Appl. Entomol. Zool. 45 (2): 259–266 (2010)
http://odokon.org/

The 2008 overseas mass migration of the small brown planthopper, *Laodelphax striatellus*, and subsequent outbreak of rice stripe disease in western Japan

Akira OTUKA,[1] Masaya MATSUMURA,[1,*] Sachiyo SANADA-MORIMURA,[1] Hiroaki TAKEUCHI,[1] Tomonari WATANABE,[2] Reiko OHTSU[3] and Hideaki INOUE[4]

[1] National Agricultural Research Center for Kyushu Okinawa Region; Koshi, Kumamoto 861–1192, Japan
[2] National Agricultural Research Center; Tsukuba, Ibaraki 305–8666, Japan
[3] Nagasaki Plant Protection Station; Isahaya, Nagasaki 850–0062, Japan
[4] Kagoshima Prefectural Institute for Agricultural Development; Minami-Satsuma, Kagoshima 899–3401, Japan

(Received 4 September 2009; Accepted 22 December 2009)

Abstract
The small brown planthopper, *Laodelphax striatellus* (Fallén), is one of the major insect pests of rice in East Asia. This species is known as a vector insect of *Rice stripe virus*, and has been believed to show strong indigenousness, unlike other migratory rice planthoppers, the brown planthopper and the whitebacked planthopper. Large trap catches of *L. striatellus* with high viruliferous rates were recorded in western Japan on a windy day in early June 2008, and subsequently, rice stripe diseases spread in these regions. The migration source was estimated using backward trajectory analysis, and found to be Jiangsu Province, China. *Laodelphax striatellus* with high viruliferous rates and rice stripe diseases has occurred markedly throughout Jiangsu Province since 2004, and early June is the wheat harvest season, which could serve as a stimulus for planthopper emigration. Insecticide susceptibility of populations collected in rice fields both in western Japan and Jiangsu were compared by a topical application method. Both Chinese and immigrant populations showed resistance only against imidacloprid, whereas Japanese local populations showed resistance only against fipronil. Collectively, this evidence suggested that the overseas migration of viruliferous *L. striatellus* from China to western Japan occurred and subsequently caused rice stripe diseases in the areas to which insects immigrated.

Key words: Backward trajectory analysis; long-distance migration; imidacloprid; fipronil; insecticide susceptibility

INTRODUCTION

The small brown planthopper, *Laodelphax striatellus* (Fallén), is a major insect pest of rice in East Asia. This species transmits *Rice stripe virus* to rice plants, and causes rice stripe disease (Kuribayashi, 1931a; Kisimoto and Yamada, 1998). An outbreak of this disease was first recorded in Nagano Prefecture, central Japan in 1903 (Kuribayashi, 1931b). Large outbreaks of the disease occurred mainly in the Kanto region in 1977 and 1984 (Shinkai, 1985). After these outbreaks, the total occurrence area continuously decreased to 15,000 ha by 2000 (Ministry of Agriculture, Forestry and Fisheries (MAFF), 2009); however, the occurrence area of rice stripe disease has recently shown an increasing trend (MAFF, 2009). The viruliferous rate of *L. striatellus* in Kyushu region, western Japan, has also indicated an increasing trend since 2000, and had an average value around 5% in 2008, and over 10% at some points within the region (Matsumura and Otuka, 2009).

Meanwhile, on the other side of the East China Sea, *L. striatellus* and rice stripe disease have been increasing since 2000 in southeastern provinces, such as Jiangsu and Zhejiang, China (Sogawa, 2005; Zhu, 2006; Wang et al., 2008).

Since *L. striatellus* is able to overwinter in temperate zones, including all regions in Japan, by diapausing as third- or fourth-instar nymphs (Ito and

---

* To whom correspondence should be addressed at: E-mail: mmasa@affrc.go.jp
DOI: 10.1303/aez.2010.259

Okada, 1985; Noda, 1990), outbreaks of rice stripe disease in Japan have been believed to be caused by domestic populations of *L. striatellus*. A few reports have implied that overseas migration and subsequent outbreak of rice stripe disease might have occurred in the western Kyushu region in 1985 (Fukamachi et al., 1986; Kimura et al., 1986; Sogawa, 1992), but little evidence was available to link overseas migration to rice stripe disease outbreaks in Japan.

The insecticide susceptibility of *L. striatellus* has been changing in East Asia. Recently, Chinese populations collected in Jiangsu and Zhejiang Provinces in 2006 developed resistance to imidacloprid (Ma et al., 2007), whereas some Japanese populations in the Kyushu region showed resistance to fipronil (Murakami et al., 2007; Nishimoto et al., 2008).

Under these circumstances, large trap catches of *L. striatellus* were recorded in western Kyushu in early June, 2008 and a subsequent epidemic of rice stripe diseases occurred in areas where large immigrations occurred, as described in detail below.

This study investigated the possibility that long-distance migration served as a cause of the epidemic. Several methods were employed to elucidate the overseas migration and subsequent outbreak of rice stripe disease, including the use of trap catches, source estimation by backward trajectory analysis (Otuka et al., 2005a), and evaluation of insecticide susceptibility by a topical application method. This paper presents, for the first time, positive evidence for the hypothesis that *L. striatellus* migrates for a long distance from overseas and causes ripe stripe disease in Japan.

MATERIALS AND METHODS

Trap catches. Two different types of traps were used for monitoring *L. striatellus*; one was a tow net trap with a 1-m ring mounted at the top of a pole 10 m above the ground, and the other was a Johnson and Taylor suction trap installed on the roof of a three-story building. The net trap is located at Nagasaki Plant Protection Station, Isahaya City, Nagasaki Prefecture (32.83°N and 130.02°E), and the suction trap is located at Kagoshima Plant Protection Station, Minami-Satsuma City, Kagoshima Prefecture (31.48°N and 130.34°E) (Fig. 1). These traps are separated north to south by 300 km and began operation in April 2008. Insects caught by the traps were collected at 9:00 every morning and were identified by well-trained plant protection officers using a stereoscopic microscope. The density of immigrants was investigated in an observational rice field near the suction trap on 9 June. Rice seedlings were transplanted in late May. Immigrant density in early June was not investigated in Nagasaki.

Backward trajectory analysis. Backward trajectory analysis was conducted to estimate the possible migration source for trap catches in Kyushu (Otuka et al., 2005a). Backward trajectory is the backward trace of three-dimensional insect position. The starting time of backward trajectories was set every 1 h within 24 h of each catch date. For each starting time, 20 backward trajectories were calculated with different initial heights ranging from 100 to 2,000 m at an interval of 100 m above the trap site. Overall, 480 trajectories were calculated for each catch date and terminal time. The insect was assumed to fly at the same speed as the wind; therefore, for each time step, the insect's position goes back by a small position vector [m] of wind speed [m/s] multiplied by a time step [s]. Wind speed was simulated by a weather prediction model (Otuka et al., 2005a). After travelling over the sea, the backward trajectory was terminated at three different times; dusk, 12:00 Coordinated Universal Time (UTC) 2 days before the catch, dawn, 21:00 UTC, and dusk, 12:00 UTC, on the previous day. Dawn and dusk are the times when planthoppers were assumed to fly out of the source areas. These terminal times were three values closer to the catch date. They were used not only because they reduced flight durations, but also because backward trajectories with such terminal times could reach possible source areas. Terminal points of trajectories were distributed over a region depending on their starting time and height (terminal point distribution), and were plotted on a map to identify possible source areas. In the analysis, air temperature at the flying height was not considered, although insects may stop beating their wings or fly at a slower speed than wind in cooler air at high altitudes.

Evaluation of insecticide susceptibility. To determine the insecticide susceptibility of immigrant populations of *L. striatellus*, macropterous adults of the two immigrant populations (Japan-KG-08 and Japan-KMA-08) were collected from rice fields in Kyushu, Japan on 9 and 7, June 2008, respectively, just after the mass migration (Fig. 1; Table 1). For comparison of insecticide susceptibility between immigrant and domestic populations in Japan, three domestic populations of *L. striatellus* were collected from wheat fields in 2006–2008 (Japan-SG-06, Japan-GF-07, and Japan-KMK-08) (Fig. 1; Table 1). For comparison of insecticide susceptibility between immigrant populations in Japanese and Chinese populations, three Chinese populations of *L. striatellus* were collected from rice fields in Jiangsu and Zhejiang Provinces during September to October 2008 (China-JSY-08, China-JSC-08, and China-ZJ-08) (Fig. 1; Table 1).

The collected populations were derived from more than 100 adults with the same number of males and females. These populations were maintained in the laboratory for 2–5 generations prior to testing using rice seedlings (var. Reihou) growing at a temperature of 25°C under light conditions of 16L8D.

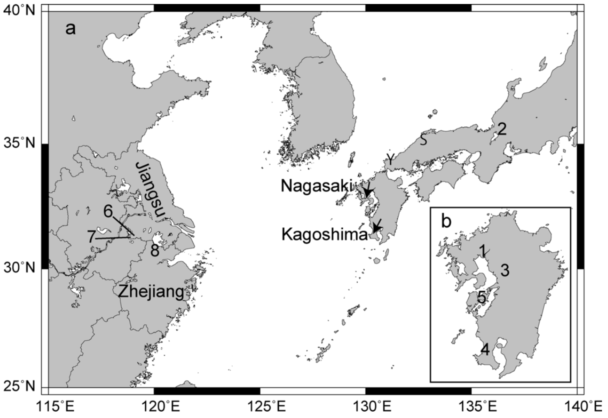

Fig. 1. Locations of trap and collection sites. Upper and lower arrows in the figure indicate trap locations in Isahaya, Nagasaki Prefecture and Minami-Satsuma, Kagoshima Prefecture, respectively. Numbers shown in figures a and b indicate collection sites of *Laodelphax striatellus* populations shown in Table 1. Letters Y and S denotes Yamaguchi and Shimane Prefectures, respectively.

The insecticide susceptibility of the eight populations was monitored by a standard topical application method (Fukuda and Nagata, 1969) on imidacloprid (98.5%), fipronil (90.7%), BPMC (96.9%), dinotefuran (99.8%), and etofenprox (99.9%). Dinotefuran and etofenprox were not tested for populations collected before 2008 and 2007, respectively. These insecticides were provided by Bayer CropScience K. K. (Tokyo, Japan) for imidacloprid, BASF Agro. Ltd. (Tokyo, Japan) for fipronil, Sumitomo Chemical Co. Ltd. (Tokyo, Japan) for BPMC, and Mitsui Chemical (Tokyo, Japan) for dinotefuran and etofenprox.

Long-winged female adults within 7 days after emergence were anaesthetized with carbon dioxide for about 5 s prior to treatment. A 0.08 μl droplet of acetone solution was applied topically on the dorsal surface of the thorax with a hand microapplicator (Burkard Manufacturing Company Ltd.). The treated insects were kept in a transparent plastic box (5 cm diameter, 10 cm high) with rice seedlings at 25°C and relative humidity of 55±15% under light conditions of 16L8D. Mortality was determined 24 h after treatment for all insecticides. All tests were conducted on 2–5 generations after collection. More than 45 females were used for each insecticide concentration. Tests were carried out on 5–6 concentrations. The average body weight of the tested insects was 1.24±0.05 mg (mean±S.E.).

The LD_{50} value, 95% confidence interval, and slope of the regression line were calculated by

Table 1. Locality and collection date of tested populations of *Laodelphax striatellus*

No.[a]	Population	Locality	Lat/Long	Collection date	Collected field
1	Japan-SG-06	Kawazoe, Saga, Japan	33.22°N, 130.30°E	31 May 2006	Wheat
2	Japan-GF-07	Ohno, Gifu, Japan	35.46°N, 136.60°E	1 June 2007	Wheat
3	Japan-KMK-08	Koshi, Kumamoto, Japan	32.92°N, 130.76°E	22 May 2008	Wheat
4	Japan-KG-08	Minami-Satsuma, Kagoshima, Japan	31.48°N, 130.33°E	9 June 2008	Rice
5	Japan-KMA-08	Amakusa, Kumamoto, Japan	32.41°N, 130.27°E	7 June 2008	Rice
6	China-JSY-08	Yaxi, Gaochun, Jiangsu, China	31.39°N, 119.06°E	2 October 2008	Rice
7	China-JSC-08	Chinxi, Gaochun, Jiangsu, China	31.34°N, 118.86°E	2 October 2008	Rice
8	China-ZJ-08	Huzhou, Zhejiang, China	30.84°N, 120.10°E	30 September 2008	Rice

[a] See Fig. 1 for the location of the collection sites.

Bliss's (1935) probit method using PoloPlus software (LeOra Software Company, 2003). To compare resistance levels between populations, likelihood ratio tests of equality for slopes and intercepts of probit regression lines were conducted using PoloPlus (LeOra Software Company, 2003; Robertson et al., 2007). The significance level of each test was adjusted with the sequential Bonferroni method (Rice, 1989) to control Type I error across pairwise comparisons.

RESULTS

Trap catches

The number of *L. striatellus* caught in the net trap in Nagasaki and the suction trap in Kagoshima from May to early June is shown in Fig. 2. In Kagoshima, 106 macropterous adults (female 52, male 54) of *L. striatellus* were caught on 6 June 2008. No *L. striatellus* was caught previously from 1 May to 5 June. Strong westerly winds were recorded in Kagoshima on the catch date. A field survey was performed on 9 June, and it was found that the population density of adult *L. striatellus* was 4.5 individuals per hill. This value was the highest ever recorded at this location for this season.

Sixty-three *L. striatellus* were caught in Nagasaki. This catch number was the highest trap catch in June for the last 10 years. Small catches were seen in late May that may be due to emigrants from harvested wheat fields in the region.

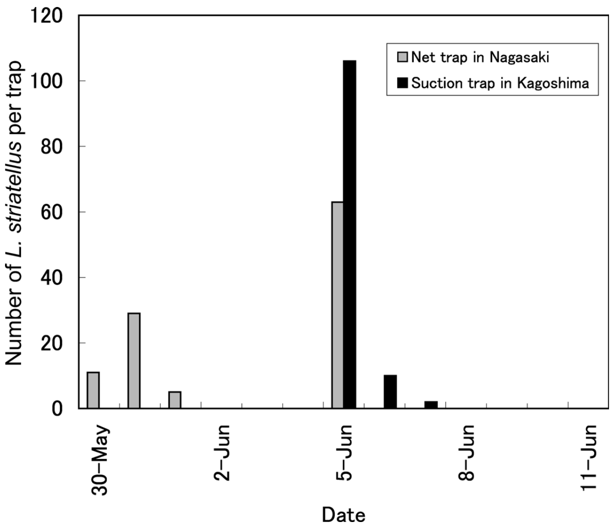

Fig. 2. Trap catches of *Laodelphax striatellus* in Isahaya, Nagasaki Prefecture and Minami-Satsuma, Kagoshima Prefecture in 2008. A tow net trap for Nagasaki and a Johnson and Taylor suction trap for Kagoshima were used. Trap locations are indicated in Fig. 1.

Source estimation

Distributions of terminal points of backward trajectories that started over Kagoshima (a) and Nagasaki (b) on 5 June 2008 are shown in Fig. 3. Although the terminal time for both cases differed depending on different wind conditions on the trajectories, a large portion of the terminal points was distributed over Jiangsu Province, China. Hence, the possible source of *L. striatellus* immigration to

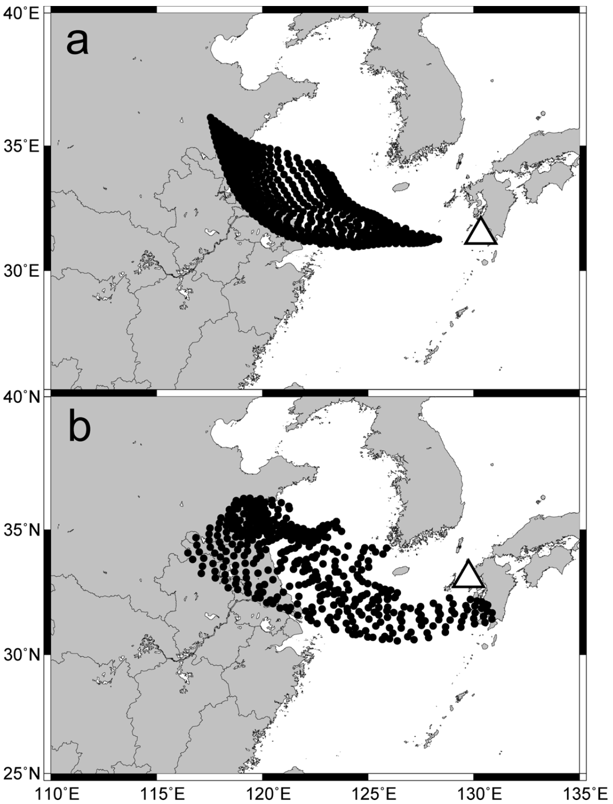

Fig. 3. Distribution of terminal points of backward trajectories. a) Trajectories that started over Minami-Satsuma, Kagoshima Prefecture (triangle) terminated at 20:00 Chinese Standard Time (12:00 UTC) on 4 June 2008. b) Trajectories that started over Isahaya, Nagasaki Prefecture (triangle) terminated at 05:00 Chinese Standard Time (21:00 UTC) on 4 June 2008. The starting time of the trajectories on a catch date ranged over 24 h at intervals of 1 h. Since trajectories have different flight durations depending on their starting times, the terminal points are distributed mainly in the wind direction. Terminal points over the sea were disregarded for source estimation because the sea cannot be a source; therefore, the figures show that terminal points were distributed over Jiangsu Province in both cases.

Table 2. LD_{50} values (μg/g) of *Laodelphax striatellus* populations collected in 2006–2008 in Japan and China[a,b]

Population	BPMC			Imidacloprid			Fipronil			Dinotefuran			Etofenprox		
	LD_{50}[c]		*b*	LD_{50}[c]		*b*	LD_{50}[c]		*b*	LD_{50}[c]		*b*	LD_{50}[c]		*b*
Japan-SG-06	67.5 ab	(54.3–81.4)	2.9	0.19 a	(0.10–0.32)	1.4	19.9 a	(8.2–52.7)	0.5	—[d]			—[d]		
Japan-GF-07	67.0 ab	(52.3–88.4)	1.9	0.20 a	(0.15–0.25)	1.6	10.5 a	(6.0–18.4)	0.7	—[d]			1.5 ab	(1.01–2.3)	1.9
Japan-KMK-08	114.5 cd	(91.3–142)	2.6	2.1 b	(1.3–4.6)	1.3	39.8 a	(15.0–184)	0.4	2.8 a	(1.6–4.4)	2.3	3.3 b	(2.2–5.9)	1.3
Japan-KG-08	52.1 a	(29.3–112)	2.1	10.5 c	(4.8–23.6)	1.0	0.09 b	(0.05–0.14)	1.8	1.6 bc	(0.48–3.2)	1.3	2.1 ab	(0.89–4.5)	1.4
Japan-KMA-08	159.7 ce	(125–209)	2.1	16.8 c	(8.4–34.6)	1.2	0.15 bc	(0.09–0.27)	3.3	4.6 d	(3.4–6.5)	1.4	3.1 b	(2.2–4.9)	1.3
China-JSY-08	210.4 e	(181–245)	3.6	16.3 c	(11.2–23.7)	1.2	0.38 d	(0.30–0.52)	2.0	1.4 b	(1.0–1.8)	1.9	2.4 ab	(1.8–3.2)	1.4
China-JSC-08	188.7 ce	(137–246)	2.5	13.5 c	(6.5–24.0)	0.9	0.34 cd	(0.17–0.86)	2.1	2.7 acd	(2.0–3.4)	2.0	2.7 b	(1.7–3.9)	2.3
China-ZJ-08	93.9 bd	(72.8–116)	2.7	0.83 b	(0.43–1.4)	1.2	44.3 a	(19.5–170)	0.7	2.9 acd	(2.0–3.8)	1.6	5.5 c	(4.4–6.8)	2.7

[a] LD_{50} value, 95% confidence interval in parentheses in μg/g, and slope of the regression line (*b*) are shown.

[b] All the LD_{50} values were determined 24 hours after treatment.

[c] Different letters indicate a significant difference between regression lines of populations by likelihood ratio tests of equality (slopes and intercepts) ($p<0.05$).

[d] Not observed.

western Japan on 5 June was found to be Jiangsu Province.

Insecticide susceptibility among immigrant, domestic, and Chinese populations

Large differences in LD_{50} values and regression lines of imidacloprid and fipronil were found between immigrant and domestic populations of *L. striatellus* in Japan (Table 2). For imidacloprid, the LD_{50} values of immigrant populations (Japan-KG-08 and Japan-KMA-08) were 5- to 88-fold larger than those for domestic populations (Japan-SG-06, Japan-GF-07, and Japan-KMK-08). The regression lines of imidacloprid were also significantly different between immigrant and domestic populations (Table 2). In contrast, LD_{50} values of domestic populations exposed to fipronil were 70- to 442-fold larger than those of immigrant populations. Regression lines of fipronil were also significantly different between immigrant and domestic populations (Table 2).

LD_{50} values and regression lines of imidacloprid and fipronil in the two immigrant populations (Japan-KG-08 and Japan-KMA-08) were similar to those in the two Jiangsu populations in China (China-JSY-08 and China-JSC-08), but were significantly different from those of the Zhejiang population in China (China-ZJ-08) (Table 2).

No large differences in the LD_{50} values and regression lines of BPMC, dinotefuran, and etofenprox (less than 4-fold) were found among the populations (Table 2).

ADDITIONAL PIECES OF EVIDENCE KNOWN SO FAR

In this section, three additional pieces of evidence obtained in previous studies are summarized for later discussion. These include the viruliferous rate of immigrants, the occurrence of rice stripe disease in invaded regions of western Japan in 2008, and the recent occurrence of *L. striatellus* and rice stripe disease in Jiangsu Province.

Viruliferous rate of immigrants

The viruliferous rate of *L. striatellus* caught on 9 June 2008 in the observation rice field near the suction trap in Kagoshima was investigated with ELISA (Clark and Adams, 1977) by Kagoshima Plant Protection Office (Fukuda et al., unpublished). The rate of viruliferous *L. striatellus* female adults was found to be 9.2% (*N*=120) (Fukuda et al., 2009). The viruliferous rate of 11.5% (*N*=200) for *L. striatellus* caught in a net trap in Yamaguchi Prefecture from 1 to 5 June in 2008 was previously reported (Nakagawa et al., 2009; letter Y in Fig. 1 denotes the location). The viruliferous rates for overwintering populations collected in Yamaguchi and Nagasaki Prefectures were 2.9 (*N*=175) and 4% (*N*=2,019), respectively (Nakagawa et al., 2009; Ohtsu et al., unpublished). The rates of immigrant populations were larger than those of overwintering populations. Based on statistical tests, the viruliferous rate of the immigrant population in Yamaguchi Prefecture (11.5%) was significantly higher than of the two overwintering populations, although no significant difference was found between the Kagoshima population and the overwintering populations (multiple comparison test for proportions (Zar, 1996), $p<0.05$).

Outbreak of rice stripe disease in western Japan

According to plant protection offices in Nagasaki and Yamaguchi Prefectures, ghost syndromes of rice stripe disease were first noticed by farmers in late June (Nakagawa et al., 2009; Ohtsu et al., unpublished). The timing of the outbreak corresponded to about one month after the immigration date. The total occurrence area of rice stripe disease in Nagasaki in 2008 was 10,720 ha, which had increased by 126% since the previous year based on the governmental statistics (MAFF, 2009). Especially in severely damaged areas, field and hill occurrence rates hit 100% and more than 50%, respectively (Ohtsu et al., unpublished). These occurrence rates were high along western coastal regions in Nagasaki, where imidacloprid was applied in seedling box treatments (Ohtsu et al., unpublished). The rice stripe disease occurrence area in Shimane Prefecture in 2008 was 3,770 ha, of which 10% was heavily damaged (MAFF, 2009; letter "S" in Fig. 1 denotes the location).

Recent occurrence in Jiangsu Province

In response to our analysis of the potential source of migration, the authors visited the Plant Protection Station of Jiangsu Province, China, and interviewed Vice Director, Dr. Ye-Qin Zhu on the recent occurrences of *L. striatellus* and rice stripe disease. The outbreak area of the disease has continuously increased within the province since 1997 and a heavy outbreak area spread throughout the province in 2004 and 2005 (Zhu, 2006). Average viruliferous rates of *L. striatellus* in the province from 2004 to 2008 were 24, 29, 23, 23 and 17%, respectively, based on data obtained during the interview. The rate peaked in 2005 and has since gradually decreased; however, viruliferous rates are still very high compared to those in Japan. Population density in rice fields on 5 June 2008 was one million per mu (1 mu=6.67 a), or 60 insect per hill (Zhu, personal communication). Early June corresponds with the peak season for wheat harvesting.

DISCUSSION

Overseas migration and subsequent rice stripe disease

Summarizing our results along with the known facts, this study presents six pieces of distinct evidence to link overseas migration of *L. striatellus* to subsequent outbreaks of rice stripe disease in Japan: i.e. (1) immigration peaks captured on 5 June 2008 in western Japan under windy weather conditions, (2) resistance of immigrants to the insecticide imidacloprid and high viruliferous rates (3) outbreaks of rice stripe disease in invaded areas, and heavy occurrence, especially in imidacloprid-applied rice fields (4) backward trajectory analysis estimated the source to be Jiangsu Province, China, (5) heavy outbreak of *L. striatellus* and rice stripe disease in Jiangsu Province, and (6) coincidence of insecticide susceptibility and high viruliferous rates between immigrants and the Jiangsu population. Collectively, the evidence supports the hypothesis that long-distance migration of *L. striatellus* from Jiangsu Province to western Japan occurred on 5 June 2008 and caused severe outbreaks of rice stripe disease in Japan.

Impact of immigrants on insecticide resistance of local population

Our results showed that insecticide resistance of the immigrant populations of *L. striatellus* was completely different from that of domestic insects, i.e., immigrants were only resistant to imidacloprid, whereas domestic insects were only resistant to fipronil. Because *L. striatellus* is able to overwinter successfully in Japan, this would be the case if intercrossing between immigrant and domestic populations produces different characteristics of insecticide resistance in local populations in Japan. The consequences of intercrossing could depend greatly on the relative abundance of immigrant and domestic populations, and also on the genetic background of insecticide resistance against imidacloprid and fipronil. The genetic basis of insecticide resistance in *L. striatellus* against these insecticides has been poorly studied and should be investigated in the future.

Ma et al. (2007) reported that the Chinese populations of *L. striatellus* collected in Jiangsu and Zhejiang Provinces in 2006 developed resistance to imidacloprid but not to fipronil; however, similar results were only detected in Jiangsu populations, but not in Zhejiang population collected in 2008. The 2008 Zhejiang population only developed resistance to fipronil. This observation could be due to the heavy use of fipronil to control rice stem borers in the province (Zhu, Z.R., personal communication). The present results revealed that insecticide resistance of *L. striatellus* in China varies considerably among regions. Thus, continued monitoring of the status of insecticide susceptibility of *L. striatellus* is needed in central China, where a possible source exists for overseas migration to Japan.

Migration prediction of *L. striatellus*

Prediction of these expected overseas migrations may be feasible and could be conducted by a modified version of the real-time prediction system for the brown planthopper, *Nilaparvata lugens* (Stål) and the white-backed planthopper, *Sogatella furcifera* (Horváth) (Otuka et al., 2005b). The current system predicts the migration of the two species mainly from southern China to Japan in the *Bai-u* rainy season. Parameters of prediction calculations, such as the take-off date and take-off areas located in the possible source, are adapted to *N. lugens*. The temperature ceiling is also used in the prediction (Otuka et al., 2005b). This is a level of air temperature of 16.5°C, across which no simulated insects enter upper cooler air. This modelling is based on an observation that 50% of *N. lugens* stop beating their wings at an air temperature of 16.5°C (Ohkubo, 1973). For migration prediction of *L. striatellus*, the take-off date ranges from late May to early June, which corresponds to the wheat harvesting period in the source region. The take-off area was Jiangsu Province or possibly the surrounding provinces. The temperature ceiling value could be changed to be lower, because *L. striatellus* can overwinter in temperate regions and could have stronger tolerance to cool temperatures than other tropical rice planthoppers. A better estimate of the temperature ceiling value may be estimated by a flight experiment using controlled air temperatures. This experiment is planned for the future.

In conclusion, the severe occurrence of *L. striatellus* with high viruliferous rates continues in Jiangsu Province (Zhu, personal communication), and the incidence of rice stripe disease in Zhejiang Province has spread from the northern to southern part (Wang et al., 2008). If the density of viruliferous *L. striatellus* in southeastern Chinese provinces remains high in the future, overseas migrations similar to the 2008 case could occur repeatedly. Careful attention should be paid to the period from the end of May to early June because this is the wheat harvest season in the source areas (Sogawa, 2005). In fact, a previous study observed the coincidence between the peak time of wheat harvesting and the peak of *L. striatellus* catches by a net trap in Kyushu (Ito and Okada, 1985).

Finally, this study importantly demonstrated that backward trajectory analysis together with insecticide resistance testing of immigrants is an improved method to estimate migration sources. When insecticide resistance differs between the source and destination of migration, analysis of insecticide resistance is expected to be an appropriate method for determining migration sources, as exemplified by the 2008 case in Kyushu. The estimation accuracy of the proposed method is expected to become better than backward trajectory analysis alone.

ACKNOWLEDGMENTS

The authors thank Takeshi Fukuda, Hiroyuki Etoh, Miyuki Sakai, Fumitaka Kuchiki, Hideyuki Ichihashi, Zeng-Rong Zhu, Yi-Jun Zhou, and Ye-Qin Zhu for their help in collecting *L. striatellus*. Thanks are due to Shinji Sakumoto, Kayoko Abe, Reiko Yamada, and Akiko Okada for their assistance in monitoring insecticide resistance and laboratory insect rearing.

REFERENCES

Bliss, C. I. (1935) The calculation of the dosage-mortality curve. *Ann. Appl. Biol.* 22: 134–167.

Clark, M. F. and A. N. Adams (1977) Characteristics of the microplate method of enzyme-linked immunosorbent assay for detection of plant viruses. *J. Gen. Virol.* 34: 475–483.

Fukamachi, S., H. Muranaga, M. Horimoto and S. Higo (1986) Outbreaks of rice stripe in Kagoshima prefecture in 1985. *Proc. Assoc. Pl. Prot. Kyushu* 32: 5–7 (in Japanese).

Fukuda, H. and Nagata, T. (1969) Selective toxicity of several insecticides on three planthoppers. *Jpn. J. Appl. Entomol. Zool.* 13: 142–149 (in Japanese with English summary).

Ito, K. and M. Okada (1985) Bionomics of the small brown planthopper in relation to the transmission of rice stripe disease. *Plant Prot*. 39: 525–530 (in Japanese).

Kimura, S., Y. Ogawa, K. Katayama, K. Ono, Y. Nagata, K. Hirata, T. Nakasuga and K. Teramoto (1986) Occurrence of rice stripe disease in Nagasaki prefecture in 1985. *Proc. Assoc. Pl. Prot. Kyushu* 32: 1–4 (in Japanese).

Kisimoto, R. and Y. Yamada (1998) Present status of controlling rice stripe virus. In *Plant Virus Disease Control* (A. Hadidi, R. K. Khetarpal and H. Koganezawa, eds.). APS Press, Saint Paul, MN, pp. 470–483.

Kuribayashi, K. (1931a) Research on rice stripe disease. *Report of Nagano Agricultural Experimental Station* 2: 45–69 (in Japanese).

Kuribayashi, K. (1931b) Relationship between transmission of rice strip disease and the small brown planthopper. *Byouchugaizasshi* 18: 565–571 (in Japanese).

LeOra Software Company (2003) *PoloPlus: Probit and Logit Analysis. User's Guide, Version 2.0*. LeOra Software Company, Petaluma, CA. 39 pp.

Ma, C.-Y., C.-F. Gao, H.-J. Wei and J.-L. Shen (2007) Resistance and susceptibility to several groups of insecticides in the small brown planthopper, *Laodelphax striatellus* (Homoptera: Delphacidae). *Chinese J. Rice Sci.* 21: 555–558 (in Chinese with English summary).

MAFF (2009) Statistics of occurrence area of diseases and insect pests. Ministry of Agriculture, Forestry and Fisheries (in Japanese).

Matsumura, M. and A. Otuka (2009) Recent occurrence of the small brown planthopper and the rice stripe virus disease in Japan. *Plant Prot*. 63: 293–296 (in Japanese).

Murakami, H., Y. Shiroto and S. Urakawa (2007) Occurrence of rice stripe in Fukuoka and insecticide susceptibility of its vector insect, the small brown planthopper. *Proc. Assoc. Pl. Prot. Kyushu* 53: 133 (in Japanese).

Nakagawa, K., S. Mizobe and T. Tonokawachi (2009) Outbreak of rice stripe in Yamaguchi prefecture in 2008. *Proc. Assoc. Pl. Prot. Kyushu* 55 (in press).

Nishimoto, Y., S. Sakumoto, H. Gyotoku, K. Yamada and K. Komaki (2008) Insecticide susceptibility of the small brown planthopper collected in Kumamoto in 2006. *Proc. Assoc. Pl. Prot. Kyushu* 54: 158 (in Japanese).

Noda, H. (1990) Graphic variation of nymphal diapause in the small brown planthopper, *Laodelphax striatellus. Plant Prot.* 44: 437–441 (in Japanese).

Ohkubo, N. (1973) Experimental studies on the flight of planthoppers by the tethered flight technique. *Jpn. J. Appl. Entomol. Zool*. 17: 10–18 (in Japanese with English summary).

Otuka, A., J. Dudhia, T. Watanabe and A. Furuno (2005a) A new trajectory analysis method for migratory planthoppers, *Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *Agric. For. Entomol.* 7: 1–9.

Otuka, A., T. Watanabe, Y. Suzuki, M. Matsumura, A. Furuno and M. Chino (2005b) Real-time prediction system for migration of rice planthoppers *Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *Appl. Entomol. Zool*. 40: 221–229.

Rice, W.-R. (1989) Analyzing tables of statistical tests. *Evolution* 43: 223–225.

Robertson, J.-L., R.-M. Russel, H.-K. Preisler and N.-E. Savin (2007) *Bioassays with Arthropods.* 2nd Edition. CRC press, Boca Raton, FL. 199 pp.

Shinkai, A. (1985) Present situation of rice stripe disease. *Plant Prot.* 39: 503–507 (in Japanese).

Sogawa, K. (1992) Recent biological and ecological problems of the rice planthoppers. *Plant Prot*. 46: 183–186 (in Japanese).

Sogawa, K. (2005) Epidemic of rice stripe virus disease in Jiangsu province, China. *Nogyo Gijutsu* 60: 405–409 (in Japanese).

Wang, H.-D., J.-P. Chen, H.-M. Zhang, X.-L. Sun, J.-L. Zhu, A.-G. Wang, W.-X. Sheng and M. J. Adams (2008) Recent rice stripe virus epidemics in Zhejiang province, China, and experiments on sowing date, disease–yield loss relationships, and seedling susceptibility. *Plant Disease* 92: 1190–1196.

Zar (1996) *Biostatistical Analysis.* 3rd Edition. Prentice Hall, Upper Saddle River, NJ. 662 pp.

Zhu, Y.-Q. (2006) The occurrence of small brown planthopper (SBPH) and controlling techniques of the *Rice stripe virus* (RSV). In *Proc. Int. Workshop on Ecology and Management of Rice Planthoppers*, Hangzhou, China, pp. 16–17.