

High-Altitude Windborne Transport of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Mid-Summer in Northern China

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*The high-altitude windborne transport of the second-generation moths of *Helicoverpa armigera* (Hübner) was observed with radar in July 2001 and 2002 at Langfang, Hebei province, China. Moths of local populations took off at dusk, with “area density” peaking ca. 0.5 h later. The variation of area density through the night suggested that the maximum flight duration was about 8.5 h. The moths generally ascended to altitudes of up to 1500 m above ground level (AGL) and formed layer concentrations at ca. 300, 500, and 1000 m AGL. Multiple layering was very common and layers were located at zones of maxima in wind speed or in wind shear rather than in temperature inversions. Both the displacement direction and the orientation of the insect were at an acute angle to the downwind direction, rather than being distributed at random, and varied as the wind direction changed. The windborne moths were mainly transported into northeastern China where maize at the silking stage would have provided good hosts for the subsequent (third) generation of *H. armigera*. These population movements may account for*

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the nondevelopment of resistance to Bt cotton in H. armigera in northern China.

KEY WORDS: windborne transport; *Helicoverpa armigera*; flight behavior; radar observation.

INTRODUCTION

The cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is one of the most important agricultural pests of the Old World. Its wide distribution and pest status has been attributed to its polyphagy and its ability to undergo both facultative diapause and seasonal migration (Fitt, 1989). The species is migratory in all four Old World continents, in all of which it is a key pest (Fitt, 1989; Riley *et al.*, 1992; Gregg *et al.*, 1993; Vaishampayan and Singh, 1996; Wu *et al.*, 1998; Zhou *et al.*, 2000a; Torres-Vila *et al.*, 2002).

Chinese populations of *H. armigera* infest crops in the northeast (Liaoning province) of the country, where they cannot overwinter (Wu and Guo, 1997). These observations have led to the hypothesis that *H. armigera* moths trapped in late June in northeastern China are immigrants from Shandong, Hebei, and Henan provinces further south (summarized by Wu, 1998). Insecticide-resistance monitoring and RFLP (Restriction Fragment Length Polymorphism) analysis of the genetics of populations collected from different geographical regions of China showed that there are frequent gene exchanges between populations in different ecological regions within China (Wu and Guo 2000; Xu *et al.*, 2002). Xu *et al.* (1999), by identifying pollen attached to the probosces of *H. armigera* trapped in Liaoning province, Beijing city, Henan province and over the Bohai Sea, documented this species' long-distance migration from northern China (especially Shandong, Hebei, and Henan provinces) into northeastern China (especially Liaoning province). This northeastward migration of the first generation of *H. armigera* moths, which occurs in late June and involves an acrossing of the Bohai Sea, was also confirmed from observations of the ovarian development of the migrants (Zheng *et al.*, 2000; Wu *et al.*, 2002b) and by capture of *H. armigera* over the Bohai Sea (Wu *et al.*, 1998). Long-distance windborne nocturnal migrations by this species have also been observed directly, though at other seasons or in different regions, with entomological radars (Schaefer, 1976; Wu *et al.*, 2001; Feng *et al.*, 2004a).

In the present study, radar observations were made of the flight behavior of the second-generation *H. armigera* moths during their high altitude windborne transportation through northern China during

mid-summer 2001 and 2002. The take-off, duration and height of flight, and the orientation and displacement direction of the moths are described in detail, and relationships between these flight behaviors and the wind are identified.

METHODS

The observations were carried out at the Langfang Experimental Station of the Chinese Academy of Agricultural Sciences (CAAS) (39°30'42" N, 116°36'07" E, 28 m above sea level), in Hebei province (Fig. 6), northern China between early July and mid-August of 2001 and 2002. Crops growing in this season around the radar site were mainly maize and cotton.

Radar Observations

Observations were made with the CAAS scanning radar (X-band, 3.2 cm wavelength) which was standing on a 2-m high platform (antenna 6.2 m above ground level). The radar was operated with a display range of 1.5 nautical miles, a pulse length of 0.08 μ s and a pulse repetition frequency of 2 kHz; the antenna was directed at a sequence of elevation angles of 3°, 5°, 8°, 12°, 18°, 28°, 45°, and 58° as proposed by Drake (1981). Observations began at sunset and continued until sunrise (Feng *et al.*, 2003). A digital data-acquisition system was employed to capture the PPI screen images and analyze them to retrieve aerial insect densities and track vectors (Cheng *et al.*, 2002). The area density of large insects (insects/km²) was calculated by summing the sequence of products of the volume density and the height interval over which each density was measured (Feng *et al.*, 2003). Dates for observations and trap catch reported in this paper indicate the evening of that date through to sunrise the next. Times in this paper are all given in Beijing time (GMT + 08 : 00 h).

Target Air Speed and Direction

A meteorological balloon with a radiosonde attached was released and tracked with a theodolite every night except when it was raining. The radiosondes ascended at a rate of 100 m/min and provided estimates of wind velocity at 50-m intervals and of air temperature approximately every 8 m, the data being automatically recorded into a laptop computer (Feng *et al.*, 2003). Using these wind estimates, the air speed and direction of individual

insect targets were calculated from the radar data by vector-subtraction (Riley and Reynolds, 1979). (It was assumed that the speed and direction of the wind did not change within 30 min of an ascent, and air-speed estimates were calculated only for this period.) To minimize error, the radar beam was positioned at the elevation angle of the balloon during each ascent, so as to record targets as close as possible to the height where wind data were being acquired (Feng *et al.*, 2003).

The air speeds estimated in this way were used to identify the radar targets according to the criteria described by Riley (1999): that targets with air speeds of less than 6–7 ms^{-1} and generating continuous wing-beat modulation above 14 Hz will almost certainly be insects. Species identification was inferred from the accompanying trap catches (Riley, 1999).

The heading directions were tested for collective orientation by the Rayleigh Test (Mardia and Jupp, 2000). The direction of displacement and wind direction were tested for directionality by the Rayleigh's Test as well. Directions in this paper are all given as $\bar{\theta} \pm \nu$ (mean \pm circular standard deviation). The directions of orientation and of displacement of the insects were compared with the wind direction by circular–circular rank correlation (Mardia and Jupp, 2000). The circular–circular rank correlation coefficient r_0 was calculated using $r_0 = \max(\bar{R}_+, \bar{R}_-)$, where $\bar{R}_\pm^2 = (T_{cc} \pm T_{ss})^2 + (T_{sc} \mp T_{cs})^2$ with $T_{cc} = \frac{1}{n} \sum_{i=1}^n \cos \beta_i \cos \gamma_i$ and $T_{cs} = \frac{1}{n} \sum_{i=1}^n \cos \beta_i \sin \gamma_i$. The β_i and γ_i are defined by $\beta_i = \frac{2\pi r_i}{n}$ and $\gamma_i = \frac{2\pi s_i}{n}$ ($i = 1, 2, \dots, n$) with r_1, \dots, r_n and s_1, \dots, s_n the circular ranks of $\theta_1, \dots, \theta_n$ and ϕ_1, \dots, ϕ_n . For $n > 10$, the approximation $P_r(2(n-1)r_0 > \mu)$ is approximately equal to $1 - (1 - e^{-\mu/2})^2$, therefore, the probability of correlation p was calculated (Feng *et al.*, 2004a).

Sampling High-Flying Insects

A ground based vertical-pointing searchlight trap located close to the radar was used to sample insects from altitudes of up to 500 m above ground level (AGL) (Feng *et al.*, 2003). The searchlight (GT70, Shanghai Yayuan Light Electronic Company Limited, Shanghai, China), which equipped with a 1-kW metal-halide lamp, had a parabolic reflector which generated a narrow vertical beam of light. Below the lamp was an inverted metal cone which collected the insects and directed them into a plastic basin containing 1% detergent solution to kill and retain them. Since microinsects such as aphids, ants, planthoppers, and leafhoppers could not be detected with the radar within the working range of the radar PPI display, they were excluded from the catch counts (Feng *et al.*, 2003).

RESULTS

Radar Targets

The air speeds of most radar targets were in the range 1.4–7.0 m/s, which indicates that they were insects rather than birds. *H. armigera* was the most numerous macroinsect species in the searchlight trap catches during the radar observation periods 11–25 July 2001 and 24–30 July 2002 (Fig. 1), the proportion exceeding 70% on some peak nights in 2001 but only reaching 40% in 2002.

Variation of Area Density

H. armigera moths took off at dusk (19.56–20.12 h in mid-July) around the radar site and then the area density of insects increased quickly, peaking ca. a half hour (30 ± 10 (SD, $n = 11$) and 28 ± 3 (SD, $n = 4$) min in 2001 and 2002 respectively) later (e.g. 19 July 2001, Fig. 2). The maximum area

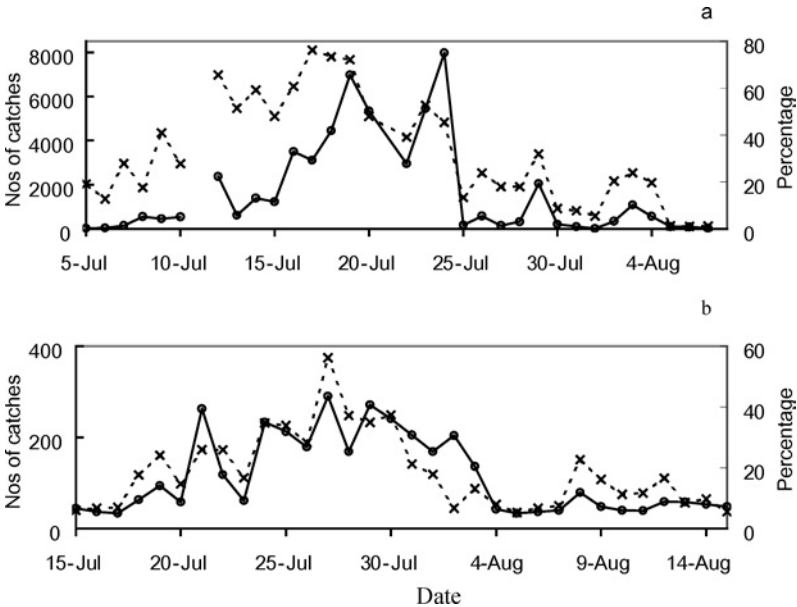


Fig. 1. Number of daily catches (—○—) of 2nd generation moths of *H. armigera*, and the proportion (···×···) of this species amongst all macroinsects in the catch, for the searchlight trap at Langfang in (a) 2001 and (b) 2002.

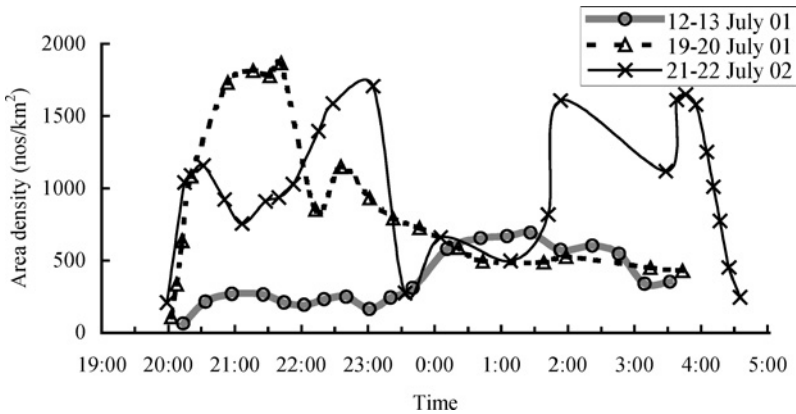


Fig. 2. Variation of area density of insect targets through the night at Langfang for selected nights in 2001 and 2002.

density was 1864 and 2021 insects/km², recorded in 2001 and 2002 respectively. After this peak (ca. a half hour), area density generally decreased quickly to a low level which then persisted through the rest of the night. A peak of insect density, thought to be due to a dawn take-off, was recorded about a half hour before dawn (04.30 h) on 21, 24, 26, and 28 July 2002. The area density decreased quickly after this peak and insect targets became very rare (e.g. 21–22 July 2002, Fig. 2). The variation of area density through the night suggests the maximum duration of flight was ca. 8.5 h (Fig. 2).

A longer dusk peaking duration (ca. 1 h) of area density was recorded on 19 July 2001, which could be attributed to lower wind speeds and therefore slower transport of the insects over the radar site. During the evenings of 15, 16, 18, 19 and 25 July 2001, there were one or two lesser peaks following the dusk peak (Fig. 2), and these were thought to be due to arrivals of moths which had taken off further away from the radar site. On 12 July 2001, the highest densities of insects were detected after midnight (Fig. 2), and this was interpreted as an immigration. On nights with intermittent showers, the insect density varied abruptly (e.g., 21–22 July 2002, Fig. 2).

Height of Flight and Vertical Distribution of Insects

Helicoverpa armigera-type targets generally flew <1500 m AGL, although some insects extended up to 2000 m (Fig. 3 and Table I). Multiple layering was common, often occurring at altitudes of ca. 300, 500, and

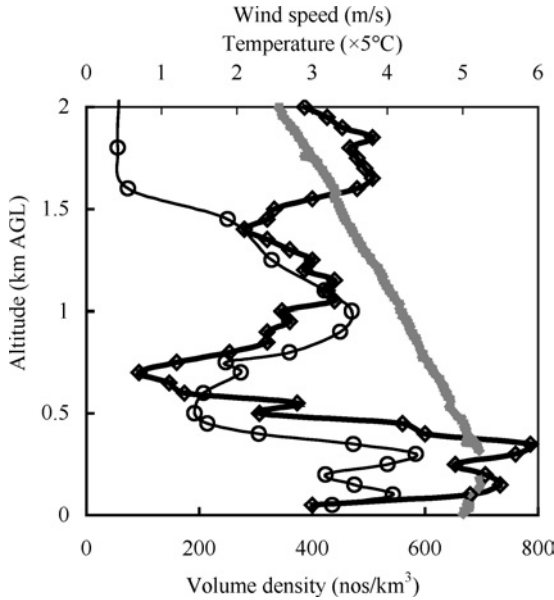


Fig. 3. Profiles of wind speed (—◇—), temperature (—) and insect density (—○—) during the balloon ascent that started at 22.22 h on 14 July 2001.

1000 m AGL. In 2001, the maximum insect density was frequently observed to coincide closely with a zone of wind shear rather than a temperature inversion (Table I). An example of the close correlation of insect density with the wind speed, at heights below 1500 m, is shown in Fig. 3. However, the maximum insect density was not located exactly at the height of maximum wind speed, but 50 m lower where the wind was a little slower. A regression analysis showed that a significant linear relationship of insect density at height of h ($h = 50\text{--}1250$ m), D_h to wind speed at 50 m above h , V_{h+50} , described by $D_h = 61.57V_{h+50} + 173.17$ ($P < 0.01$), during the period of balloon ascent on 14 July 2001 (Fig. 3). In 2002, however, the maximum insect density was not closely related to either wind shear or temperature inversions (Table I).

On a small number of nights, the profiles of both wind speed and wind direction had a simple form like the letter J with little variation with height above ca. 200 m (e.g. Fig. 4a). On one such night, 16 July 2001, a layer of insects at a height of 400–600 m was observed at 22.49 h but had disappeared by 23.08 h and was still absent at 23.20 h (Fig. 4b), after the J-shaped wind profile was detected at 22.50–23.00 h. The following night, when a J profile

Table I. Height of Wind Shear, Temperature Inversion, and Insect Density Maximum for Nights of Peak *H. armigera* Moth Migration in July 2001 and July 2002

Date	Altitude (m AGL)	Wind	Temperature	Insect density
14 Jul '01	150	>	>	>
	1000	/		>
	300 ^a	/>		>
	1000 ^a	/>		>
15 Jul '01	100		>	
	300	>		>
	1650	>		>
16 Jul '01	250	>	>	
	300			>
17 Jul '01	300	>	>	>
18 Jul '01	250			>
19 Jul '01	100		>	
	1000	/<		>
	1300		>	
24 Jul '02	150		>	>
	250		>	
25 Jul '02	250–300	/		>
26 Jul '02	150	>	>	>
27 Jul '02	200	>	>	
	250			>
28 Jul '02	350	>		
	450			>
29 Jul '02	100		>	
	900			>

Note. Key: > maximum, < minimum, / wind shift.

^aBoth the temperature and the wind were measured twice on 14 July 2001, and these entries were for the second time.

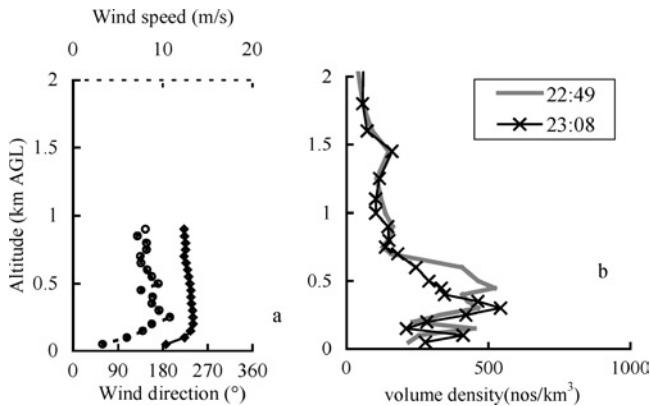


Fig. 4. Profiles of (a) wind speed (—○—) and, direction (—◇—) and (b) insect density, during the balloon ascent that started at 22.50 h on 16 July 2001.

was also present, no layer concentrations formed at heights above 250 m. A similar absence of high-altitude flight in the presence of a J-shaped wind profile was also observed on 12 July 2001.

Displacement and Orientation

The insect displacement speed ranged from 6.1 to 14.4 m/s and the displacement direction was mainly towards the northeast in 2001 and towards either the west or the northeast in 2002 (Table II). On 29 July 2002, when the population was moving toward the northeast following a change of wind direction, from easterly to southwesterly, the catches in the searchlight trap were predominantly (78%) of newly emerged *H. armigera* moths; however, samples of the local flying population, caught in a traditional light-trap contained no newly emerged moths.

The insect targets at higher altitudes were observed moving in an opposite direction to those at lower altitude when the wind direction turned to an opposite direction above ca. 700 m on 14 July 2001, and there was a significant change in displacement direction as the wind shifted at ca. 350 m on 11 July and 1000 m on 15 July 2001 (Tables II and III). When tested by Rayleigh’s Test of randomness, the displacement directions of the insect

Table II. Velocity of Displacement of Insect Targets on Peak Nights of *H. armigera* at Langfang in July 2001 and July 2002

Date	Altitude	Direction (deg) ($\bar{\theta} \pm \nu$)	Speed (m/s) ($\bar{x} \pm SD$)	n
11 July '01	50–250	164 ± 39	6.1 ± 1.3	241
	400–1000	44 ± 19	11.6 ± 2.7	155
12 July '01	50–1500	357 ± 49	8.3 ± 6.5	904
	50–500	0 ± 37	6.1 ± 3.4	794
14 July '01	800–1500	171 ± 25	6.7 ± 1.6	129
	50–1000	49 ± 19	8.5 ± 5.5	790
15 July '01	1000–2000	349 ± 26	10.6 ± 3.1	73
	50–1500	42 ± 13	12.0 ± 2.7	569
17 July '01	50–1500	33 ± 11	14.4 ± 2.1	419
18 July '01	50–1500	39 ± 16	12.1 ± 2.6	732
19 July '01	50–1500	20 ± 27	8.2 ± 3.3	362
24 July '02	50–800	17 ± 17	9.1 ± 1.2	60
25 July '02	50–1500	272 ± 53	7.7 ± 1.6	2061
26 July '02	50–1500	257 ± 69	8.4 ± 3.8	1023
27 July '02	50–1500	264 ± 37	9.7 ± 2.7	283
28 July '02	50–1500	261 ± 40	7.6 ± 1.8	455
29 July '02	50–1500	24 ± 17	10.3 ± 1.4	477
30 July '02	50–1500	40 ± 19	10.3 ± 2.8	205

Note. Directionality was significant at 0.01 confidence level.

Table III. Directions of Displacement and of Orientation of Insect Targets, and Wind Direction During the Periods of Balloon Ascent on Peak Nights of *H. armigera* Moth Migration at Langfang in July 2001 and July 2002, and Their Relationships

Date	Altitude	Direction (deg) ^a			Relationship					
		Displacement	Orientation	Wind ^b	Displacement and wind		Orientation and wind		t ₀	n
					Angle ^c	t ₀	Angle ^c	t ₀		
11 Jul '01	50-250	167 ± 36	176 ± 48	155 ± 4	6 ± 34	0.12**	27 ± 51	0.07**	78	
	400-1000	39 ± 9	48 ± 49	41 ± 12						
12 Jul '01	50-900	38 ± 14	34 ± 38	39 ± 5	-7 ± 13	0.13*	-5 ± 38	0.05	36	
14 Jul '01	50-500	307 ± 10	303 ± 18	314 ± 6	-18 ± 28	0.21**	-23 ± 38	0.22**	78	
	800-1200	167 ± 25	147 ± 33	194 ± 6						
15 Jul '01	150-900	55 ± 19	73 ± 39	39 ± 6	9 ± 21	0.10	32 ± 39	0.07	36	
16 Jul '01	150-700	45 ± 13	46 ± 36	50 ± 3	-10 ± 12	0.01	-3 ± 36	0.01	23	
2001 (sum)					-4 ± 27	0.33**	2 ± 45	0.11**	251	
25 Jul '02	50-1500	258 ± 48	243 ± 61	283 ± 23	-23 ± 38	0.07**	-35 ± 50	0.03**	313	
27 Jul '02	50-650	257 ± 44	158 ± 62	263 ± 26	-15 ± 37	0.13**	-110 ± 56	0.05**	77	
28 Jul '02	250-1050	285 ± 37	307 ± 44	253 ± 5	27 ± 38	0.08*	54 ± 45	0.06*	66	
2002 (sum)					-15 ± 39	0.03**	-25 ± 58	0.03**	458	

^aDirectionality was significant at 0.01 confidence level.

^bDirection towards which wind was blowing.

^cMinus value means angle is counterclockwise from the downwind direction, positive value means it is clockwise.

**Significant at 0.001 confidence level, and *significant at 0.05 confidence level.

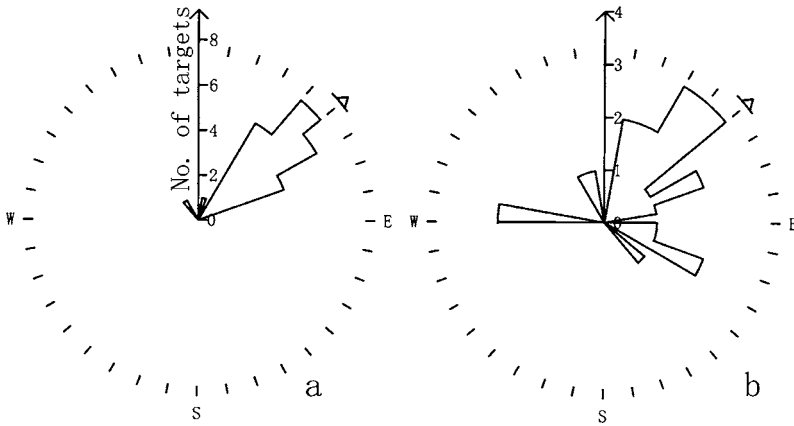


Fig. 5. Rose diagrams showing distributions of (a) displacement direction ($45^\circ \pm 13$, $P < 0.001$) and (b) heading direction ($46^\circ \pm 36$, $P < 0.001$) of the 2nd generation moths of *H. armigera* at altitudes below 1000 m on 16 July 2001, during the balloon ascent that started at 22.50 h. Total number of targets = 23, Δ indicates the direction towards which the wind was blowing, and the arc shows the circular standard deviation of the wind.

targets were found to be not distributed at random but were directed downwind, when the wind direction was stable (Table III and Fig. 5a). Similarly, the distribution of heading directions of individual targets calculated from vector differences showed that *H. armigera* had a common orientation toward the downwind direction (Table III and Fig. 5b). The directions of displacement and of orientation of the insect targets were related to the wind direction and lay either clockwise or counterclockwise to the downwind direction in both 2001 and 2002 (Table III). On 15 and 16 July 2001, the correlations between the directions of insect displacement, insect orientation and wind direction were not significant, but this can be attributed to small deviations ($<10^\circ$) in the wind direction.

DISCUSSION

In July 2001 and 2002, the 2nd generation *H. armigera* moths, took off at dusk and were generally moving towards the NE rather than moving at random. Related studies have shown that 2–3 days of successive migration could have occurred before reproduction (Riley *et al.*, 1992; Zheng *et al.*, 2000; Zhou *et al.*, 2000b), and flight durations inferred from the variation of insect density with time showed that many migrants flew about 8.5 h per night. Therefore, under the observed displacement speeds of 6.1 to 14.4 m/s, *H. armigera* moths migrating towards northeast could have moved as far

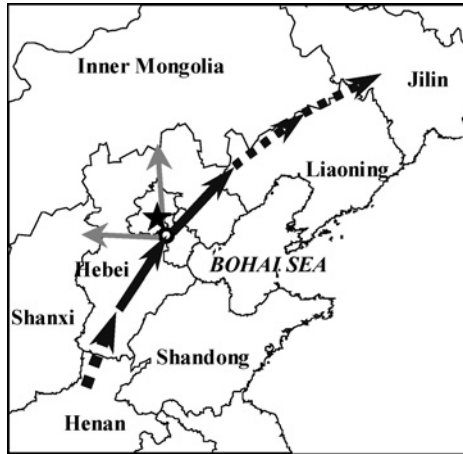


Fig. 6. Possible pathway of windborne transport of *H. armigera* in July in 2001 and 2002. Black arrows show a general path and gray arrows show some minor special paths. The dashed line shows the possible path during up to three nights' transport. The circle shows the location of Langfang, the radar site and the star the location of the city of Beijing.

as Liaoning province (Fig. 6) where in addition to cotton, abundant spring maize would be important alternative hosts.

Since 1997, when Bt cotton was first extensively planted in northern China, the population of the second generation of *H. armigera* has been suppressed to a very low level and maize now provides an important refuge for the species (Wu *et al.*, 2004). However, the summer maize grown in northern China is too young for 3rd generation larva to survive on it, but the spring maize in northeastern China is in the silking stage in mid- and late July, this is the most favorable stage for laying by this species on this host. Therefore, the windborne transport of the second-generation moths of *H. armigera* observed in the present study, may play an important role in population survival. In addition, the huge number of moths emerging from maize would dilute any gene providing resistance to Bt cotton when these moths return to northern China in fall (Wu *et al.*, 2001), and this might account for the species' failure so far to develop the resistance to Bt cotton that has been predicted (Wu *et al.*, 2002a; Tabashnik *et al.*, 2003).

In the present study, insect concentrations often formed at heights above 500 m AGL, which is higher than those observed during spring or fall migrations of the oriental armyworm *Mythimna separata* (Chen *et al.*, 1989) and the beet armyworm *Spodoptera exigua* (Feng *et al.*, 2003) in China, in a

mixed moth population in Australia (Drake, 1985), and in unidentified insects in southern North America (Beerwinkle *et al.*, 1994). This difference could be attributed to the high air temperature in summer at Langfang. It has been hypothesized that the insects often seek the warmest air for migration and in many early studies the maximum densities were found where temperatures were highest (Schaefer, 1976; Riley and Reynolds, 1979; Drake, 1984). In spring, temperature inversion was often accompanied by a wind maximum, so layering may then have been a response to either feature (Feng *et al.*, 2004b). Recent studies (Domino *et al.*, 1983; Drake, 1985; Wolf *et al.*, 1986; Hobbs and Wolf, 1989; Beerwinkle *et al.*, 1994; Riley *et al.*, 1995; Feng *et al.*, 2004b), however, suggested that peak density of insects was associated with a maximum in the wind speed or in wind shear rather than with a temperature inversion. Honeybees are able to sense the wind so as to maintain accurate compensation for lateral wind drift (Riley *et al.*, 2003), similarly, the *H. armigera* moths seemed to sense the wind speed and tend to fly in fast moving airflows for obtaining maximum windborne transport. This provided more evidence for the later hypothesis. To be a contrast to the common stratified feature, the wind was detected to be almost constant both in speed and direction above 200 m, forming a J-shaped profile for several nights in the present study. The vertical distribution of insect density and its variation through time suggested that insects were confined to lower altitudes under these conditions. It might be because that no more benefits would be obtained by ascending higher once >200 m. There are clearly a number of mechanisms involved in multiple layering phenomena and require further study.

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