Microsatellite analyses reveal the sources and genetic diversity of the first-introduced Q-biotype population and the well-established B-biotype populations of *Bemisia tabaci* in China

CHU Dong1,2, LI Xian-Chun3, ZHANG You-Jun2,*

1. Key Laboratory of Integrated Crop Pest Management of Shandong Province, College of Agronomy and Plant Protection, Qingdao Agricultural University, Qingdao, Shandong 266109, China; 2. Department of Plant Protection, Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences, Beijing 100081, China; 3. Department of Entomology, College of Agriculture and Life Sciences, University of Arizona, 410 Forbes, PO Box 210036, USA

Abstract: The invasive *Bemisia tabaci* (Gennadius) (Hemiptera; Aleyrodidae) biotype Q (hereafter referred to as Q) was first detected in China in 2003, it gradually displaced the well-established biotype B (hereafter referred to as B) and has become the dominant whitefly in China by 2008. The goal of the current study was to provide insight into the rapid invasion of *B. tabaci* Q and the domination of *B. tabaci* Q over B in China. In this study we used 11 microsatellite loci to analyze and compare the genetic structure of one Q and 11 B introduced populations collected in China in 2003 with those of two native Q populations from Spain, one invasive Q population and one native B population from Israel, and five introduced B populations from Spain, the USA, and Australia. The results revealed that the first *B. tabaci* Q population in China was probably introduced from the western Mediterranean region rather than from the eastern Mediterranean region. The 11 *B. tabaci* B populations in China, however, might be the progeny of multiple primary introductions from the source region or represent secondary spread from an invaded region. Chinese B had greater genetic diversity than B from Spain, Australia, and the USA, suggesting that Chinese B might have more than one source. Both the first-introduced Chinese Q population and the well-established B populations have not experienced a substantial decrease in genetic diversity relative to their source populations, suggesting minimal bottleneck or founder effects. Genetic diversity for the invasive Q population was greater than the B populations in China, which might contribute to Q’s strong ecological adaptability to the new environments in the introduced regions and thus might explain why it has rapidly spread and displaced the well-established B populations in China.

Keywords: *Bemisia tabaci* biotype Q; *Bemisia tabaci* biotype B; microsatellite marker; genetic diversity; invasion biology

1 INTRODUCTION

The sweet potato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera; Aleyrodidae), is a serious pest in many agricultural systems worldwide. It damages crops in the field and in greenhouses primarily by feeding on phloem and by transmitting plant viruses (Brown et al., 1995). The pest has been considered as a species complex comprising at least 36 biotypes (De Barro et al., 2011). Among them, biotypes B and Q (hereafter referred to as *B. tabaci* B and Q, respectively) are the most invasive and destructive biotypes, and have recently been regarded as Middle East-Asia Minor 1 and Mediterranean species, respectively (Dinsdale et al., 2010; De Barro et al., 2011). In the past 20 years or so, *B. tabaci* B has spread from its native region, the Middle East-North Africa, to more than 50 countries. In the last decade, *B. tabaci* Q has spread from the Mediterranean region to more than 10 countries (De Barro et al., 2011) including China (Chu et al., 2006), Japan (Ueda and Brown, 2006), Mexico (Martinez-Carillo and Brown, 2007), and the USA (Dennehy et al., 2010).

*Bemisia tabaci* B was introduced into China in the mid-1990s (Luo et al., 2002) whereas *B. tabaci* Q was first recorded in the country (Yunnan Province) in 2003 (Chu et al., 2006). After its introduction, *B. tabaci* Q spread and displaced the well-established B populations in many provinces,

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作者简介：褚栋，男，1977 年生，山东莘县人，博士，教授，主要从事生物入侵研究。E-mail：chinaudong@sina.com
*通讯作者 Corresponding author, E-mail: zhangyi@mail.cas, net.cn
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and it has been the dominant whitefly in both field and greenhouse agricultural systems since 2008 (Chu et al., 2010; Teng et al., 2010; Pan et al., 2011). The displacement of B. tabaci B by Q indicated that B. tabaci Q has performed better than B in field and in greenhouse systems in China. Several studies have also suggested that application of insecticides and host adaptability might help B. tabaci Q displace B in agricultural systems (Mujíz, 2000; Mujíz and Nombela, 2001; Nombela et al., 2001).

While the effects of ecological factors on the competitive displacement of one species by another have been well studied (Reitz and Trumble, 2002), few studies have examined the genetic diversity and differences between invasive competitors (Sakai et al., 2001). Such is the case for the invasive B. tabaci B and Q. The genetic and geographic diversity of the first introduced B. tabaci Q population and its well-established B. tabaci B competitor in China have not been investigated (Simón et al., 2007; Tsagkarakou et al., 2007). In this study, we used 11 microsatellite loci to analyze the genetic diversity and structures of one Q population and 11 B populations collected in China in 2003, as well as two native Q populations from Spain, one invasive Q population and one native B population from Israel, and five introduced B populations from Spain, the USA, and Australia, respectively. The data obtained suggest that greater genetic diversity of B. tabaci Q may explain why it has been rapidly displacing B. tabaci B in China.

2 MATERIALS AND METHODS

2.1 Whitefly populations

From September to October of 2003, living adults of B. tabaci were collected from representative locations throughout China and placed in tubes containing 95% ethanol. At each location, at least 100 adults were collected from different plant species. The genetic group or species of the whitefly populations was determined based on mitochondrial cytochrome oxidase I (mtCOI) marker by Chu et al. (2006) (Table 1). The Yunnan Q population (YN) is the earliest detected Q population, which was also the only Q-biotype population in China in 2003.

2.2 DNA extraction, PCR, and microsatellite loci

Individual whiteflies were ground for genomic DNA extraction following the procedures of Frohlich et al. (1999). In De Barro et al. (2003), 8–15 individuals were used in the analyses. In our study, 16 individuals from each whitefly population were analyzed using 11 polymorphic microsatellite loci (BEM06, BEM11, BEM15, BEM18, BEM23, BEM25, BEM31, BEM37, BEM40, BT-b53, and BT-b103) as described by De Barro et al. (2003) and Tsagkarakou and Roditakis (2003) (Table 2). The PCR reaction conditions for each locus were 35 cycles of denaturation at 94°C for 1 min, annealing at temperatures listed in Table 2 for 1 min, and extension at 73°C for 1 min.

2.3 Electrophoresis and silver staining

The PCR product was mixed with 6 × loading buffer, denatured for 3 min at 96°C, loaded on a 7% polyacrylamide-urea gel, and subjected to electrophoresis in 0.5 × TBE at 50 W. After electrophoresis, the gel was silver stained as follows: the gel was fixed in 10% acetic acid, washed with ultrapure water, and incubated for 30 min in a solution of silver nitrate (1 g/L) and was washed and developed in a sodium carbonate/formaldehyde solution (30 g/L Na2CO3, 0.15% formaldehyde, and 200 μL of 0.002% thiosulfate sodium) after incubation. The reaction was stopped with 10% acetic acid, and the gel was washed with water and air-dried at room temperature. The DNA-size ladder (EcoR I/Hind III λDNA) (Promega, USA) was used to determine the microsatellite alleles.

2.4 Genetic structure analysis

The alleles for each locus among B. tabaci Q or B populations were calculated, and the allele-sharing among B. tabaci Q or B populations was estimated. For analysis of the genetic differentiation of B. tabaci Q and B populations, neighbor-joining (NJ) dendrograms were constructed using Da distance (Nei et al., 1983) in the software package POPULATIONS (Langella, 1999) with 1 000 bootstrap replicates. The individuals with the same alleles in the 11 microsatellite loci were labeled with two numbers following the population designation; for example, SPIQ1 [3] refers to three individuals with the same allele as the first individual (SPIQ1) in the SPIQ population, and the “1” following the Q indicates that it was the first individual detected in that population. Genetic diversities of B. tabaci Q and B populations were evaluated in POPGENE version 1.31 (Yeh et al., 1999). The difference in the genetic diversity of Q (Spanish and Yunnan populations) and B was analyzed with an independent sample t-test. Because Israeli Q population belongs to Q2 clade while Spanish and Yunnan populations belong to Q1 clade (Chu et al., 2008a), the Israeli population was not used to estimate the difference in the genetic diversity of Q and B.
### Table 1 Characteristics of *Bemisia tabaci* populations used in this study

<table>
<thead>
<tr>
<th>Population site</th>
<th>Population code</th>
<th>Individual code</th>
<th>Host plant</th>
<th>Genetic group</th>
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<tr>
<td>Native populations of Q</td>
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</tr>
<tr>
<td>Spain</td>
<td>SPIQ</td>
<td>SPIQ1 – 16</td>
<td>Solanum lycopersicum</td>
<td>Q (2)</td>
</tr>
<tr>
<td>Spain</td>
<td>SP2Q</td>
<td>SP2Q1 – 16</td>
<td>Solanum lycopersicum</td>
<td>Q (1)</td>
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<tr>
<td>Introduced population of Q</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kunming, Yunnan, China</td>
<td>YN</td>
<td>YNI – 16</td>
<td>Euphorbia pulcherrima</td>
<td>Q (2)</td>
</tr>
<tr>
<td>Israel</td>
<td>ILQ</td>
<td>ILQ1 – 16</td>
<td>Gossypium hirsutum</td>
<td>Q (2)</td>
</tr>
<tr>
<td>Native populations of B</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Israel</td>
<td>ILB</td>
<td>ILB1 – 16</td>
<td>Gossypium hirsutum</td>
<td>B (2)</td>
</tr>
<tr>
<td>Introduced populations of B</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Haidian, Beijing, China</td>
<td>Bji</td>
<td>BJI – 16</td>
<td>Cucumis sativus</td>
<td>B (3)</td>
</tr>
<tr>
<td>Haidian, Beijing, China</td>
<td>Blii</td>
<td>BLI1 – 16</td>
<td>Capsicum annuum</td>
<td>B (3)</td>
</tr>
<tr>
<td>Haikou, Hainan, China</td>
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<td>HuiN1 – 16</td>
<td>Solanum melongena</td>
<td>B (1)</td>
</tr>
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<td>Zhengzhou, Henan, China</td>
<td>HeiN</td>
<td>HeiN1 – 16</td>
<td>Ipomoea batatas</td>
<td>B (7)</td>
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<tr>
<td>Nanjing, Jiangsu, China</td>
<td>JS</td>
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<td>Gossypium hirsutum</td>
<td>B (1)</td>
</tr>
<tr>
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<td>SDZZ1 – 16</td>
<td>Cucumis sativus</td>
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</tr>
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<td>Shanghai, China</td>
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</tr>
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<td>B (1)</td>
</tr>
<tr>
<td>Hangzhou, Zhejiang, China</td>
<td>ZJ</td>
<td>ZJ1 – 16</td>
<td>Gossypium hirsutum</td>
<td>B (1)</td>
</tr>
<tr>
<td>Spain</td>
<td>SPB</td>
<td>SPB1 – 16</td>
<td>Solanum lycopersicum</td>
<td>B (2)</td>
</tr>
<tr>
<td>California, USA</td>
<td>CL</td>
<td>CL1 – 16</td>
<td>Euphorbia pulcherrima</td>
<td>B (1)</td>
</tr>
<tr>
<td>Texas, USA</td>
<td>TX</td>
<td>TX1 – 16</td>
<td>Solanum lycopersicum</td>
<td>B (1)</td>
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<td>Arizona, USA</td>
<td>AZ</td>
<td>AZ1 – 16</td>
<td>Hibiscus rosinianus</td>
<td>B (1)</td>
</tr>
<tr>
<td>Australia</td>
<td>AUS</td>
<td>AUS1 – 16</td>
<td>Euphorbia pulcherrima</td>
<td>B (1)</td>
</tr>
</tbody>
</table>

* 1 – 16 refers to the 16 individuals; Genetic group classification was determined based on the mtCOI marker, and the number of the individuals assessed is indicated in parentheses.

### Table 2 Primers of the microsatellite loci used in the study

<table>
<thead>
<tr>
<th>Microsatellite locus</th>
<th>Primer sequences (5’ – 3’)</th>
<th>Annealing temperature (°C)</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>BEM06</td>
<td>F: TTACACTTAAACCAAGAACT</td>
<td>55</td>
<td>De Barro et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>R: GATGCCTTATGATATATACT</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>R: CAAAATAATACACATTATA</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>R: CATTCTTTGCGGTGTTAGATT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BEM23</td>
<td>F: CGACGTGTCGCGGCTGCT</td>
<td>60</td>
<td>De Barro et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>R: CCGGTTTTATCATGTCCTCGT</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>R: TGAACAAATAGAAATAAAGG</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BEM31</td>
<td>F: AAGAATCTGACGGACCAAAC</td>
<td>60</td>
<td>De Barro et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>R: GTCTATTGTGGACTGGCA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BEM37</td>
<td>F: TGACGACTTGCAGGTGCA</td>
<td>60</td>
<td>De Barro et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>R: TGGACGGCAACAGACGCAA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BEM40</td>
<td>F: TGGAGAAATTGATAAAGTGCA</td>
<td>60</td>
<td>De Barro et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>R: GAAAGCTGGGAGCCTGGTGCA</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>R: AAGCCTTACGTCTACTAAAGCC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BT-b103</td>
<td>F: GC7CAACCGCAAATACCTCAC</td>
<td>50</td>
<td>Tsagkarakou and Roditakis (2003)</td>
</tr>
<tr>
<td></td>
<td>R: AACTCTAAAGCGAGCGCTGAA</td>
<td></td>
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</tbody>
</table>
3 RESULTS

3.1 Allele-sharing among B. tabaci Q or B populations

Analysis of the 11 microsatellite loci revealed 14 alleles in the invasive Israeli Q population ILQ, 22 alleles in the native Spanish Q population SPIQ, and 21 alleles in the native Spanish Q population SP2Q. The introduced Yunnan population YN had 20 alleles, of which 9, 15, and 14 alleles could also be found in the ILQ, SPIQ, and SP2Q populations. In other words, the Yunnan population YN shared 45.0%, 75.0% and 70.0% of alleles with ILQ, SPIQ and SP2Q populations, respectively. Eighty-five percent of the alleles in the Yunnan population (YN) could be found in the Spanish populations.

Results revealed 16 alleles in the native Israeli B population ILB. The introduced B populations from Arizona, Texas, California, Spain, and Australia had 16, 14, 16, 14, and 16 alleles, respectively. The introduced B populations from 11 Chinese populations had 13 – 17 alleles. The Chinese populations shared 66.7% – 92.3% of alleles with the native Israeli population. In addition, the 11 Chinese populations shared 70.6% – 100%, 70.6% – 100%, 64.7% – 92.9%, 60.0% – 81.3%, and 64.7% – 85.7% of alleles with B populations from Arizona, Texas, California, Spain, and Australia, respectively (Table 3).

<table>
<thead>
<tr>
<th>Table 3 Allele-sharing among B. tabaci B populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bji (16)</td>
</tr>
<tr>
<td>ILB (16)</td>
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<tr>
<td>AZ (16)</td>
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<tr>
<td>TX (14)</td>
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<tr>
<td>CL (16)</td>
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<tr>
<td>SPB (14)</td>
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<tr>
<td>AUS (16)</td>
</tr>
</tbody>
</table>

The value in parentheses following the population designation in column and row headings indicates the number of alleles detected for the 11 microsatellite loci. The values in the table cells indicate the number (and percentage) of shared alleles; the percentages were calculated with respect to the number of alleles in the Chinese populations listed in the column headings.

3.2 Genetic differentiation of B. tabaci Q or B populations

The neighbor-joining (NJ) dendrograms based on the microsatellite data revealed that at least three groups existed in the populations of B. tabaci Q in this study (Fig. 1). All individuals from Yunnan (YN) clustered into Group I. Group II only included the individuals from Israel (ILQ). Group III included some individuals from Spain (SPIQ, SP2Q).

For populations of B. tabaci B, the NJ dendrograms based on the microsatellite data revealed at least six groups existed in this study (not shown). Group I included the individuals from Beijing (Bji, BJii), Shandong (SDTA, SDZZ), Jiangsu (JS), Shanghi (SH), Xinjiang (XJ), Hainan (HaiN), Shanxi (SX), Spain (SPB1), and the USA (AZ, TX, CL). Group II included the individuals from Beijing (Bji), Henan (HeN), Zhejiang (ZJ), Spain (SPB), and Australia (AUS). Group III included the individuals from Beijing (Bji, BJii), Shandong (SDTA, SDZZ), Jiangsu (JS), Xinjiang (XJ), Henan (HeN), Shanxi (SX), Israel (ILB), Australia (AUS), and the USA (CL, TX, AZ). Group IV included the individuals from Xinjiang (XJ), Shandong (SDTA), and the USA (AZ, CL, TX). Group V included the individuals from Beijing (Bji) and Israel (ILB). Group VI included individuals from Hainan (HaiN), Shanxi (SX), Beijing (BJii), Xinjiang (XJ), Shandong (SDTA), Henan (HeN), Israel (ILB), and the USA (TX, AZ). The NJ dendrograms of B. tabaci B based on the microsatellite markers showed that the individuals from Israel, Spain, Australia, or USA populations existed in three, two, two, and four groups, respectively. Individuals from Chinese B populations existed in all the six groups.

3.3 Genetic diversity of B. tabaci Q and B populations

Among the B. tabaci Q populations (Table 4), the Israeli population had the lowest genetic diversity while the Spanish SPIQ population had the highest genetic diversity. The value of Na (average number of alleles detected per locus) in SPIQ, SP2Q, ILQ, and YN populations was 2.000, 1.909, 1.364, and 1.818, respectively. The genetic diversity of both of the native Spanish populations was higher while that
of the invasive Israeli population was lower than that of the introduced population in Yunnan, China.

The Na values of the B. tabaci B populations ranged from 1.1818 to 1.5455 (Table 4). The genetic diversity of three of the introduced populations in China (Blji, JS, and SDZZ) was higher than that of the native population from Israel (ILB). Only a few of the introduced populations in China seem to have experienced moderate bottleneck or founder effects; for example, the Na value of the Shanxi population (SX) was the lowest in this study. The B. tabaci Q population in China also seems not to have experienced a significant bottleneck or founder effect because its Na value was nearly as high as the Na values of native populations in Spain and was higher than that of the introduced Q population in Israel (Table 4).

Based on the Na values, the genetic diversity of Q populations (Spanish and Yunnan populations, belonging to the Q1 subclade) was higher than that of B populations whether the populations were considered from across the world or only from China (P < 0.05).

4 DISCUSSION

4.1 Potential sources of B. tabaci Q and B introduced in China

The allele-sharing analysis and NJ dendrogram suggest that all B. tabaci Q individuals of the first Q population found in Yunnan, China, originated from a western Mediterranean population (e.g. Spanish
<table>
<thead>
<tr>
<th>Population</th>
<th>Diversity index</th>
<th>Microsatellite locus</th>
<th>Average η SE</th>
</tr>
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<tbody>
<tr>
<td>B. tabaci Q</td>
<td></td>
<td></td>
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<tr>
<td>SP1Q</td>
<td>Na</td>
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<tr>
<td></td>
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<td>0.000</td>
</tr>
<tr>
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<td>SP2Q</td>
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Na: The average number of alleles per locus; H0: The observed heterozygosity; He: The expected heterozygosity.
rather than from an eastern Mediterranean population (Israeli Q). This inference is consistent with Chu et al. (2008a), which also concluded that B. tabaci Q is a genetically differentiated species with at least two subspecies, labeled as Q1 and Q2. The Israeli Q populations belong to the Q2 subscale, and the Spanish Q and Chinese Q populations belong to the Q1 subscale. Using the mtCOI and microsatellite markers, Chu et al. (2011) concluded that the introduced Q populations in Shandong Province of China originated mainly in the western Mediterranean region (Morocco and/or Spain). These studies might indicate that the Q populations that subsequently established in Shandong and other provinces of China probably have spread from Yunnan Province, where ornamental plants are cultured and transported throughout China.

Recent research has revealed that, for many different kinds of organisms, only a subset of native populations become invasive (Winkler et al., 2008; Lee and Gelembiuk, 2008). The accumulated data indicate a similar phenomenon for B. tabaci Q that the invasive Q in China evidently originated only from the western Mediterranean rather than from the eastern Mediterranean (Chu et al., 2011).

Based on the worldwide mtCOI network, De Barro and Ahmed (2011) demonstrated that the invasive B. tabaci B might have originated in Israel. Our analysis of microsatellite markers shows, however, that the alleles within the Israeli B population in this study do not include all the alleles within the Chinese B populations or the populations from Spain, Australia, and USA. Our data therefore suggest that Chinese B populations might have multiple origins, which might be a consequence of multiple introductions or secondary spread from an invaded region. If Israel is the only original source, the introduced B populations in China might come from different Israeli populations. Some Chinese populations and those from Spain, Australia, and the USA have a high percentage of allele-sharing, suggesting that they might have the same origin.

4.2 Genetic characteristics of introduced B. tabaci Q and B populations

The comparison of the genetic diversity of Q and B will be helpful for unraveling their distribution patterns in China. The genetic diversity index of the introduced Yunnan Q population (YN) was not substantially smaller than those of the native Spanish Q populations, suggesting that bottleneck or founder effects in China were not severe. Similarly, the genetic diversity indexes of the introduced B. tabaci B populations from China, Spain, the USA, and Australia were not much smaller than that of the presumptive original Israeli population. However, the genetic diversity was generally higher for the introduced Q population in Yunnan than for the introduced B populations in China. Comparative studies of the genetic diversity of Q and B based on RAPD or ISSR markers (Chu et al., 2007, 2008b) also revealed that Q populations have higher diversity than B populations.

Many studies have shown that Q has greater resistance to neonicotinoids or pyriproxyfen than B (Horowitz et al., 2005; Dennehy et al., 2010). In addition, Q populations are also superior to B populations in colonizing some host plants (Muñiz, 2000; Muñiz and Nombela, 2001; Nombela et al., 2001), and Q populations may also have a greater ability to adapt to a wider range of plant species and cultivars than B populations (Iida et al., 2009). The current study suggests that greater genetic diversity, which would presumably facilitate adaptation to the invaded environment, may explain why B. tabaci Q has displaced B. tabaci B in China (Chu et al., 2010; Teng et al., 2010; Pan et al., 2011).

Recent studies revealed that B populations in Israel dominated in open field while the invasive Q populations were mainly found in greenhouses and nethouses (Kontsedalov et al., 2012), which is obviously different from the status in China where Q populations dominate in both open field and protected systems (Chu et al., 2010; Teng et al., 2010; Pan et al., 2011). Our study revealed that the genetic diversity of invasive Q population from Israel was lower than that of B population from Israel, which is different from that of Q and B populations in China and thus might explain the different invasive pattern of Q population in the two invaded regions.

Acknowledgements

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基于微卫星标记对中国 Q 型烟粉虱早期入侵种群与 B 型烟粉虱种群的遗传结构分析

褚 栋1,2, 李显春3, 张友军2,*

1. 中国农业科学院农业资源与环境研究所，北京 100094；2. 中国农业科学院蔬菜花卉研究所

摘要：2003 年首次在云南昆明发现 Q 型烟粉虱 Bemisia tabaci (Gennadius) 传入中国。随后几年时间内，它在许多省份逐渐取代了 B 型烟粉虱种群。2008 年后，Q 型烟粉虱基本上成为中国多数省份区的优势生物型。为了进一步揭示 Q 型烟粉虱在中国快速扩散以及取代 B 型烟粉虱的遗传学基础，本研究运用 11 个微卫星位点分析并比较了 2003 年中国云南昆明 Q 型烟粉虱入侵种群及其他地区的 11 个 B 型入侵种群。以色列 1 个 Q 型入侵种群，以色列 1 个 B 型土著种群，以及西班牙、美国与澳大利亚的 5 个 B 型入侵种群的遗传结构。结果表明，中国 Q 型烟粉虱早期种群（云南昆明种群）可能来自于西部地中海地区。中国 B 型烟粉虱种群遗传多样性高于西班牙、澳大利亚、美国 B 型种群，中国 B 型可能存在多次传入或某个混合种群的再次传入。相对而言，中国 Q 型烟粉虱早期入侵种群与 B 型烟粉虱种群遗传多样性并没有明显降低，表明 Q 型与 B 型

关键词：烟粉虱 Q 型；烟粉虱 B 型；微卫星标记；遗传多样性；入侵生物学

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