb | 1829kb | 1711kb | 963kb | 1172kb | 213kb | 1200kb | 5155kb | 4843kb | 294kb | 1493kb | 4208kb | 213kb | 5454kb | 294kb | 1493kb | 4208kb | 213kb | 5454kb |

* SSR – Simple Sequence Repeat, PCR products size polymorphism; STS – Sequence tag site, PCR products size polymorphism; SNP – Single nucleotide polymorphism.