Limited Gene Flow Among Cydia pomonella (Lepidoptera: Tortricidae) Populations in Two Isolated Regions in China: Implications for Utilization of the SIT

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Limited gene flow among *Cydia pomonella* (Lepidoptera: Tortricidae) populations in two isolated regions in China: Implications for utilization of the SIT

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Abstract

 Codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), a highly invasive species, recently became established in the Hexi Corridor, which is a long narrow passage area with many oases surrounded by deserts and tall mountains in Gansu province, China. The corridor is an important temperate fruit growing region in northwestern China as well as a natural barrier to prevent *C. pomonella* from invading other fruit growing areas of the country. Since the codling moth was firstly reported, pome fruit damage in this corridor has been severe. The sterile insect technique (SIT) is considered a possible effective control tactic for integration in a future area-wide integrated pest management (AW-IPM) program against *C. pomonella* in the corridor. Knowledge of population genetics and more specifically of genetic differentiation and gene flow patterns may be important for developing AW-IPM strategies that include the SIT. In the current study, we collected *C. pomonella* samples from 8 populations distributed across 2 adjacent regions in the Hexi corridor that are geographically separated by stone deserts and high mountains. Eight microsatellite loci were used to investigate the genetic diversity, structure and differentiation of these 8 populations. Significant genetic differentiation was found between populations of each of the 2 regions, whereas populations within each region showed a similar genetic structure, demonstrated by higher *N_A* and lower *F_ST* values for population pairs within the same region than in pairs between the regions. Our findings indicate limited gene flow of *C. pomonella* between the 2 regions, which suggests that SIT can be implemented to control the pest in the Hexi Corridor of China.

Key Words: codling moth; fixation index (*F_ST*); migrants; molecular markers; genetic differentiation; genetic structure

Resumen

El gusano de la manzana, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), una especie altamente invasora, recientemente se estableció en el Corredor Hexi, que es una área larga y estrecha de paso con muchos oasis rodeado de desiertos y montañas altas en la provincia de Gansu, China. El corredor es una región templada importante donde siembran frutas en el noroeste de China, así como una barrera natural para prevenir la invasión de *C. pomonella* en otras áreas donde siembran frutales en el país. Desde que se informó de la presencia del gusano de la manzana, el daño de frutas de huevo en este corredor ha sido grave. Se considera la técnica del insecto estéril (TIE) una posible táctica de control eficaz para la integración de un programa de manejo integrado de plagas en un área amplia (MIP-AA) en el futuro contra el *C. pomonella* en el corredor. El conocimiento de la genética de poblaciones, y más específicamente de los patrones de diferenciación genética y de flujo de genes pueden ser importantes para el desarrollo de estrategias MIP-AA que incluyan el TIE. En el presente estudio, se recolectaron muestras de *C. pomonella* de 8 poblaciones distribuidas en 2 regiones adyacentes al corredor de Hexi que están separadas geográficamente por los desiertos de piedra y las altas montañas. Se utilizaron ocho loci de microsatélites para investigar la diversidad genética, la estructura y la diferenciación de estas 8 poblaciones. Se encontró una diferenciación genética significativa entre las poblaciones de cada una de las 2 regiones, mientras que las poblaciones dentro de cada región mostraron una estructura genética similar, demostrado por un valor mayor *N_A* y un valor menor *F_ST* para los pares de la población dentro de la misma región que en pares entre las regiones. Nuestros hallazgos indican un flujo genético limitado de *C. pomonella* entre las 2 regiones, lo que sugiere que la TIE puede ser implementada para controlar la plaga en el Corredor de Hexi de China.

Palabras Clave: gusano de la manzana; índice de fijación (IDF); migrantes; marcadores moleculares; diferenciación genética; estructura genética

The codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is one of the most destructive pests of pome fruits (apple, pear and quince) and walnut orchards in most temperate regions of the world (Barnes 1991; Willett et al. 2009; Vreyesen et al. 2010). It is generally assumed that the codling moth originated from southeastern Europe from where it spread around the world as a result of expanding apple

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tain and deserts (Zhang 1957). Although C. pomonella has been the object of both internal and external quarantines in China, it still managed to spread from Xinjiang Province to the neighboring Hexi Corridor of Gansu Province in 1989 as a direct result of dense traffic and commercial transport (Shi et al. 2008). Thereafter, it took 20 years for codling moth to spread along the Hexi Corridor, which is composed of a 1,000 km long string of oases along the northern edge of the high Tibetan Plateau, and is bordered on the north by the Gobi Desert and the grasslands of Outer Mongolia (Fig. 1). Irrigated by water from the snow-capped mountains, the oases of the Hexi Corridor are the main farming regions that supply most of the food including fruit to the arid Gansu Province. Apple and pear trees are planted widely in the oases and in the last several decades approximately 40% apple losses due to the codling moth have been reported in the corridor (Zhai et al. 2010).

Intensive spraying of chemical insecticides during the growing season is the main measure for controlling C. pomonella in China. However, the continuous use of broad-spectrum insecticides has not only become a serious concern for the environment and human health, but has also resulted in increased insecticide resistance of codling moth and in the loss of natural pest control (Bloem & Carpenter 2001; Reyes et al. 2009; Vreysen et al. 2010). The use of more environment-friendly pest management strategies such as the sterile insect technique (SIT) would have several advantages for the control of C. pomonella in China (Liu et al. 2012). The SIT is highly species-specific and friendly to the environment (Klassen 2005; Vreysen et al. 2010), and has been used successfully against a number of pest species, such as the Mediterranean fruit fly, Ceratitis capitata (Wiedemann) (Diptera: Tephritidae), the melon fly, Bactrocera cucurbitae (Coquillet) (Diptera: Tephritidae), the pink bollworm, Pectinophora gossypiella (Saunders) (Lepidoptera: Gelechiidae), the false codling moth, Thaumatotibia leucotreta (Meyrick) (Lepidoptera: Tortricidae), the New World screwworm, Cochliomyia hominivorax (Coquerel) (Diptera: Calliphoridae) and the tsetse fly Glossina austeni Newstead (Diptera: Glossinidae) (Tan 2000; Vreysen et al. 2000; Wyss 2000; Bloem & Carpenter 2001; Hendrichs et al. 2005; Klassen & Curtis 2005; Parker & Mehta 2007). The successful suppression of the codling moth in the Okanagan Valley of British Columbia, Canada for the last 20 years is arguably one of the most successful AW-IPM programs that integrated the SIT with other control tactics (Klassen 2005; Bloem et al. 2007b; Vreysen et al. 2010). Given that the invasion of the Hexi Corridor by the codling moth is fairly recent, and that the oases of the corridor are isolated, the SIT could be considered as a potential part of an effective strategy of managing codling moth in the Hexi Corridor (Li 2013).

Population genetics data and more specifically genetic differentiation and gene flow patterns of target insect populations can provide sound baseline information to develop efficient insect pest-management strategies including the SIT (Klassen 2005; Krafsur 2005; Timm et al. 2006; Chen & Dorn 2010; Vreysen et al. 2010; Zheng et al. 2013). These data can reveal the distance over which members of a given species typically disperse, estimate the degree of genetic isolation of target populations from each other and from untargeted populations, determine whether a sub-population or sibling species exists, and establish the origin of outbreaks or reintroductions (Krafsur 2005; Chen & Dorn 2010). In practice, if immigration of gravid female moths into a given agro-ecosystem can be kept to a minimum, the SIT would be more effective. As moths released in AW-IPM programs with a SIT component should be capable of mating with females from different geographic regions, it is important to know to which degree an insect species migrates between different field populations (Krafsur 2005; Chen & Dorn 2010). Moreover, knowledge on the genetic differentiation and rate of gene flow among populations can provide an estimate of the rate of invasion or reinvansion of eradicated areas by unchallenged populations (Krafsur 2005).

Fig. 1. Sampling regions and locations of Cydia pomonella in Hexi Corridor of China. (I) map of China, the Hexi Corridor is indicated in the dash box; (II) enlarged map of Hexi Corridor, the 2 sampling regions are indicated as (A) Jiuquan region and (B) Zhangye region; (III) enlarged map of the sampling regions and sampling locations. The sampling locations includes JiuTa (JJT), YinDa (JYD), XiDong (JXD), and ZongZai (JZZ) of the Jiuquan Region, and Luo Tuocheng (ZLT), Niliaying (ZNJ), MinYong (ZMY) and XiaoMan (ZXM) of the Zhangye Region.

Although the Hexi Corridor has always been considered an important natural barrier that prevents C. pomonella from invading the more southerly major fruit growing areas, C. pomonella has been established in several oases of the Hexi Corridor. However, the genetic differen-
tiation and gene flow of the different codling moth populations is still unknown. In this study, we collected *C. pomonella* samples from 2 geographically adjacent regions (Jiuquan and Zhangye) in the Hexi Corridor separated by unpopulated tall mountains and stone deserts serving as a geographic barrier. Using microsatellites and the method developed by Men et al. (2013) we aimed to characterize the genetic structure and gene flow pattern of the *C. pomonella* populations in the 2 regions. The findings are of interest for the development and implementation of a rational AW-IPM strategy that includes a SIT component.

### Materials and Methods

#### INSECT SAMPLING

*Cydia pomonella* was sampled in 2 isolated adjacent regions (Jiuquan and Zhangye) of the Hexi Corridor (Fig. 1). Adult moths were sampled with 6 pheromone traps deployed for 5 consecutive days in apple orchards. Traps were replaced every 24 h and relocated to a new site within each sublocation. This resulted in a total of 30 traps per sublocation. To avoid sibling sampling, only one individual was taken from each trap and preserved in a 10 mL Falcon tube filled with ethanol. The same sampling procedure was repeated 3 times in each sublocation during the apple growing season giving a total of 45–65 moths collected in each sublocation. Around half of the samples of each region were randomly selected for genotyping in the current study. We use the term “population” for *C. pomonella* samples from a single orchard (sampling unit). Samples from 4 locations in each of the 2 regions were used (Fig. 1).

#### DNA EXTRACTION AND MICROSATTELITE GENOTYPING

Genomic DNA was extracted from 8–10 mg of insect material using the Easy Pure™ Genomic DNA Kit (TransGen Biotech Co., Ltd., Beijing, China) according to the manufacturer’s protocol for animal tissues. DNA was eluted in 200 μL of ultra pure water and stored at −20 °C. All samples were genotyped at 8 polymorphic microsatellite loci (*Cp1.62, Cp2.39, Cp2.P, Cp3.56, Cp3.169, Cp3.K, Cp4.56 and Cp4.129*) isolated from *Cydia pomonella* (Franck et al. 2005). Three primers, which included the forward primer synthesized with an M13 (−21) at the 5’ end, the reverse primer and the FAM fluorescent dye labeled M13 (−21) primer, were used for amplification each microsatellite locus in a PCR reaction (Schuelke 2000). PCR reactions for the 8 loci were carried out in a mix of 12.5 μL 2 × Taq Master Mix (containing 0.05 U/μL Taq DNA Polymerase, 2 × Taq PCR Buffer, 3 mM MgCl₂, and 400 μM dNTP mix) (Beijing CoWin Biotech Co, Ltd, Beijing, China), 0.2 μM of each forward primer, 0.8 μM of each reverse primer, 0.8 μM M13 primer, and 1 μL genomic DNA (10–30 ng/μL). The PCR involved denaturation at 95 °C for 10 min, followed by 30 amplification cycles consisting of 95 °C for 30 s, 45 s at the primer-specific annealing temperature (57 °C for *Cp1.62, 60 °C for *Cp2.39, 58 °C for *Cp2.P, 60 °C for *Cp3.56, 54 °C for *Cp3.169, 48 °C for *Cp3.K, 60 °C for *Cp4.129 and 56 °C for *Cp4.56*), 72 °C for 45 s, then 8 cycles consisting of 95 °C for 30 s, 53 °C for 45 s and 72 °C for 45 s, and a final step at 72 °C for 10 min. Genotyping was carried out on an ABI3730XL automated DNA sequencer (Applied Biosystems, Foster City, California, USA) and GENEMAPPER version 4.0 (Applied Biosystems, Foster City, California, USA).

#### DATA ANALYSIS

Null allele and frequency were checked with Micro-Checker version 2.2.3 (Van Oosterhout et al. 2004). FSTAT Version 2.9.3.2 (Goudet 2001) was utilized for calculating the number of alleles (*Na*), and for calculating the mean allelic richness per locus (*R*) for all the sampling populations with a rarefaction method that adjusted the observed number of alleles to a common size for each population sample. Observed heterozygosity (*Hₑ*) and expected heterozygosity (*Hₑ*) were calculated using microsatellite analyzer (MSA) version 3.15 (Dieringer & Schlötterer 2003). The Hardy-Weinberg equilibrium (HWE) and *P* value for Hardy-Weinberg equilibrium (HWE-P) were calculated using GENEPOP version 4.0.1 (Rousset 2008).

Analysis of molecular variance (AMOVA), inbreeding coefficients (*Fₛ*), fixation index among groups (*Fₛₛ*), fixation index among populations within groups (*Fₛₛ*) and fixation index within populations (*Fᵢᵢ*) were performed using ARLEQUIN version 3.5.1.2 (Weir & Cockerham 1984; Excoffier & Lischer 2010). We calculated the number of migrants moving between each pair of populations (*Nₑ*) per generation as (*1/Fₑₑ* − 1/4) (*Excoffier & Lischer 2010; Munshi-South 2012). For AMOVA, samples were arbitrarily grouped according to the collection regions: (1) Jiuquan and (2) Zhangye. The matrices of genetic distance (*Fₑₑ* (1 − *Fᵢᵢ*)) and the geographic distance (*In*) between 8 *C. pomonella* populations were used to test isolation by distance (IBD) with 10,000 permutations (Mantel 1967). The IBD analysis was performed using the ZT software package (Bonnet & Van der Peer 2002).

The Bayesian clustering approach was used to estimate the population structure in STRUCTURE version 2.3.3 (Pritchard et al. 2000) with a burn-in period of 50,000 iterations and 1 million Markov chain Monte Carlo (MCMC) repetitions. We set the number of the cluster (*K*) from 1 to 10 and repeated 10 times, and the most likely number of clusters was calculated by delta *K* methods (Evanno et al. 2005). The graphical display of genetic structure was produced by DISTRUCT (Rosenberg 2004). A neighbor-joining (NJ) tree based on Nei’s genetic distances among populations was constructed by MEGA version 5 (Tamura et al. 2011).

### Results

#### GENETIC DIVERSITY

A total of 214 *C. pomonella* individuals were genotyped across all 8 microsatellite loci. All 8 loci were polymorphic and the number of alleles at each locus ranged from 7 to 25. The frequency of null alleles ranged from 0.049 to 0.241, which is similar to previous reports of *C. pomonella* (Franck et al. 2007; Men et al. 2013) and is typical for Lepidoptera (Dakin & Avise 2004; Meglécz et al. 2004). The average number of alleles per population ranged from 4.3 to 6.9 (Table 1). The allele richness value per locus per population was between 4.07 and 6.64. The value of observed heterozygosity (*Hₑ*) was between 0.190 and 0.569, and the expected heterozygosity (*Hₑ*) values ranged from 0.311 to 0.534, whilst the expected heterozygosity (*Hₑ*) values ranged from 0.111 to 0.569. Three populations revealed significant departures from HWE, together with large mean values of the inbreeding coefficient (*Fᵢᵢ*), ranging from 0.422 to 0.543. This indicates the existence of heterozygote deficiencies in these 3 populations. The genetic indices indicated that the 8 populations showed similar genetic diversity over the 8 microsatellite loci.

#### GENETIC DIFFERENTIATION

AMOVA results (Table 2) indicated significant genetic differentiation at the 3 hierarchical levels (*Fᵢᵢ* = 0.097, *P* < 0.001; *Fₛᵢᵢ* = 0.085, *P* < 0.001; *Fₛₛ* = 0.173, *P* < 0.001) with populations grouped according to the 2 sampling regions. Although the proportion of explained variance was low (9.7%), significant genetic differentiation existed among populations from the 2 regions.

Gene flow over generations as revealed by *Nₑ* is shown in Table 3. The results indicate that *Nₑ* values within populations from Jiu-
The flight capacity of a large proportion of a *C. pomonella* population is low, and only a small proportion of a population is capable of long distance flights (Schumacher et al. 1997; Dorn et al. 1999). In the current study, AMOVA analyses among the 8 populations from the 2 sampling regions showed significant genetic differentiation. Based on cluster analysis, populations sampled in the 2 regions differed in genetic structure, and they formed 2 distinct clades in the NJ tree. The codling moth has traditionally been regarded as a sedentary insect (Keil et al. 2001; Timm et al. 2006; Thaler et al. 2008; Chen & Dorn 2010), and the limited gene flow implied by the significantly different population genetic characteristics of the 2 separate regions is likely the result of the limited dispersal capacity of *C. pomonella*. This was verified by mark-release-recapture studies in the field and flight mill experiments in the laboratory (Schumacher et al. 1997; Dorn et al. 1999; Keil et al. 2001). Our results are consistent with findings in South Africa, northern Italy and Switzerland, where limited gene flow and significant genetic differentiation between different local geographic regions were found (Timm et al. 2006; Thaler et al. 2008; Chen & Dorn 2010).

**Table 2. Analysis of molecular variance of populations from Jiuquan and Zhangye regions of the Hexi Corridor.**

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Variance components</th>
<th>Percentage of variation</th>
<th>Fixation Indices</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among groups</td>
<td>1</td>
<td>59.502</td>
<td>0.22430</td>
<td>9.69</td>
<td>F_{ST} = 0.097</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>Among populations within groups</td>
<td>6</td>
<td>68.072</td>
<td>0.17712</td>
<td>7.65</td>
<td>F_{ST} = 0.085</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>Within populations</td>
<td>420</td>
<td>803.793</td>
<td>1.91379</td>
<td>82.66</td>
<td>F_{ST} = 0.17</td>
<td>P &lt; 0.001</td>
</tr>
</tbody>
</table>
Similar results were also reported in the closely related species with small flight capacity, *Grapholita molesta* (Timm et al. 2008; Torriani et al. 2010; Kirk et al. 2013a, b; Zheng et al. 2013), as well as in aphids (Lodake et al. 1993; Miller et al. 2003).

We found similar genetic diversities and similar genetic structures within each region in this study. In the current analysis, \( N_m \) values were greater and \( F_{st} \) values were smaller within population pairs from the same region in comparison to those found in population pairs from the 2 regions, indicating limited gene flow between the regions. Dispersal caused by humans might have contributed to these results (Mazzi & Dorn 2012; Kirk et al. 2013a, b). Population genetics of local populations of sedentary species such as *Cydia pomonella* and *G. molesta* can obviously be affected by anthropogenic influences including neurotoxic pesticide spraying, regional fruit transportation, the recent spread of modern fruit culture and regional integrated production and marketing programs (Chen & Dorn 2008; Torriani et al. 2010; Mazzi & Dorn 2012). Anthropogenic influences are considered important reasons for the small genetic differentiation of *Cydia pomonella* as found in populations in France, Chile and Croatia (Franck et al. 2007; Fuentes-Contreras et al. 2008; Voudouris et al. 2012). Actually, local Chinese governments promote centralized purchasing of fruit and distribution of apple and pear cultivars that might promote gene flow and facilitate genetic exchange of *G. molesta* populations within regions, as is also the case for cooperatives in Italy (Torriani et al. 2010). Two populations (JIT and JYD) from the Jiuquan region were very similar in genetic diversity and showed very large \( N_m \) values, which can be explained by the frequent fruit transportation between the 2 regions offering ample opportunity for interbreeding between the populations of the 2 sublocations.

The SIT has been successfully used to suppress *Cydia pomonella* in the fruit growing Okanagan Valley of British Columbia in Canada (Klassen 2005; Bloem et al. 2007b; Vreyesen et al. 2010). The Hexi Corridor is considered an important natural barrier that prevents the codling moth from invading into the more southerly major fruit growing areas of China. Our results show that gene flow between the 2 investigated regions is limited, which creates the possibility of developing and implementing a sequential eradication strategy for the sustainable removal of the codling moth populations in the 2 regions. The use of the SIT is considered a possibility for use in an AW-IPM strategy in view of the absence of mating barriers between codling moth populations worldwide (Taret et al. 2010; Liu et al. 2012; Li 2013).

### Table 3. Pairwise population differentiation estimates (\( F_{st} \)) averaging 8 loci between 8 populations of *Cydia pomonella* with \( P \) value (below the diagonal) and gene flow \( (N_m) \) values (above the diagonal).

<table>
<thead>
<tr>
<th></th>
<th>JIT</th>
<th>JYD</th>
<th>JXD</th>
<th>JZZ</th>
<th>ZLT</th>
<th>ZNJ</th>
<th>ZMY</th>
<th>ZXM</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>JIT</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>JYD</strong></td>
<td>0.002**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>JXD</strong></td>
<td>0.066**</td>
<td>0.106**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>JZZ</strong></td>
<td>0.043**</td>
<td>0.036**</td>
<td>0.103**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ZLT</strong></td>
<td>0.115**</td>
<td>0.123**</td>
<td>0.143**</td>
<td>0.084**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ZNJ</strong></td>
<td>0.277**</td>
<td>0.278**</td>
<td>0.259**</td>
<td>0.225**</td>
<td>0.093**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ZMY</strong></td>
<td>0.120**</td>
<td>0.114**</td>
<td>0.195**</td>
<td>0.097**</td>
<td>0.050**</td>
<td>0.184**</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ZXM</strong></td>
<td>0.228**</td>
<td>0.206**</td>
<td>0.244**</td>
<td>0.132**</td>
<td>0.071**</td>
<td>0.120**</td>
<td>0.140**</td>
<td></td>
</tr>
</tbody>
</table>

\* \( P < 0.05 \), ** \( P < 0.001 \); NS = non-significant. The significances were tested for multi comparisons by the Bonferroni method for \( k = 28; P < 0.05 \).
Acknowledgments

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