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Research Article

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Seasonal Migration Pattern of *Nilaparvata lugens* (Hemiptera: Delphacidae) Over the Bohai Sea in Northern China

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Abstract

The brown planthopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) is a major, regionally migratory pest of rice crops in Asia. Despite intensive studies, the seasonal pattern of migration in this species remains largely unknown, especially in northern China. Analysis of monitoring data of light trapping at Beihuang island in northern China showed that brown planthopper migrants could be found at the island in any month from July to October. However, the daily number of brown planthopper migrants varied considerably from day to day, month to month, and year to year. Most of migrants were caught from July to September, with fewer in October. Simulation of backward trajectories showed that there was temporal variation in the source areas of brown planthopper migrants trapped at Beihuang. A majority of migrants trapped at Beihuang in July came from south of Beihuang. In contrast, migrants caught in August and September could be from any direction around the island. Results suggested that the brown planthopper migrants likely traveled northward in July, and Multidirectionally in August and September in northern China. Some of brown planthopper in northeastern China could escape the 'Pied Piper effect' and migrate southward in September.

Key words: brown planthopper, *Nilaparvata lugens* (Stål), migration, HYSPLIT, trajectory analysis

Brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), is an important rice pest across Asia. The pest of brown planthopper not only causes direct damages to rice plants but also transmits plant viruses that may do additional harm to plants at the same time (Otuka 2013). In China, the pest of brown planthopper has caused huge yield losses in rice production during the past decades. The serious problem caused by brown planthopper in China dated back to 1960s when susceptible hybrid rice varieties were planted (Heinrichs and Mochida 1984, Cheng 2001). To address the issue, a research team called the National Cooperated Research Group of Brown Planthopper (NCRGBPH 1981) was formed in China to coordinate the nationwide research. One of the major findings by NCRGBPH was that brown planthopper could overwinter only in south of isotherm of 10°C in January. Results by NCRGBPH have also revealed the migratory patterns of brown planthopper in southern and central China. The earlier generation of brown planthopper adults would usually migrate northward or northeastward from tropical and subtropical regions in spring and summer, and the later generation of adults then migrate southwestward for overwintering in autumn (Otuka et al. 2008).

The pest of brown planthopper has been known to migrate passively with prevailing winds. Adults of brown planthopper usually migrate into southern China from tropical regions in March and continue to northern China with the prevailing winds in later season. Some individuals can reach northeastern China, the Korean Peninsula, and Japan. In Autumn, brown planthopper adults of brown planthopper migrate southwestward from northern China, Japan, and the Korean Peninsula to their overwintering region with prevailing winds (NCRGBPH 1981).

Previous studies on brown planthopper migration have been focusing on the tropical and subtropical regions, and southern and eastern China (Riley et al. 1991, Riley et al. 1994). In contrast, studies on the migratory dynamics of brown planthopper in northern Asia have been rare, partly because the pest was thought less important in northern region. However, literatures show that as brown planthopper is capable of migrating farther north, this pest species has become an increasing problem in northern and northeast Asia (Feng et al. 1992, Heong and Hardy 2009). In 1991, for instance, a mass population of brown planthopper arrived at the coast of Bohai Sea, which is 1,500 km from the planthopper source area (Feng et al. 2002). Therefore, there is a pending need to address this pest in northern region. Related issues include seasonal variation in population size and seasonal pattern in migratory directions and so on. So far, these issues have not been addressed, especially with detailed data.

To address the issues mentioned above, we conducted a 5-yr monitoring study at Beihuang island (BH). We aim to understand the migratory pattern of brown planthopper in northern China and Asia.

Materials and Methods

Searchlight Trapping Data

Searchlight trap monitoring for brown planthopper was carried out from Spring to Autumn (April to September in 2012–2015 and April to October in 2016–2017) at BH (38.24′N; 120°55′E) in Shandong Province (Fig. 1). BH is a small island (about 2.5 km^2), where no crop was planted. The searchlight trap was equipped with a 1-kW metal-halide lamp and incorporated a parabolic reflector that can generate a narrow vertical light beam. The searchlight trap could attract insects flying 500 m above the ground level (AGL) (Feng et al. 2009) and had been used to capture long-distance migrants of brown planthopper in Southern China (Qi et al. 2014). The searchlight trap was turned on at sunset and off at sunrise every day, except for power loss or bad weather. Trapped insects were collected with a nylon net bag (60 mesh) beneath the trap and kept in a freezer at −20°C before being identified.

Mixed-Effect Regression Analysis

The data of daily (or nightly) catches of brown planthopper adults were analyzed using a generalized linear mixed-effect regression. Because the daily number of catches was a count number within a time interval, a Poisson or negative binomial distribution for this variable was expected. Preliminary test analysis showed that a negative binomial distribution was acceptable. Therefore, a link function of log was used. To deal with possible violation of model assumption, a method of robust covariance was adopted for parameter estimation. Because the seasonal effect was the main concern of this study, month was considered a fixed effect and year a random effect. This mixed-effect regression analysis tested the significance of both the fixed effect of month and random effect of year and estimated the expected values of daily number of catches for each month from July to October.

Simulation of Backward Trajectories

Migration trajectory was simulated by the TrajStat module in MeteoInfo (version 1.3.3) (Wang 2014), a GIS software for meteorological data visualization and analysis. In the TrajStat module, trajectories were calculated by the method of Hybrid Single Particle Lagrangian Integrated Trajectory (HYSPLIT), which was developed by the United States National Oceanic and Atmospheric Administration Air Resources Laboratory (Stein et al. 2015). The detailed method of HYSPLIT had been described in elsewhere (Qi et al. 2014, Westbrook et al. 2016). The detail information of meteorological data Global Data Assimilation System (GDAS) used in trajectory simulation was described below.

Meteorological Data

Aerial temperatures was one of the key elements for trajectory simulation. The data of hourly temperature around BH during the migration season were extracted from the GDAS, with a spatial resolution of 1° latitude × 1° longitude and temporal resolution of 6 h (Mcpherson et al. 1979). Box plot was used to analyze the aerial temperature at a series of pressure levels.

Flight Height, Speed, Time and Duration

Because brown planthopper could hardly fly with an aerial temperature lower than 16.5°C (Baker et al. 1980), the up-limited flight altitude was set to where the aerial temperature was above 16.5°C. Brown planthopper could takeoff or land in either dusk or dawn (Deng 1981, Riley et al. 1991, Riley et al. 1994), thus 0500, 0600, 0700, 1900, 2000, and 2100 hours were set as the valid takeoff time and landing time in the backward trajectory simulation. Local time used was Beijing Time (UTC+8 h). The searchlight trap site was set as the end location. Flight speed of brown planthopper was set the same as the wind. The max flight duration of brown planthopper

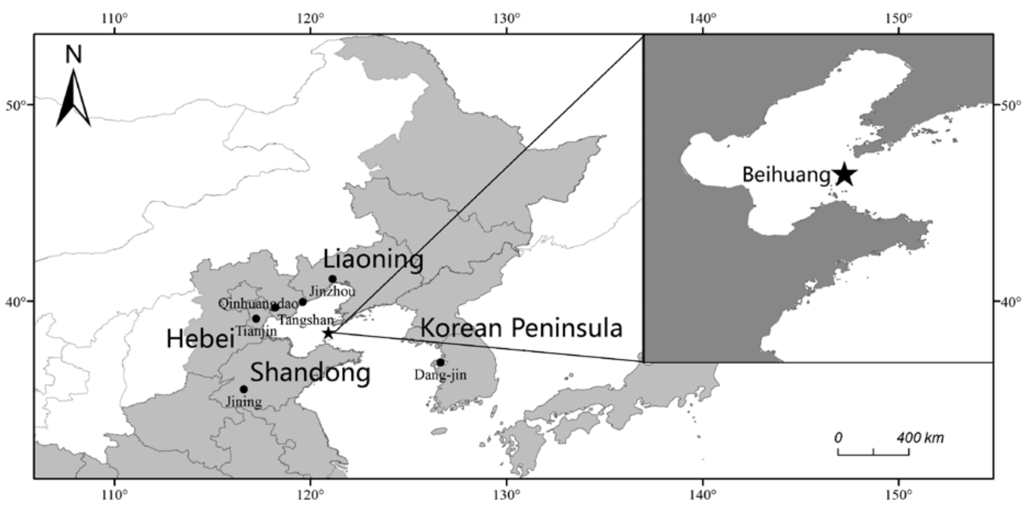

Fig. 1. Maps of the main rice-growing region in China and other Asian countries. Black dots represent the stations in surrounding regions of Beihuang with occasional brown planthopper outbreaks.

was set to 36 h according to previous research (Rosenberg and Magor 1983, Qi et al. 2014).

Source Area Analysis

Source areas of brown planthopper trapped in BH were determined by the endpoints of trajectory. In July, all days with at least one trapped adult were selected as migration events. In August and September, only those days with the number of trapped adults greater than five were selected as migration events. In October, brown planthopper was only trapped on 3 d in 2016, and the number of trapped brown planthopper was only one in each day. The trapped brown planthopper at BH in October may be resident populations landing on BH on previous dates. Thus the days with trapped brown planthopper in October were excluded as migration events for further trajectory simulation. Finally, a total of 49 migration events or days (6 in July, 22 in August, and 21 in September) with migration occurrence were selected for trajectory simulation.

To show the spatial difference in source areas, we divided the mainland surrounded BH into four regions by four directions of BH, region I (including Shandong and neighbor provinces), region II (including Hebei and neighbor provinces), region III (including Liaoning and neighbor provinces), and region IV (including the Korean Peninsula and Japan). We then displayed the spatial distribution of backward trajectory endpoints over the four regions.

Because brown planthopper is monophagous and feeds solely on rice, and the macropterous adults usually emerge at the ripening stage of rice, especially at yellow-ripe stage (Cheng et al. 1979), the following criteria were used in analyzing the direct sources of brown planthopper migrants. First, ripening rice existed in the locations. Second, there were macropterous adults of brown planthopper in the paddy fields. Third, the takeoff time of the migrants was at dusk or dawn.

Results

Seasonal Pattern in the Number of Light-Trapped Brown Planthopper Migrants

The adults of brown planthopper were trapped on BH in 4 mo from July to October. The daily number of adults varied considerably from day to day, month to month, and year to year (Fig. 2). In 2012–2014 and 2016, the initial capture occurred in July, while

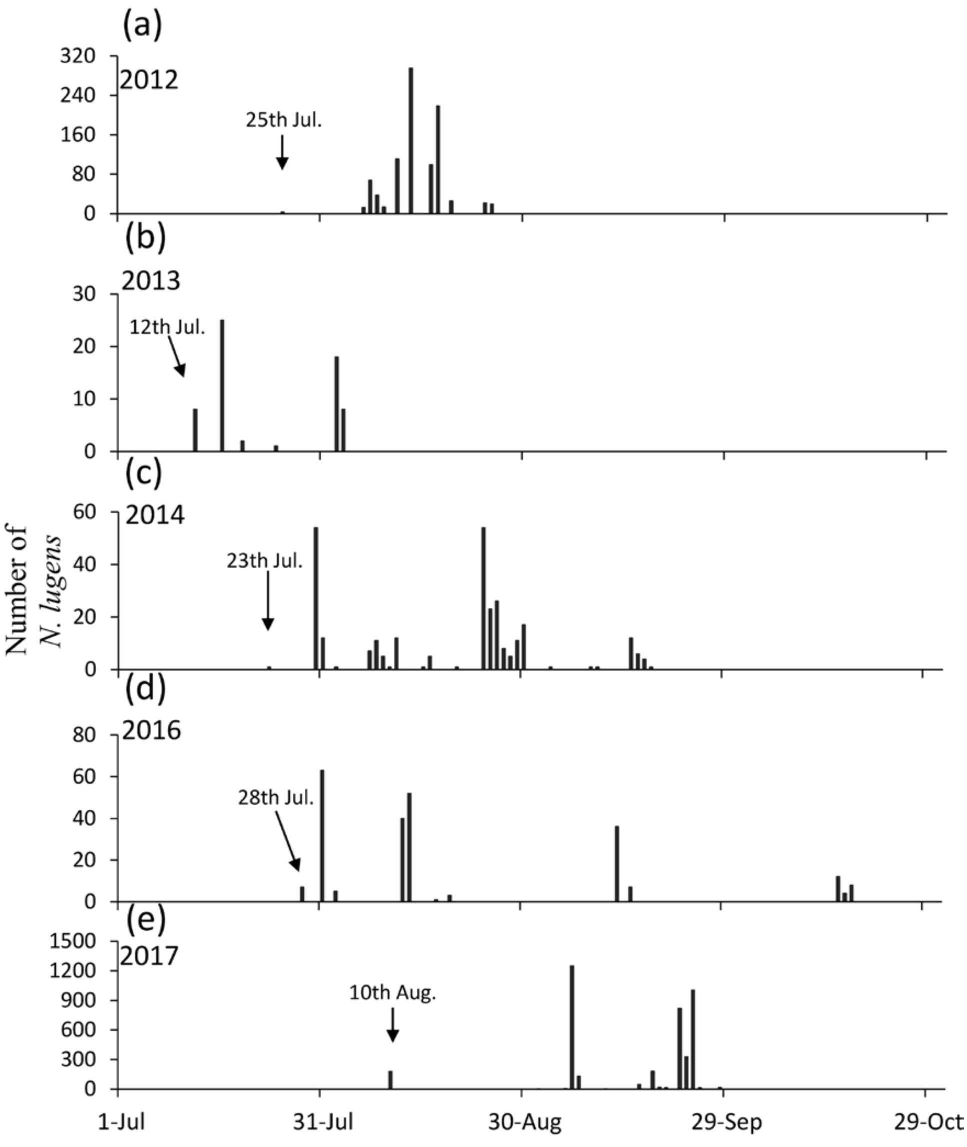

Fig. 2. Daily number of catches of brown planthopper adults in the searchlight trap from July to October. The data include 5 yr in 2012–2014 (panels a–c) and 2016–2017 (panels d and e). No adults were trapped in 2015. The arrow in each panel indicates the date of first catches in a specific year.

in 2017, the initial capture occurred in August. During the study period, the earliest capture occurred on the 12 July while the latest on the 18 October.

To examine the seasonal differences in the daily number of catches, a generalized linear mixed-effect regression was conducted (see Methods). The analysis demonstrated that there were significant seasonal differences in the daily number of catches, particularly between October and the rest of 3 mo ($P = 0.007$; Table 1). The random effect of year was not significant ($P = 0.268$; Table 1). Model estimation showed that the average number of daily catches was highest in September and lowest in October. The expected daily numbers of catches from July to October were 10.1, 10.2, 15.3, and 3.2, respectively.

Seasonal Pattern in Flight Altitude of Brown Planthopper Migrants

The aerial temperature at night was a crucial element for determining the flight altitude of brown planthopper migrants. Box-plot analysis showed that in July and August, the average air temperatures at 0200 hours were higher than 16.5°C when atmospheric pressure was below 850 hPa (approximately 1,500 m above sea level [a.s.l.]) (Fig. 3). In September, the average air temperatures at 0200 hours were higher than 16.5°C only when atmospheric pressure was below 900 hPa (approximately 1,000 m a.s.l.). Thus, the flight heights of brown planthopper at different months were set as follows: 1,500, 1,000, and 500 m in July and August, and 1,000 and 500 m in September. In October, the aerial temperature at all altitudes is below16.5°C and cannot support long time flight of brown planthopper, which indicates that days with trapped brown planthopper in October could hardly be migration events.

Mainland Source of Brown Planthopper Migrants

By backward simulation of trajectory, a total of 5,669 endpoints were identified. Since brown planthopper is monophagous and just feed on rice, endpoints located in the sea or areas with no host plants for brown planthopper were determined to be invalid and therefore not considered for further analyses. Based on this criterion, only 2,548 endpoints were determined to be valid. Among the valid endpoints, the farthest was located in south Japan, about 1,500 km away from BH.

The spatial distribution of valid endpoints per month from July to September indicated seasonal variation in source area of brown planthopper migrants captured at BH. In July, most of backward trajectory endpoints were located in south region of BH (region I), and some of the endpoints were located in north region of BH (regions II and III) (Fig. 4). The farthest endpoints on mainland were in south of Jiangsu Province. In July, the rice planted in the peripheral regions around Bohai Sea (Shandong, Hebei and Liaoning) is at tillering stage and is also similarly as the mid and lower Yangtze River basin at brown planthopper immigration period and is impossible to provide macropterous brown planthopper to the island. During this period, the source population of brown planthopper should be only come from the early rice cropping areas in central eastern China at 26–30°N (Hunan, Jiangxi, Fujian, and Zhejiang). Our results demonstrate that brown planthopper mainly come from South of BH, while rice in this region cannot provide macropterous brown planthopper, which means that this region is not the direct source of brown planthopper trapped at BH. In other words, in July, brown planthopper cannot reach BH from source region with once migration.

In August, endpoints distributed in four regions (I, II, III, and IV) around BH (Fig. 5). Although rice in these neighbor regions of BH could host brown planthopper adults, the development stage of rice cannot trigger the outbreak of enormous macropterous brown planthopper. The direct source areas of brown planthopper in August should be located the mid and lower Yangtze River basin at 30–32°N (Hunan, Hubei, Jiangxi, Zhejiang and Anhui) where the early rice is at the ripening stage. Our results demonstrated that brown planthopper trapped at BH may take multiple re-emigrations and then reach BH. We can also infer that brown planthopper may have no ability to select the migrating dates to reach suitable regions for their survival. By re-emigration, brown planthopper could, to some extent, resolve this problem and to ensure their landing in desirable regions. The endpoints in the Korean Peninsula indicated that, in August, brown planthopper take frequent transnational communication in northern China.

In September, most endpoints were located in China (regions I, II, and III), and only a few of them were in the Korean Peninsula (region IV) (Fig. 6). In this month, the single rice planted in north of 32°N (Jiangsu, Anhui, Henan, Shandong, Hebei, Liaoning) gradually ripe from south to north. The new emerged macropterous brown planthopper in this region will emigrate riding on the wind with different directions, some of them may arrive at BH.

The endpoints in northern region of BH indicated that the newly emerged macropterous brown planthopper during the ripe stage of rice migrated southward into warm regions in September. While a large number of endpoints in south of BH demonstrated that some brown planthopper might still take northward migration.

Table 1. Summary of the generalized linear mixed-effect regression

	Factor	*F*	df1	df2	*P*-value		
	Month	240.1	3	226	0.000		
	Level	Coef.	SE	*t*	*P*-value	LB	UB
Fixed effect	Intercept	2.725	1.153	2.364	0.019	0.454	4.996
	July	−0.409	1.330	−0.308	0.759	−3.029	2.211
	Aug.	−0.398	0.834	−0.478	0.633	−2.402	1.245
	Oct.	−1.551	0.565	−2.745	0.007	−2.664	−0.437
	Sept.	0[a]					
Random effect	Factor	Variance	SE	*Z*	*P*-value	LB	UB
	Year	1.519	1.372	1.107	0.268	0.259	8.918

LB and UB: lower and upper bound of the 95% confidence interval. The target is the number of brown planthopper adults caught per night by a light trap during 2012–2017. The fixed and random effects are month and year, respectively.

[a]Redundant parameter (corresponding to intercept).

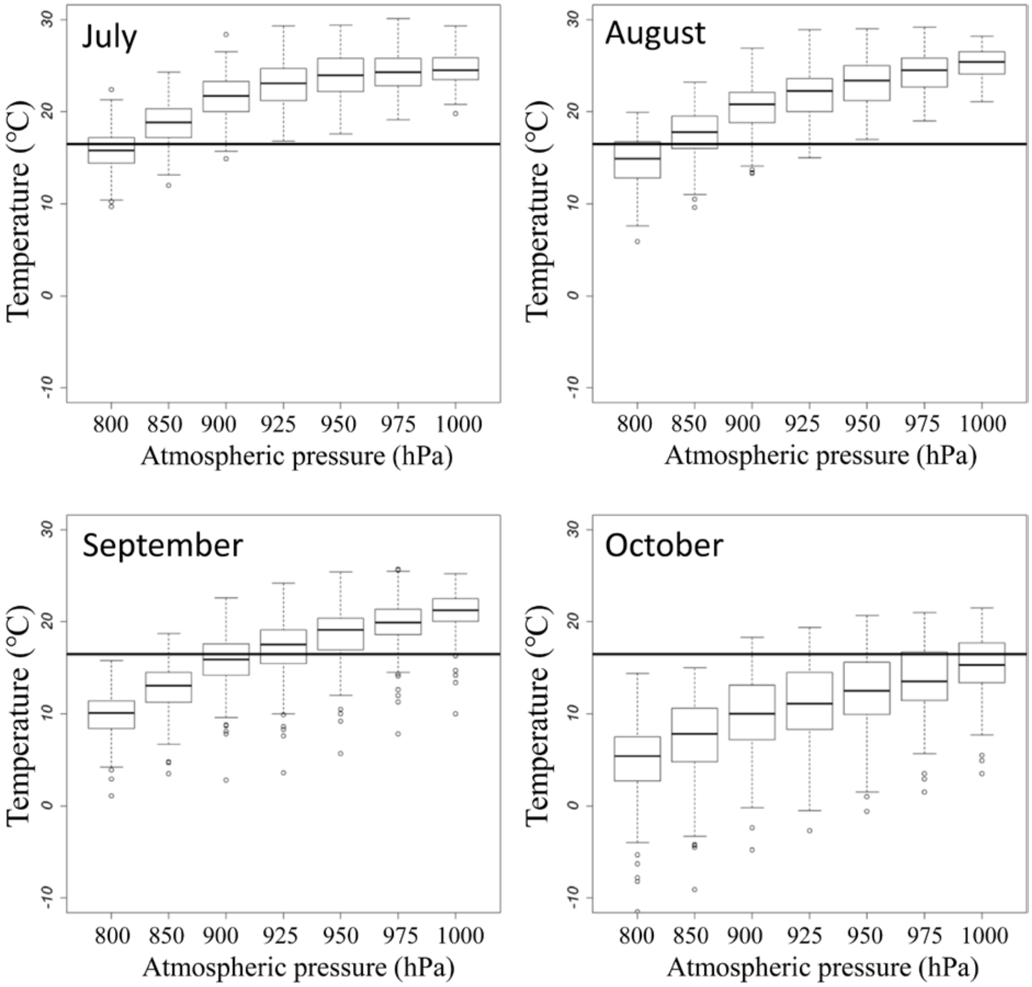

Fig. 3. Aerial temperature against atmospheric pressure at 0200 hours in July, August, September, and October. The horizontal black line in each panel indicates the threshold temperature of 16.5°C below which brown planthopper cannot fly.

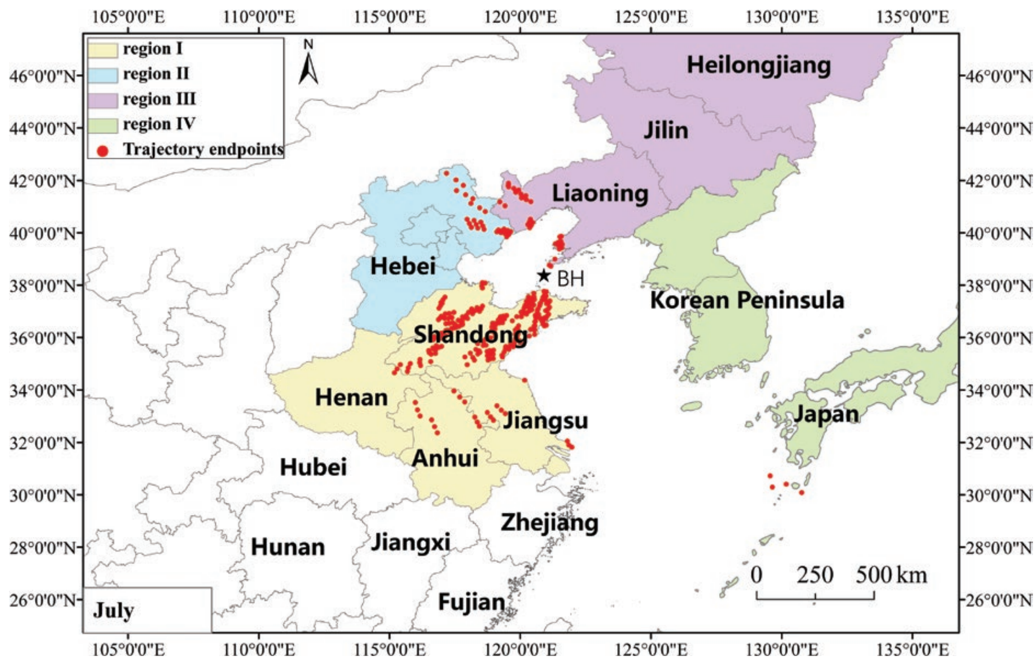

Fig. 4. Spatial distributions of backward trajectory endpoints in July.

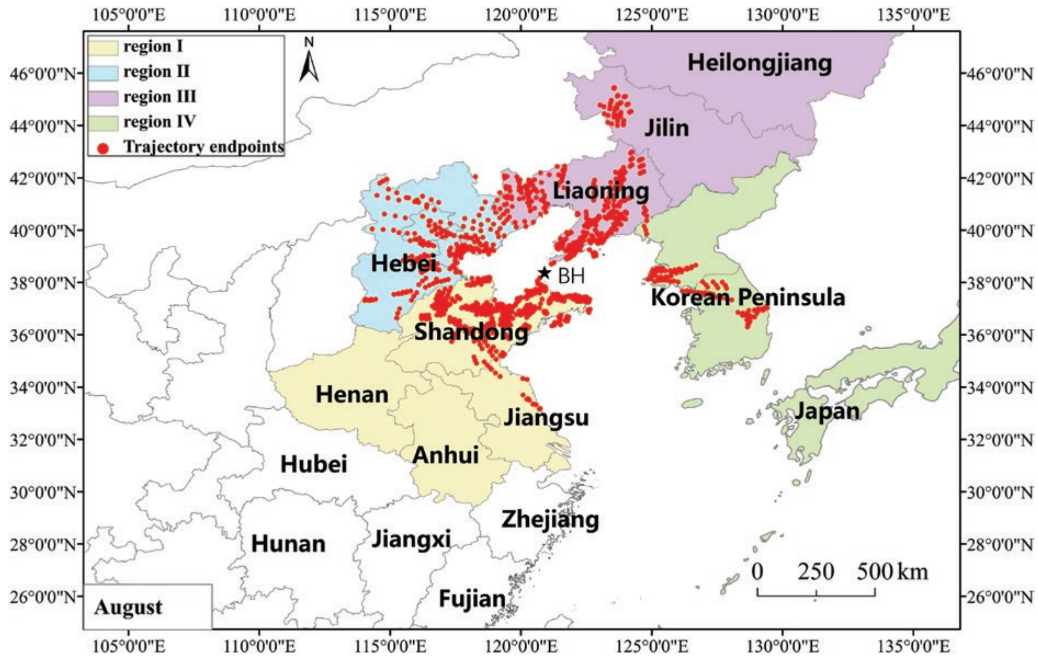

Fig. 5. Spatial distributions of backward trajectory endpoints in August.

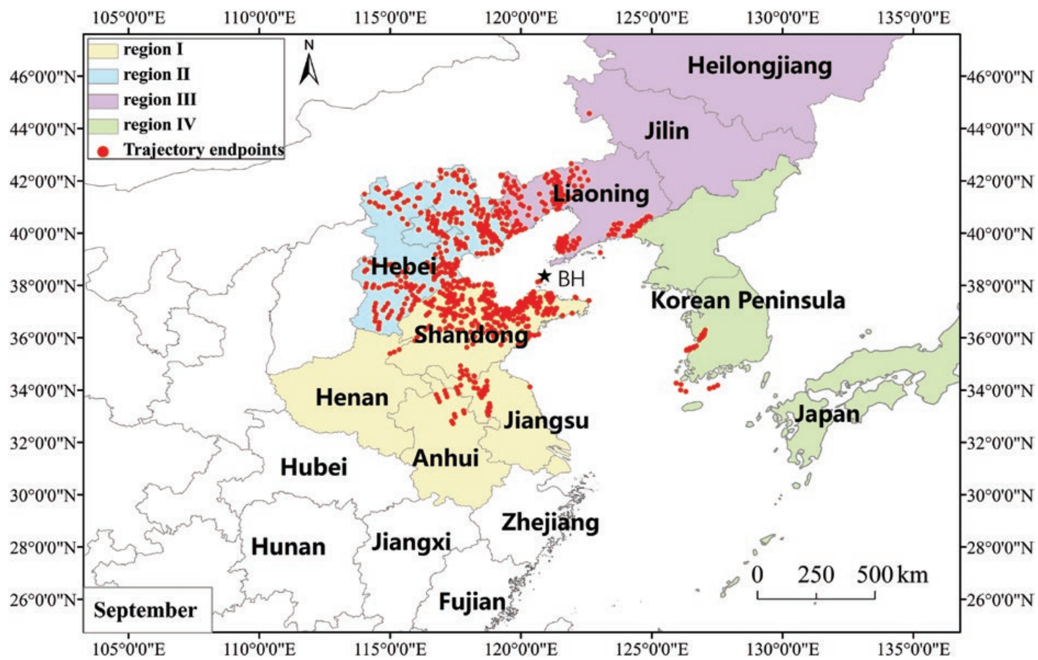

Fig. 6. Spatial distributions of backward trajectory endpoints in September.

Discussion

The monitoring data reported here showed that the Bohai Strait was an important pathway for migration of brown planthopper in northern China and BH was an ideal location for monitoring the migratory pattern. The brown planthopper migrants could be found at BH in 4 mo from July to October, but the daily number of brown planthopper migrants varied considerably from day to day, month to month, and year to year. The migrants of brown planthopper trapped at BH might come from all directions in August and September, but mainly from south in July.

The migrants of brown planthopper trapped at BH in October was notably fewer than other months. This was likely related to the 'Pied Piper effect' (Mcneil 1987), where the cool air temperature limited the migratory capability of the insect. In October of northern China, the ground and air temperature was usually below 16.5°C, which greatly limited the long-distance migration of brown planthopper. This was in contrast with the cases in August and September when air temperature was higher. Therefore, migration of insect was not affected by the Pied Piper effect.

The number of brown planthopper migrants trapped at BH was far fewer than that in southern China, where about 10,000 brown planthopper adults were trapped nightly (Qi et al. 2014). This was expected because the population sizes were much larger in the temperate southern regions. It also worth to note that there were substantial annual fluctuations in the migratory population over the Bohai Sea. These fluctuations were likely caused by the population fluctuations in central and southern China as well as the annual variation in monsoon airflows (Feng et al. 1992).

Analysis of air temperature distribution demonstrated that flight altitudes of brown planthopper differed substantially at BH among the 4 mo. This was consistent with studies elsewhere. In Central China, by means of airplane collections, Deng (1981) found brown planthopper distributed at height of 0.3–2.5 km and 0.1–1.5 km in summer and autumn, respectively. In southern China, brown planthopper individuals were caught at 1–1.5 km in spring, 0.6–1.5 km in autumn, 0.2–0.8 km in late autumn (Rosenberg and Magor 1983).

Our results here suggested that brown planthopper in northern China could migrate northward in prevailing southerly winds in July, August, and September, and return in prevailing northerly winds in August and September. The migratory pattern was generally consistent with East Asian monsoon airflows.

Previous studies have found that the traveling brown planthoppers could migrate again if the landing region was not suitable and the energy was enough for further migration (Liang et al. 1991). However, the re-emigration capacity of brown planthopper was expected to be relatively weak, and the ratio of brown planthopper population with re-emigration was usually very low in temperate region (Feng et al. 2001). Therefore, we did not consider such a migrating behavior in the present study. Future study to consider re-emigration behavior may be needed.

Acknowledgments

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