

Quantification of diapausing fourth generation and suicidal fifth generation cotton bollworm, *Helicoverpa armigera*, in cotton and corn in northern China

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Abstract

Cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is a major pest of cotton and corn crops in northern China. A phenological differentiation between fourth generation cotton bollworms from cotton and those from corn fields was observed in northern China during 1999–2000. The proportion of pupation in late fall was marginally higher in cotton fields compared to that in corn fields; however, the proportions of fall emergence of moths from cotton fields were significantly higher than those from corn fields. The proportion of spring emergence of moths was also significantly higher for larvae collected from cotton (28.0%) than from corn (14.5%). The overwintering duration of females was significantly shorter than that of males in both crops. Moreover, the overwintering duration of bollworm populations from cotton was significantly longer than that from corn. The early spring population of *H. armigera* came from both cotton and corn fields, but the spring emergence of moths from larvae collected from cotton took about 5 days longer to reach 100% emergence compared to that from corn.

Introduction

The cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is one of the most important field crop pests in the world. In most subtropical and temperate regions of the world, all species of the genera *Heliothis* and *Helicoverpa* have the ability to overwinter in a state of facultative pupal diapause (Roome, 1979; Key, 1982), and the diapausing pupae have greater cold hardiness (Eger et al., 1982). While most bollworm populations enter diapause for overwintering in temperate regions, Hackett & Gatehouse (1982) reported that only 2–4% of bollworm pupae entered diapause in the tropics.

In northern China, the cotton bollworm passes through four or five generations each year, and enters diapause as pupae in the fourth generation (Li & Xue, 1981). The first generation bollworm feeds primarily on wheat, while cotton supports the second to fourth generations; corn

overlaps with cotton to support third and fourth generation bollworms. The final instars of the fourth generation bollworm could either pupate normally to give rise to a fifth generation in the fall, or they enter diapause as pupae. If bollworms produce a fifth generation, the larvae die due to the adverse winter conditions, and this can then be seen as a suicidal generation. If bollworms enter diapause as pupae, the adults that emerge the following spring lay eggs in wheat to produce the first generation. It is therefore important to examine the population characteristics of diapausing fourth generation and suicidal fifth generation bollworms.

Much is known about the survival of the overwintering population and spring emergence of the bollworm worldwide (Slosser et al., 1975; Caron et al., 1978; Wilson et al., 1979; Eger et al., 1983; Rummel et al., 1986; Fitt & Daly, 1990; Zhou et al., 2000; Parajulee et al., 2004). However, information on the fall-emerging moths producing the 5th generation is lacking. Sheng (1993), Liu et al. (1998), and Lu & Xu (1998) reported that the cotton bollworm

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produces five generations in northern China, and that the fifth generation larvae have potential to cause significant economic damage to fall crops. Nevertheless, the proportions of fourth generation bollworms that either enter diapause or develop into adults have not been quantified. Moreover, little information is available on the overwintering potential of bollworms in different cropping systems. This study was conducted to quantify the overwintering potential of bollworms, and to examine the implications of diapausing (fourth) and suicidal (fifth) generations of bollworms on cotton management in northern China.

Materials and methods

A 2-year study was conducted to evaluate the overwintering potential of bollworms in Raoyang County (38°15'N, 115°40'E), Hebei Province of China. Two cropping systems, cotton (*Gossypium hirsutum* L., var. Shimian321, Malvaceae) and corn (*Zea mays* L., var. Yedan10, Gramineae), were examined. Cotton (60 000 plants per ha) and corn (75 000 plants per ha) were planted on 25 April and 25 May in 1999 and 2000, respectively. The soil type was very fine sandy loam (ca. 20–22% clay). Crops were managed following standard production practices recommended for the region.

Large (final instar) larvae of bollworms were randomly collected from both cotton and corn at 5-day intervals during the late summer/early fall. A total of nine collections was made between 26 August and 5 October 1999, and eight collections were made between 17 August and 20 September 2000. Over 50 larvae were collected per collection interval, hereafter referred to as a cohort, with 340 and 380 larvae collected from cotton and 450 and 400 larvae collected from corn in 1999 and 2000, respectively.

The collected bollworm larvae were placed individually in soil-filled plastic cups; soil was obtained from the same field from which the larvae had been collected. The size of the pupation cup was 10 cm diameter × 10 cm height, sufficient to allow maximum depth of pupal tunneling (Fitt & Daly, 1990; Yang et al., 1998, 2001; Chen et al., 2002). The cups from each cohort were transferred to a plastic overwintering cage (100 × 100 × 50 cm), and the overwintering cages were placed outdoors to expose them to the prevailing local conditions. The larvae were provided with cotton squares/small bolls or tender corn, corresponding to the host plant from which they were collected. Feeding continued until larvae entered the soil to pupate. Each cup within each overwintering cage was inspected daily to monitor when the larva had entered the soil to pupate, and when successful emergence of the adult occurred. Adults were only sexed upon emergence in 1999.

Four parameters were defined for the overwintering populations, as follows: (1) proportion of pupation = number of larvae that underwent successful pupation divided by the total number of larvae deployed for pupation, (2) proportion of fall emergence = number of moths emerged in the fall divided by the total number of larvae that underwent pupation, (3) proportion of effectively overwintering diapausing pupae = number of individuals that entered the soil but did not emerge in the fall divided by the total number of larvae that underwent pupation, (4) proportion of spring emergence = number of moths emerged in the following spring divided by the total number of larvae that underwent pupation in the previous fall. Thus, proportion (2) plus proportion (4) plus the proportion mortality = 100% of the initial number of larvae.

As part of the overwintering study, we also monitored field populations of the fourth generation bollworms in both cotton and corn cropping systems to estimate the abundance of bollworms with effective overwintering potential. The field abundance was monitored on each of the sample collection dates mentioned previously for the overwintering study. We surveyed 4–12 sites, comprising 98–312 whole plants in cotton fields, and 8–17 sites comprising 200–850 whole plants in corn fields. The whole-plant sample data were converted to bollworm density per hectare for analysis.

Differences in the proportions of pupation, effectively overwintering diapausing pupae, and fall and spring emergence between cotton and corn were analyzed using a G-test (Sokal & Rohlf, 1981). The overwintering duration of cotton bollworms collected from cotton and corn were compared using a two-way analysis of variance (ANOVA) with crop, moth sex, and their interaction as sources of variability; means were compared using the least significant difference method (SAS Institute, 2000). Data on the proportion of effectively overwintering diapausing pupae, the estimated abundance of fourth generation cotton bollworms in the field, and the estimated abundance of effectively overwintering pupae were subjected to separate two-way ANOVAs, with year, crop, and their interaction as sources of variability; means were separated using the least significant difference method (SAS Institute, 2000).

Results

Proportion of pupation

Proportion of pupation was higher for larvae collected from cotton compared with those collected from corn, for all sample dates, except for the 26 August 1999 collection. Significant differences were found on 20 and 25 September in 1999 and on 27 August in 2000 (Table 1).

Table 1 The proportions (%) of pupation, effectively overwintering pupae, fall moth emergence, and spring moth emergence from *Helicoverpa armigera* larvae collected in the fall from cotton and corn, Hebei Province of China, 1999–2000

Year	Sample date	No. larvae collected		% pupation		% effectively overwintering pupae		% fall emergence		% spring emergence		
		Cotton	Corn	Cotton	Corn	Cotton	Corn	Cotton	Corn	Cotton	Corn	
1999	26 August	60	50	65.0 a ^a	70.0 a	8.3 a	15.4 a	56.7 a	54.6 a	0.0 a	2.0 a	
	31 August	59	50	83.1 a	70.0 a	25.4 a	34.0 a	57.6 a	36.0 b	0.0 b	6.0 a	
	5 September	56	50	73.2 a	56.0 a	35.7 a	39.2 a	37.5 a	16.8 b	14.3 a	16.0 a	
	10 September	53	50	75.5 a	60.0 a	75.4 a	52.0 b	0.0 b	8.0 a	30.2 a	14.0 b	
	15 September	64	50	68.8 a	64.0 a	68.7 a	64.0 a	0.0 a	0.0 a	28.1 a	20.0 a	
	20 September	39	50	79.5 a	30.0 b	79.4 a	30.0 b	0.0 a	0.0 a	23.1 a	8.0 b	
	25 September	9	50	77.8 a	28.0 b	77.8 a	28.0 b	0.0 a	0.0 a	44.4 a	12.0 b	
	30 September	–	50	–	80.0	–	80.0	–	0.0	–	–	42.0
	5 October	–	50	–	56.0	–	56.0	–	0.0	–	–	10.0
2000	17 August	50	50	66.0 a	64.0 a	6.0 a	10.0 a	60.0 a	54.0 a	0.0 a	2.0 a	
	22 August	50	50	70.0 a	56.0 a	10.0 a	16.0 a	60.0 a	40.0 b	0.0 a	4.0 a	
	27 August	50	50	74.0 a	40.0 b	16.0 a	24.0 a	58.0 a	16.0 b	10.0 a	10.0 a	
	2 September	50	50	54.0 a	52.0 a	46.0 a	50.0 a	8.0 a	2.0 b	32.0 a	18.0 b	
	5 September	50	50	40.0 a	32.0 a	40.0 a	32.0 a	0.0 a	0.0 a	26.0 a	12.0 b	
	10 September	50	50	52.0 a	42.0 a	50.0 a	42.0 a	2.0 a	0.0 a	32.0 a	14.0 b	
	15 September	50	50	40.0 a	38.0 a	40.0 a	38.0 a	0.0 a	0.0 a	30.0 a	24.0 a	
	20 September	30	50	46.7 a	36.0 a	28.0 a	36.0 a	0.0 a	0.0 a	26.7 a	32.0 a	

^aNumbers followed by the same letter within a parameter column are not significantly different ($P > 0.05$, G-statistic, Sokal & Rohlf, 1981).

The proportion of pupating larvae collected from cotton ranged from 65 to 83.1%, with an average of 74.7% in 1999, and from 40 to 74%, with an average of 55.3% in 2000. The proportion of pupating larvae collected from corn ranged from 28 to 80%, with an average of 57.1% in 1999, and from 32 to 64%, with an average of 45.0% in 2000 (Table 1).

Proportion of effectively overwintering pupae

In 1999, the proportion of effectively overwintering pupae from cotton during the early fall (i.e., before 5 September) ranged from 8.3 to 35.7% with an average of 23.1%, whereas this proportion from corn ranged from 15.4 to 39.2% with an average of 29.5%; no significant difference in the proportion of effectively overwintering pupae was observed between cotton and corn field collections of larvae in early fall (Table 1). In contrast, the proportions of effectively overwintering pupae from cotton during late fall (after 10 September) was significantly higher than that from corn in three of four collection dates (Table 1). In 2000, the proportion of effectively overwintering pupae from cotton (23.6%) during early fall was slightly lower than that from corn (26.4%), while the proportion from cotton (39.3%) was slightly higher than that from corn (38.7%) during late fall (Table 1).

Proportion of fall emergence of moths

In 1999, larvae collected after 10 September from cotton, or after 15 September from corn, did not develop into fall-emerging moths. In 1999, an average of 50.6% of larvae from cotton developed into fall-emerging moths, whereas only 28.9% of larvae collected from corn fields developed into fall-emerging moths. In 2000, larvae collected after 10 September from cotton or after 5 September from corn did not develop into fall-emerging moths. The percentage of larvae from cotton developing into fall-emerging moths ranged from 2 to 60% (mean = 31.3%), whereas 2–54% (mean = 28.0%) larvae from corn fields resulted in fall-emerging moths (Table 1). The proportion of fall-emergence was significantly higher in cotton compared with that in corn, on 31 August and 5 September in 1999, and on 22 and 27 August, and 2 September in 2000 (Table 1).

Proportion of spring emergence of moths

Overall, the proportion of spring emergence of moths from larvae collected from cotton in the fall was significantly higher than that from larvae collected from corn in both years, on 10, 20, and 25 September in 1999, and on 2, 5, and 10 September in 2000 (Table 1). In 1999, no larvae collected from cotton fields on or before

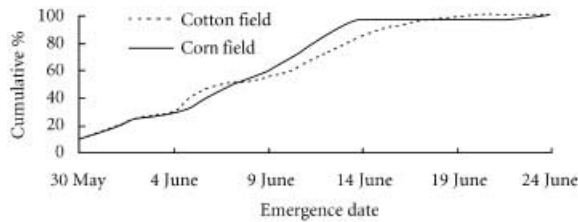


Figure 1 Spring emergence profile of cotton bollworm adults from larvae collected from cotton and corn fields in the fall of 1999, Hebei Province, China.

31 August contributed to the spring emergence of moths (Table 1). An average of 28.0% (14.3–44.4%) of larvae collected from cotton after 5 September successfully overwintered and emerged as moths the following spring, whereas only 14.4% (2–42%) of larvae collected from corn after 26 August overwintered and emerged as moths the following spring. Moth emergence began on 30 May from both cotton and corn, but 100% emergence occurred in corn about 5 days earlier than in cotton (Figure 1). In 2000, larvae collected on or before 22 August from cotton did not contribute to spring-emerging moths, whereas larvae collected from corn resulted in the spring emergence of moths for all collection dates in 2000. The average proportion of spring emergence of moths from cotton was about twice (26.1%) that of moths from corn (14.5%).

Overwintering duration of cotton bollworm (pupae in diapause)

Analysis of the 1999 data showed that the duration of overwintering female cotton bollworm pupae was significantly shorter ($F_{1,94} = 8.0$, $P = 0.005$) than that of male pupae in both cropping systems (Table 2). The

difference between the duration of female and male pupae from cotton was 6 days. However, the difference between male and female pupal duration in corn was only 1.1 days. Averaged over both sexes, the total overwintering duration of cotton bollworms was significantly longer ($F_{1,94} = 54.9$, $P = 0.0001$) in cotton than in corn, with 259.07 ± 8.3 days in cotton and 251.4 ± 8.9 days in corn fields, respectively.

Abundance of the fourth generation cotton bollworm

Overall, a significantly greater abundance of fourth generation bollworms was observed ($F_{1,24} = 7.4$, $P = 0.01$) in 1999 (7973 larvae ha^{-1}) compared to that in 2000 (2813 larvae ha^{-1}), but the abundance of fourth generation bollworms was similar between corn and cotton fields ($F_{1,24} = 0.05$, $P = 0.82$) (Table 3). There was no significant interaction between year and crop ($F_{1,24} = 0.20$, $P = 0.65$).

Field abundance of potentially effectively overwintering pupae

The field abundance of potentially effectively overwintering pupae (Figure 2) was estimated from the estimated larval density in the field (Table 3) and the proportion of effectively overwintering pupae (Table 1). In 1999, the field population of effectively overwintering pupae ranged from 1995 to 6904 pupae per hectare (average = 3961 pupae ha^{-1}) in cotton and from 1924 to 4914 pupae per hectare (average = 3675 pupae ha^{-1}) in corn, respectively. The abundances of potentially effectively overwintering pupal populations in 2000 were 1501 and 1226 in cotton and corn fields, respectively. No significant difference in the proportion of effectively overwintering pupae was found between cotton and corn fields in 1999 ($F_{1,24} = 1.2$, $P = 0.36$) or in 2000 ($F_{1,24} = 0.49$, $P = 0.48$).

Table 2 Overwintering duration (days \pm SD) of cotton bollworms collected from cotton and corn, Hebei Province of China, 1999

Sample date	Cotton			Corn		
	n (♀:♂)	Female (♀)	Male (♂)	n (♀:♂)	Female (♀)	Male (♂)
26 August	–	–	–	1 (0:1)	–	274
31 August	–	–	–	3 (2:1)	266.5 \pm 3.5	269
5 September	8 (4:4)	262.0 \pm 4.5	269.3 \pm 5.1	8 (2:6)	267.5 \pm 2.1	268.8 \pm 7.8
10 September	16 (4:12)	254.8 \pm 4.3	264.3 \pm 6.8	7 (3:4)	253.7 \pm 0.6	261.0 \pm 5.8
15 September	18 (13:5)	254.3 \pm 8.5	260.1 \pm 6.0	10 (4:6)	254.5 \pm 10.6	257.5 \pm 4.4
20 September	9 (3:6)	248.0 \pm 3.6	257.2 \pm 4.6	4 (1:3)	250	252.7 \pm 3.5
25 September	4 (1:3)	247	245.0 \pm 3.6	6 (2:4)	248.5 \pm 2.1	241.8 \pm 5.9
30 September	–	–	–	21 (6:15)	236.5 \pm 6.1	243.7 \pm 4.0
5 October	–	–	–	5 (0:5)	–	240.4 \pm 5.0
Average		254.7 \pm 7.1 A,b	260.7 \pm 8.0 A,a		250.6 \pm 12.4 B,b	251.7 \pm 11.7 B,a

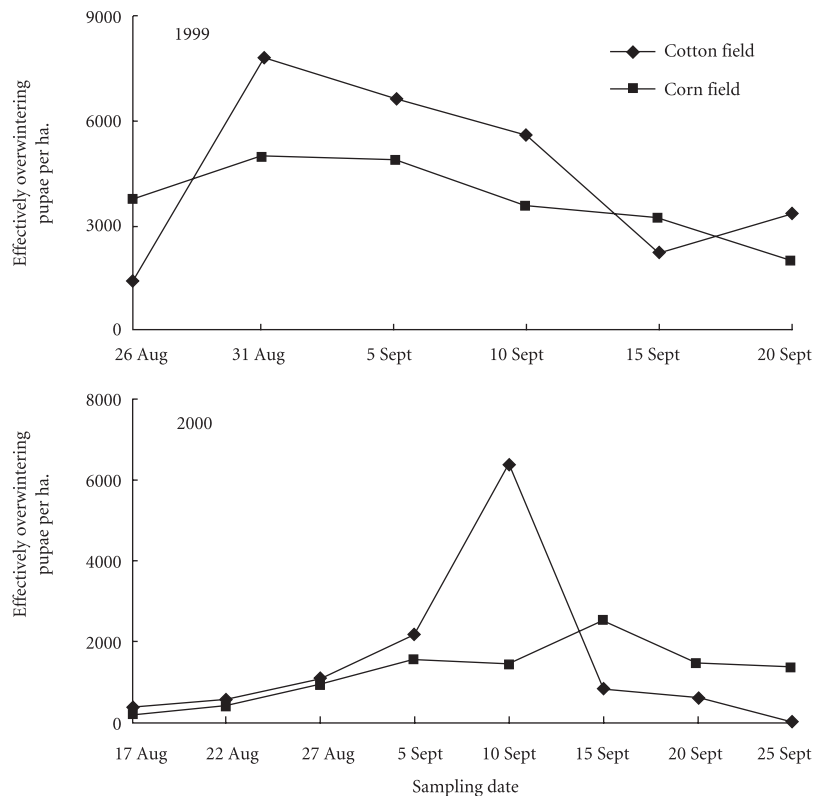
Means with different upper case letters between crops and means with different lower case letters between sexes are significantly different ($P < 0.01$). n = sampling size.

Table 3 Estimated field abundances (per ha) of late instar larvae of the fourth generation of cotton bollworms in cotton and corn, Hebei Province of China, 1999–2000

Year	Sampling date	Number of late instar larvae per ha	
		Cotton	Corn
1999	26 August	9057	1580
	31 August	17 803	23 458
	5 September	8485	14 386
	10 September	3943	5742
	15 September	2138	4161
	20 September	2632	2289
	25 September		
	30 September		
2000	5 October		
	17 August	3548	1124
	22 August	3383	1104
	27 August	3867	4784
	2 September	3358	2222
	5 September	7521	3258
	10 September	1200	3387
	15 September	723	2772
20 September	667	2151	

Discussion

Cotton bollworms typically enter the soil as larvae and then pupate for diapause in the winter (Zhang et al., 1980; Fitt, 1989). In this study, 74.7% and 55.3% of fourth generation bollworms collected from cotton fields were observed to pupate in 1999 and 2000, respectively. However, not all fourth generation larvae became effectively overwintering pupae. For example, larvae collected during early fall either did not enter the diapausing pupal stage, or only a small proportion underwent pupal diapause. An apparent differentiation in large larvae of the fourth generation was observed in our study in northern China. For example in 1999, an average of 50.6% of larvae collected from cotton fields and 28.9% of the larvae collected from corn fields emerged as adults and produced a fifth generation. Larvae of this fifth generation could cause some economic damage on fall hosts, such as grain sorghum, late-planted corn, and crucifers (Lu & Xu, 1998). Because the developmental time for the fourth generation (egg to adult) in late August/September was about 40 days, larvae of the fourth generation would not be able to complete their life cycle, nor would they enter the diapausing pupal stage. As a result, the fourth generation

**Figure 2** Number of effectively overwintering pupae of cotton bollworms per ha in cotton and corn fields, 1999–2000, Hebei Province, China.

larvae or non-diapausing pupae would die due to winter conditions. Thus, the faster the larvae of the fourth generation develop to large larvae (late instar), the lower the probability that these large larvae become effectively overwintering pupae. Our results show that a significant difference in the proportion of fall-emerging moths occurred between cotton and corn fields in both 1999 and 2000, suggesting that cotton supported a significantly greater proportion of the fifth generation bollworms, which ultimately results in a suicidal generation.

If fourth generation bollworms enter diapause as pupae and emerge as adults the following spring and lay eggs in the wheat crop, this results in 'effective overwintering.' In contrast with fall-emerging moths, the probability that the larvae develop into effectively overwintering pupae would decrease if the larvae of the fourth generation developed into large larvae earlier in the fall and became a suicidal generation. For example, no large larvae collected from cotton fields on or before 31 August 1999 or on or before 22 August 2000 were observed to emerge as adults in the following spring. Although significantly higher proportions (28.0% in 1999 and 26.1% in 2000) of spring-emerging moths resulted from the larvae collected from cotton fields than those from corn fields (14.4% in 1999 and 14.5% in 2000; Table 1), no significant difference in the production of effectively overwintering pupae was observed between cotton and corn fields in both years (Figure 2).

Bollworm overwintering survivorship is dependent on many climatic and biotic factors. For example, Slosser et al. (1975) reported that effective drainage was critical for the overwintering survivorship of *H. zea* (Hübner). Eger et al. (1983) and Rummel et al. (1986) demonstrated that soil moisture had a significant impact on the winter survival of *H. virescens* and *H. zea*. Yang et al. (1998, 2001) and Chen et al. (2003) also reported that soil moisture, as well as physical and chemical soil characteristics, greatly affected the proportion of the cotton bollworm, *H. armigera*, that successfully pupated. However, no report is available to date on the influence of host crop on the overwintering survivorship and spring emergence of heliothines (Parajulee et al., 2004). Our study suggests that the overwintering survivorship and spring emergence of late-fall collected cotton bollworm is significantly greater in cotton than in corn. Our study also indicates that the proportion of pupation of the fourth generation bollworms is generally greater in cotton than in corn. A greater proportion of pupation and better overwintering survivorship of bollworms collected from cotton can be attributed to the nutritional quality of cotton bolls compared to that of maturing corn (Ding, 1986).

A difference in overwintering duration between female and male populations was observed in both cropping

systems. The difference between female and male populations was about 6 days in cotton and about 1 day in corn. This asynchrony could be disadvantageous for the mating success of cotton bollworms in the cotton crop after overwintering. Moreover, the duration of overwintering of the fourth generation cotton bollworm from cotton fields was significantly longer than that from corn fields. Because the spring emergence of moths began simultaneously from both cotton and corn fields (30 May), cotton and corn field populations contributed equally to the early spring populations of *H. armigera*. However, the spring emergence of moths from larvae collected from cotton took about 5 days longer to achieve 100% emergence compared to that from corn. Nevertheless, both cotton and corn served as host plants for the fifth generation bollworms in the fall and for the occurrence of bollworms the following spring.

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