

Dispersal of the leafhoppers *Matsumuratettix hiroglyphicus* and *Yamatotettix flavovittatus* (Homoptera: Cicadellidae), vectors of sugarcane white leaf disease

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Abstract Sugarcane white leaf disease is a serious problem in many Asian Countries. The leafhoppers *Matsumuratettix hiroglyphicus* (Matsumura) and *Yamatotettix flavovittatus* Matsumura are the main vectors of sugarcane white leaf disease phytoplasma. Gaining a better understanding of the dispersal behavior of such insect vectors is essential for both disease epidemiology and vector control. The dispersal distances of *M. hiroglyphicus* and *Y. flavovittatus* in a sugarcane field were estimated by means of mark–release–recapture experiments. Adult leafhopper vectors collected from the fields were marked using fluorescent dye powder and released at a central release point in a sugarcane field. The marking method did not have a significant effect on the survival or flight activity of the leafhopper vectors. The overall release–recapture rates of *M. hiroglyphicus* and *Y. flavovittatus* within 50 m were 10.1 and 13.4 %, respectively. The estimated natural mean dispersal distances for *M. hiroglyphicus* and *Y. flavovittatus* were 162.1 and 387.5 m, respectively. Wind appears to be the main factor influencing the leafhopper dispersal direction.

Keywords Leafhopper vector · Dispersal distance · Mark–release–recapture · Sticky trap · Sugarcane

Introduction

Sugarcane white leaf (SCWL) is the most destructive sugarcane disease known in Asia, especially in Thailand, Taiwan, Japan, and Sri Lanka (Ling 1962; Nakashima and Murata 1993; Kumarasinghe and Jones 2001; Nakashima et al. 2001). Recently, it was reported that SCWL has spread into Lao PDR and Vietnam (T. Maleerat and T.X. Hoat, pers. commun., December 2, 2011). The disease is caused by plant-pathogenic phytoplasma, and is naturally transmitted by the leafhoppers *Matsumuratettix hiroglyphicus* (Matsumura) and *Yamatotettix flavovittatus* Matsumura (Homoptera: Cicadellidae) (Matsumoto et al. 1968; Chen 1974; Hanboonsong et al. 2002, 2006). These leafhoppers are key vectors for spreading the SCWL phytoplasma to healthy plants, and it has been reported that the transmission efficiency of *M. hiroglyphicus* (55 %) is higher than that of *Y. flavovittatus* (45 %) (Hanboonsong et al. 2006). These vectors were found in fields during different peak periods, from mid-June to the end of July in the case of *M. hiroglyphicus* and from mid-July to the beginning of September in the case of *Y. flavovittatus* (Phisitkul et al. 1989; Hanboonsong et al. 2006). SCWL phytoplasma still cannot be cultured, and there are no effective methods of controlling this disease. It is already known that the insect vector *M. hiroglyphicus* is one of the pathogen reservoirs (Hanboonsong et al. 2002), but the other host plant's pathogen reservoir has not yet been identified. Therefore, in the study described in the present paper, we investigated insect vector dispersal. Such studies are important not only for disease epidemiology but also for developing strategies to prevent the spread of disease caused by vector dispersal, which will contribute to disease management. This is the first report on the dispersal behavior of *M. hiroglyphicus* and *Y. flavovittatus* in

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sugarcane fields; however, several studies have reported that mark–release–recapture (MRR) experiments are an effective means of studying the dispersal behavior of leafhoppers (Larsen and Whalon 1988; Whitney and Meyer 1988; Zhou et al. 2003; Blackmer et al. 2006). Therefore, as it is important to quantify the spread of SCWL disease from infected fields through the transmission of insect vectors, the objective of this study was to determine the dispersal distances of *M. hiroglyphicus* and *Y. flavovittatus* from a central release point in a sugarcane field using the MRR method.

Materials and methods

Leafhopper capture and marking

The leafhoppers were collected for marking and release from the fields of high-population areas in the districts of Kumphawapi and Non Sa-at, Udon Thani Province, in northeastern Thailand. The collections were performed in the evening during the peak periods of *M. hiroglyphicus* (June–July) and *Y. flavovittatus* (July–September) using light traps to attract the insects and insect aspirators to catch the insects. Micronized (3–4 µm particle size) fluorescent dye powder in four colors—pinkish (FZ-2803), purple pink (FZ-2817), green (FZ-2802), and blue (FZ-2808) (Sinloih Co. Ltd., Kamakura, Japan)—was used for insect marking in this study (Nakata 2008), because it is the most effective means of marking insects that are small in size and large in abundance (Darling 1925). Leafhoppers were aspirated, in groups of 50, into transparent plastic tubes (12 cm in length, 3 cm in diameter) containing 20 mg of fluorescent dye powder for marking. The tubes were then shaken gently by hand for 20 s to coat the leafhoppers with the powder. Different colors of fluorescent dye powder were used to signify different release dates and leafhopper species. The marked leafhoppers were immediately transferred from the plastic tubes to open petri dishes inside transparent plastic mass-rearing cages (80 cm in height, 25 cm in diameter) containing two-month-old healthy sugarcane. Those leafhoppers that flew away from the petri dishes inside the cages were counted as released.

Effects of marking on leafhopper survival and flight activity

Our dispersal studies required the development of an effective marking method that did not affect the survival or flight activity of the SCWL leafhopper vectors. Therefore, we tested the effects of the fluorescent dye powder marking method on leafhopper survival and flight activity under greenhouse conditions. Five sets of 20 adult leafhoppers each of *M. hiroglyphicus* and *Y. flavovittatus* were treated

with one of the four colors of fluorescent dye powder, or were unmarked (used as controls). The experiment utilized a randomized block design replicated in four cages for each species. The marked leafhoppers were released into cages (70 cm in height, 20 cm in diameter) containing two-month-old sugarcane. After the release of the marked leafhoppers, the cages were placed in a greenhouse with no temperature or light-intensity control. To test the effects of the marking method on leafhopper survival, the living treated leafhoppers in each cage were counted daily (with the dead being removed) for 20 days following release.

To study the effects of the marking method on leafhopper flight activity, five sets of 50 adult leafhoppers each of *M. hiroglyphicus* and *Y. flavovittatus* were treated with one of the four colors of fluorescent dye powder, or were unmarked (used as controls). The treated leafhoppers were released together onto two-month-old sugarcane plants in a cage (2 × 1 × 1 m) covered with a nylon screen. Two yellow and two blue sticky traps made from plastic boards (12.5 × 25 cm) were placed in the cage, and trapped leafhoppers were counted daily for 20 days following release (with three replications).

Field experiments using the mark–release–recapture method

The release–recapture field site was located at Tha Phra, Khon Kaen Province, in northeastern Thailand. The field was 3 ha in size, and contained the Khon Kaen 3 variety of sugarcane, *Saccharum officinarum* L. (1 m in height). The field was bordered on the east by eucalypt trees, on the west by fallow land, and on the south and north by sugarcane fields. The pattern that sticky recapture traps were placed on the field was modified from Larsen and Whalon (1988). At the release–recapture field site, yellow and blue colored sticky traps made from plastic boards (25 × 40 cm) were fixed on bamboo sticks and placed beside each other at each location, 1.5 m above the ground, at distances of 5, 10, 20, 30, and 50 m, in six directions radiating from the release point (Fig. 1). We used two color sticky traps in this experiment because blue and yellow color sticky traps showed the same efficiency for *M. hiroglyphicus*, while the blue color sticky trap showed the best efficiency at catching *Y. flavovittatus*, followed by the yellow color sticky trap (Thein et al. 2011). The plastic boards were wrapped in transparent plastic sheets, and a colorless insect-trapping adhesive (Beetle Glue, Greenplana Co. Ltd., Thailand) was applied onto both surfaces of each board. A total of 60 traps were placed in the field.

Three releases of marked adult *M. hiroglyphicus* leafhoppers (during which 1,980, 1,200, and 800 leafhoppers were released at the central release point in the field, respectively; Fig. 1) were performed on different dates in July and August, while two releases of marked adult

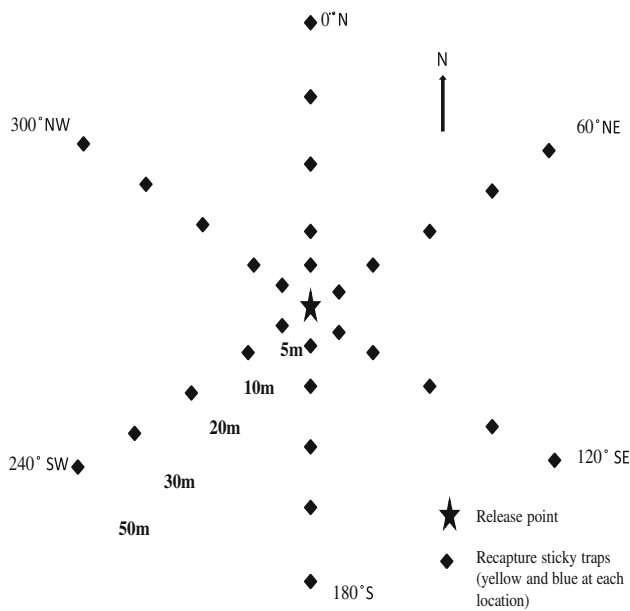


Fig. 1 Layout of the sticky traps used to recapture marked leafhoppers, *M. hiroglyphicus* and *Y. flavovittatus*, from the central release point in the sugarcane field (modified from Larsen and Whalon 1988)

Y. flavovittatus leafhoppers (during which 2,700 and 2,100 leafhoppers were released, respectively) were performed on different dates in August (Table 2). Different colors of fluorescent dye powder were used to indicate the respective release dates and leafhopper species. All sticky traps were monitored and replaced at two-day intervals until 20 days after release in all of the experiments. Trapped leafhoppers were examined under a microscope to determine their markings. Weather data were obtained from the weather station at Tha Phra, Khon Kaen Province (see the “Appendix”). The data reflecting the effects of fluorescent dye powder marking on the insect vectors’ survival and flight activity were subjected to analysis of variance (one-way ANOVA); and comparison of means was performed using the Tukey–Kramer honestly significant difference (HSD) test. All of the analysis was performed using the JMP 9 statistical software package (SAS Institute 2010).

Estimation of natural dispersal distance

We used the dispersal distance estimation method of Yamamura et al. (2003). First, we calculated the expected number of settled individuals at a distance $f(r)$, assuming that the traveling individuals settle at a position at a rate of λ :

$$f(r) = \frac{n_0}{2\pi} \lambda_D K_0 \left(r \sqrt{\lambda_D} \right), \tag{1}$$

where n_0 is the number of released insects, $K_0(\cdot)$ is a modified Bessel function of the second kind and of order

zero; and λ_D is λ/D , where D is the diffusion coefficient. λ_D is the rate of settlement scaled by the diffusion coefficient.

Then we calculated the expected number of individuals captured by the i -th trap placed at a distance r_i as

$$g(r_i) = \frac{cn_0}{2\pi} \lambda_D K_0 \left(r_i \sqrt{\lambda_D} \right), \tag{2}$$

where c is a constant.

Finally, we calculated the estimated mean dispersal distance of the individuals captured by traps as

$$E(r) = \frac{\pi}{2\sqrt{\hat{\lambda}_D}}, \tag{3}$$

where a hat (^) indicates the corresponding estimate.

The standard error (SE) is estimated as

$$SE = SE \left(\hat{\lambda}_D \right) \times \frac{\pi}{\left(4\hat{\lambda}_D^{1.5} \right)}, \tag{4}$$

where $SE \left(\hat{\lambda}_D \right)$ indicates the SE of $\hat{\lambda}_D$ (Seber 1982).

The Microsoft Excel spreadsheet for this estimation is available at http://cse.niaes.affrc.go.jp/yamamura/Yamamura_et_al_2003_estimation.xls.

Results

Effects of the marking method on survival and flight activity

The mean days of survival and days to capture for all treatments (including the control), for both *M. hiroglyphicus* and *Y. flavovittatus*, are shown in Table 1. The mean survival duration for *M. hiroglyphicus* was 11–13 days, and that for *Y. flavovittatus* was 18–20 days. The survival duration of the leafhoppers marked with the four fluorescent dye colors was not significantly different from that for the unmarked (control) leafhoppers, whether *M. hiroglyphicus* (one-way ANOVA: $F = 1.15$, $df = 4, 12$, $P > 0.05$) or *Y. flavovittatus* (one-way ANOVA: $F = 3.1$, $df = 4, 12$, $P > 0.05$). The mean days until capture on the yellow and the blue sticky-board traps as a measure of flight activity was found to be 2–3 days for both *M. hiroglyphicus* and *Y. flavovittatus*, which was also not significantly different between the marked and unmarked leafhoppers for either *M. hiroglyphicus* (one-way ANOVA: $F = 0.46$, $df = 4, 8$, $P > 0.05$) or *Y. flavovittatus* (one way ANOVA: $F = 1.13$, $df = 4, 8$, $P > 0.05$). Moreover, markings of different fluorescent dye colors were observed on the thoraces or between the heads and thoraces of leafhopper vectors throughout the experimental period of 20 days.

Table 1 Mean days of survival and days to capture by sticky traps, reflecting the effects of fluorescent dye powder marking on the survival and flight activity of *M. hiroglyphicus* and *Y. flavovittatus*

Color treatment	Days of survival (mean \pm SE) ^a		Days to capture (mean \pm SE) ^a	
	<i>M. hiroglyphicus</i>	<i>Y. flavovittatus</i>	<i>M. hiroglyphicus</i>	<i>Y. flavovittatus</i>
Blue	11.8 \pm 0.6a	18.5 \pm 0.7a	2.0 \pm 0.6a	2.7 \pm 0.3a
Green	10.5 \pm 0.9a	17.8 \pm 0.8a	2.3 \pm 0.3a	3.0 \pm 0.6a
Pinkish	13.0 \pm 1.1a	20.3 \pm 0.6a	2.7 \pm 0.3a	3.3 \pm 0.3a
Purple pink	12.3 \pm 1.0a	20.0 \pm 1.2a	3.0 \pm 0.6a	2.3 \pm 0.3a
Control	12.3 \pm 1.1a	19.3 \pm 1.1a	2.7 \pm 0.7a	3.7 \pm 0.9a

^a Means in the same column followed by the same letters were not significantly different [Tukey–Kramer honestly significant difference (HSD) test $\alpha = 0.05$]

Table 2 Number of marked leafhoppers released, number recaptured, and the percentage recapture rate for *M. hiroglyphicus* and *Y. flavovittatus*

Released date	Number of released insects	Number of recaptured insects	Recapture rate (%)
<i>M. hiroglyphicus</i>			
28th July	1,980	207	10.5
15th August	1,200	149	12.4
31st August	800	46	5.8
Total	3,980	402	10.1
<i>Y. flavovittatus</i>			
9th August	2,700	382	14.2
29th August	2,100	259	12.3
Total	4,800	641	13.4

Trap-catch patterns for the mark–release–recapture experiments

A total of 3,980 adult *M. hiroglyphicus* and 4,800 adult *Y. flavovittatus* leafhoppers were marked, released, and recaptured between July and September 2011. The recapture rate of marked *M. hiroglyphicus* leafhoppers was found to range from 5.8 to 12.4 %, and the overall release–recapture rate was 10.1 %. The recapture rate of marked *Y. flavovittatus* was found to range from 12.3 to 14.2 %, and the overall release–recapture rate was 13.4 % (Table 2). The trap-catch number of individual marked leafhoppers, for both *M. hiroglyphicus* and *Y. flavovittatus*, was highest to the southwest (240° from north), followed by to the south (180° from north) and the southeast (120° from north), and lowest to the northeast (60° from north) (Fig. 2).

The number of marked *M. hiroglyphicus* and *Y. flavovittatus* leafhoppers recaptured over the 20 days after release decreased exponentially following their release (Fig. 3). The number of *M. hiroglyphicus* leafhoppers recaptured (at two-day intervals, for three releases) was 145, 90, 61, 49, 39, 14, and 4, at 2, 4, 6, 8, 10, 12, and

14 days, respectively. No *M. hiroglyphicus* individuals were recaptured as of 12 days after the third release. The *Y. flavovittatus* leafhoppers were recaptured (in two releases) at two-day intervals for 18 days after release; 203, 148, 100, 67, 48, 39, 24, 9, and 3 were recaptured at 2, 4, 6, 8, 10, 12, 14, 16, and 18 days, respectively. The number of recaptured vectors decreased as the number of observation days increased. Simple mean dispersal distances of *M. hiroglyphicus* and *Y. flavovittatus* were determined by dividing the distance recaptured from the release point (m) by the days of observation. *M. hiroglyphicus* moved 3.56, 4.44, and 4.77 m per day during the first, second, and third releases, and the mean distance for all releases combined was found to be 4.02 m per day. *Y. flavovittatus* moved 3.56 and 3.61 m per day during the first and second releases and 3.87 m per day for the two releases combined (Table 3).

Estimation of mean dispersal distances

The average dispersal distance was estimated by combining the results for the three releases of *M. hiroglyphicus* and the two releases of *Y. flavovittatus*, respectively (Table 3). The total numbers of recaptured *M. hiroglyphicus* and *Y. flavovittatus* individuals, in all 60 traps (at 5, 10, 20, 30, and 50 m) over 20 days, were 402 and 641, respectively (Table 2). We used this cumulative number of recaptured leafhoppers to predict the cumulative dispersal distance. The maximum likelihood estimate (\pm SE) of the rate of settlement of leafhoppers scaled by the diffusion coefficient (obtained using Eq. 2) was $\hat{\lambda}_D = 9.4 \times 10^{-5} (\pm 5.5 \times 10^{-5})$ for *M. hiroglyphicus*, and $\hat{\lambda}_D = 1.6 \times 10^{-5} (\pm 1.3 \times 10^{-5})$ for *Y. flavovittatus*. The estimated mean dispersal distance (\pm SE), using Eqs. 3 and 4, was 162.1 (± 47.2) m for *M. hiroglyphicus* and 387.5 (± 156.6) m for *Y. flavovittatus*. The estimated natural mean dispersal distance was found to be less in the case of *M. hiroglyphicus* than in that of *Y. flavovittatus*, and therefore the

Fig. 2 Total number of marked leafhoppers that were recaptured during 20 days in each direction after being released at the center of release point, for all releases combined: **a** *M. hiroglyphicus*, **b** *Y. flavovittatus*. The numbers inside the circles indicate the total number of marked leafhoppers recaptured, for all releases combined

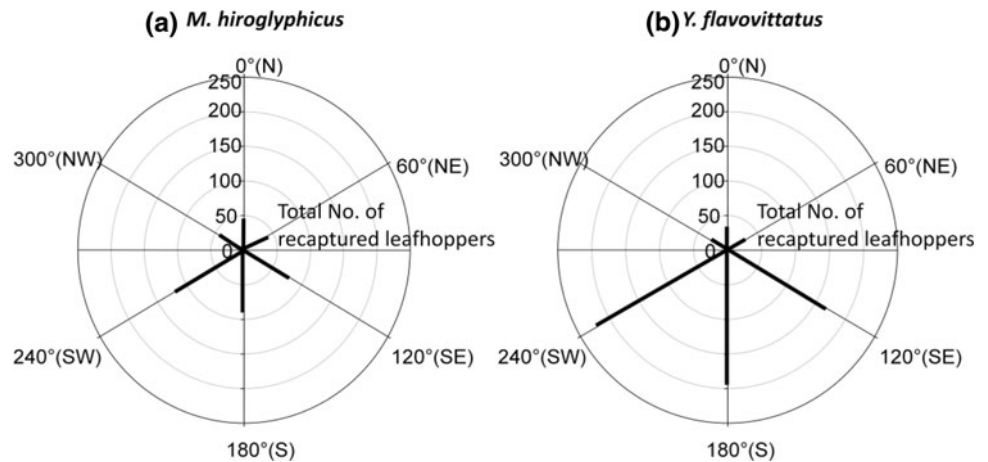
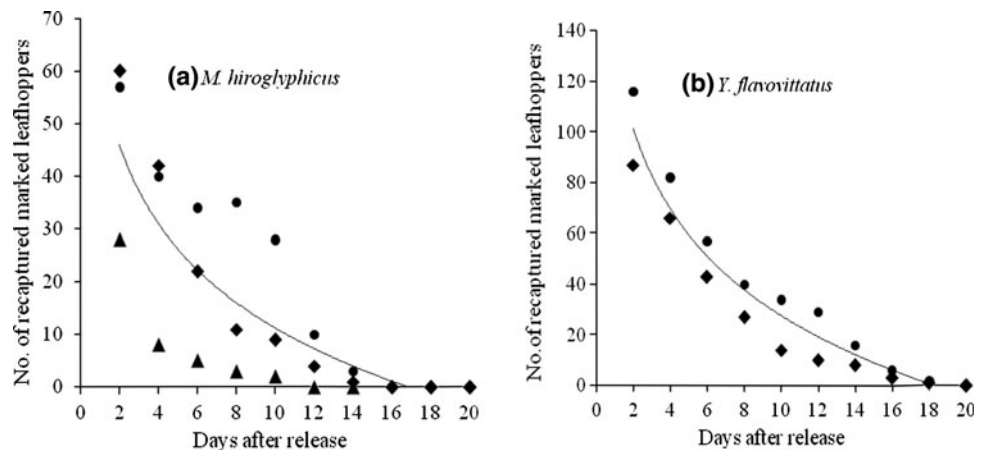


Fig. 3 Number of marked leafhoppers recaptured at each two-day interval for 20 days after release: **a** *M. hiroglyphicus*, **b** *Y. flavovittatus* (solid circles first release, solid squares second release, solid triangles third release). The curves were generated by the least squares method, assuming log approximation, combining all of the releases



rate of trapped individuals of *M. hiroglyphicus*, scaled by the diffusion coefficient, was higher than that of *Y. flavovittatus*.

Discussion

The present study revealed that the marking method using fluorescent dye powder had no significant effect on the survival or flight activity of leafhoppers under greenhouse conditions (Table 1). The marked insects were observed under a microscope, and the dye was found either around the cervix between the head and thorax or on the thorax. Among the four treatment colors of fluorescent dye, pinkish (FZ-2803) and purple-pink (FZ-2817) were found to be the most easily detectable for tracking leafhoppers. Though the marking method using fluorescent dye powder did not affect the leafhoppers’ survival and flight activity, the mean number of survival days of *M. hiroglyphicus* was found to be slightly less than that of *Y. flavovittatus*. This is not surprising, given their respective natural adult longevities. It has been reported in laboratory studies that the adult longevity of *M. hiroglyphicus* is shorter than that of

Y. flavovittatus (Hanboonsong et al. 2002; Hanboonsong 2008). In our MRR experiments in the field, marked *Y. flavovittatus* were recaptured over a period of 18 days after release, but *M. hiroglyphicus* were recaptured over 14 days in the case of the first and second releases, and over only ten days in the case of the third release. A high mortality would appear to have occurred in the third release experiment, resulting in the low recapture rate (Table 2). This could be attributable to factors such as unsuitable habitat, or abiotic factors, especially rainfall. Normally, these vectors enter fields during the rainy season of May–October, but the greatest abundance of *M. hiroglyphicus* was found to occur in June–July, and that of *Y. flavovittatus* occurred in July–August or at the beginning of September. The number of *M. hiroglyphicus* vectors decreased after July, but that of *Y. flavovittatus* decreased slightly through to October (Phisitkul et al. 1989; Hanboonsong et al. 2006). In our MRR experiments, the third release of the *M. hiroglyphicus* vector was done at the end of August, which may be a period of unstable habitat in the field, leading to changes in fitness for this species; while the greater catch numbers of *Y. flavovittatus* would suggest a relatively stable field habitat throughout the experiment.

Table 3 Simple mean dispersal distance (m) per day for *M. hiroglyphicus* and *Y. flavovittatus*

Leafhopper species	No. of release	Mean dispersal distance (m)/day \pm SE
<i>M. hiroglyphicus</i>	First release	3.56 \pm 0.22
	Second release	4.44 \pm 0.24
	Third release	4.77 \pm 0.44
	Combine three releases	4.02 \pm 0.15
<i>Y. flavovittatus</i>	First release	3.56 \pm 0.12
	Second release	3.61 \pm 0.12
	Combine two releases	3.87 \pm 0.08

Moreover, we noticed that some rain days occurred during the experimental period of July–September (rainfall >20 mm for 8 days, >10 mm for 11 days; see the “Appendix”), and it appears that *Y. flavovittatus* is more tolerant of rain effects than *M. hiroglyphicus*. This could be due to the difference in body size (length) between *M. hiroglyphicus* (2.5–3.5 mm) and *Y. flavovittatus* (3.5–4.0 mm), respectively (unpublished data).

The overall recapture rates of marked leafhoppers, *M. hiroglyphicus* and *Y. flavovittatus*, in our MRR experiments in the sugarcane field, were 10.1 and 13.4 %, respectively. This was low in comparison with some other leafhopper dispersal studies using the mark–release–recapture method [for example, 17.3–43.7 % in a report on sharpnosed leafhopper on blueberry plants (Whitney and Meyer 1988), and 5.4–32.4 % in a report on the vector leafhopper of Pierce’s disease in an alfalfa field which had only a few scattered plants (Blackmer et al. 2004)]; but was higher than the 1.8–3.7 % rate reported by Larsen and Whalon (1988) when studying the vector leafhopper of X-disease in peach and cherry orchards (some of which were commercial orchards regularly treated with pesticides). The lower rate in our study might be explained by the fact that vector movement (and thus dispersal) in a sugarcane field is comparatively difficult in comparison to that among orchards or vegetable crops, owing to the obstruction caused by the broad leaf types found in sugarcane plantations. Zhou et al. (2003) indicated that different crop types influenced the dispersal and spatial distribution of the aster leafhopper, *Macrosteles quadrilineatus*. Moreover, Taylor (1985) noted that the variance in dispersal activity present within the Cicadellidae might depend on species behavior itself.

The wind direction throughout the experimental period of our study was predominantly towards the south (S), southeast (SE), and southwest (SW) (see the “Appendix”). The total number of recaptured leafhopper individuals of both species was highest in the area south of the release point (Fig. 2), a result which appears to have been influenced by the prevailing wind direction. The release date did not influence the direction of leafhopper dispersal. The simple mean dispersal distances of *M. hiroglyphicus* and *Y. flavovittatus* in all releases

combined were found to be 4.02 and 3.87 m/day, respectively (Table 3). The rate of dispersal would suggest that both species of leafhoppers moved an average of 4.0 m per day, and it seems that they are not capable of moving faster than this speed. However, in our experiment in the field, some individuals of vector leafhopper species could not move again once they landed on the sticky traps, while some might move over 50 m outside the trapped area. Therefore, the results for simple mean dispersal distance per day may be underestimated. Moreover, the simple mean dispersal distance (m) per day of *M. hiroglyphicus* in the first release experiment was found to be less than those for the second and third releases, while *Y. flavovittatus* showed similar mean dispersal distances in both releases (Table 3). We speculate that the high variability of wind direction and speed that occurred during the first release experiment of *M. hiroglyphicus* inhibited the flight movement of this species (“Appendix”). Wind appears to be the main factor influencing leafhopper dispersal direction and distance. Larsen and Whalon (1988) and Kobori et al. (2011) each reported that wind was one of the major factors influencing the dispersal of the leafhopper *Paraphlepsius irroratus* (Say) as a vector of X-disease and citrus greening disease (Asian citrus psyllid, *Diaphorina citri* Kuwayama), respectively. On the other hand, our results showed that the estimated natural mean dispersal distances (\pm SE) of *M. hiroglyphicus* and *Y. flavovittatus* were 162.1 (\pm 47.2) m and 387.5 (\pm 156.6) m, respectively, using the Yamamura method (Yamamura et al. 2003). Our estimation assumed that each trap had the same efficiency, but this cannot be asserted with confidence; and if the trap efficiency varied, then the estimated SE is an underestimation (less than the actual distance). In addition, our estimation assumed that the vectors’ movement was isotropic, which meant that variations in wind speed and wind direction in the actual field were not factored into the analysis (see “Appendix”).

Despite these caveats, our findings would be useful not only when considering prevention techniques for SCWL disease transmitted by *M. hiroglyphicus* and *Y. flavovittatus*, but as a first step in developing spread-estimation models for SCWL disease. Based on our results, we may conjecture that the disease risk decreases with increasing distance from infected fields, and that the SCWL infection risk is higher on the leeward (downwind) side of an infected field than on the windward (upwind) side. Therefore, wind speed and direction would be important variables to consider in a dispersal model in future investigations. The results from this study indicate that the shorter-bodied *M. hiroglyphicus* can disperse further than the longer-bodied *Y. flavovittatus* by wind. However, the Yamamura method suggests that *Y. flavovittatus* is dispersed further than *M. hiroglyphicus*, although this result could be due to the higher variability in the *Y. flavovittatus* data. One important factor that requires future research is

how the body shapes, sizes, and masses of these species influence their flight and dispersal abilities. Further studies of the vectors' transmission abilities, intrinsic rates of natural increase, and movement patterns are also needed in order to enhance SCWL disease management.

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Appendix

See Table 4

Table 4 Weather parameters for the mark–release–recapture experiment in Tha Phra, Khon Kaen Province

Date	Mean (knot ^a)		Maximum (knot ^a)		Max. temp	Min. temp	Rainfall (mm)
	Wind direction	Wind speed	Wind direction	Wind speed			
28 July, 2011	ENE	0.6	N	6	32.2	22.7	0
29 July	–	0	SSW	7	33.5	24.4	0
30 July	SSE	1.9	SSW	8	27.8	26	21.2
31 July	S	5	SSW	10	25.3	23.2	7.4
1 August	S	1	SSW	9	28.3	23.7	8.4
2 August	SW	0.6	SSW	6	29.7	24	14
3 August	S	1.3	SSW	7	32.5	23.8	0.8
4 August	SSW	1.5	SSW	7	34.0	24.2	0.9
5 August	SSW	0.9	SSW	6	34.3	25.5	0
6 August	SW	1.4	S	7	33.9	25.8	1.2
7 August	–	0	W	9	33.0	25.1	17.2
8 August	S	0.8	S	7	32.2	24.8	22.2
9 August	SSW	2	SSW	7	30.3	23.2	1.6
10 August	S	1	SSW	7	30.1	23.9	10.3
11 August	S	0.6	SSW	6	29.8	24	0
12 August	S	0.1	SSW	7	31.5	23.9	11.3
13 August	–	0	S	4	33.0	23.5	0
14 August	SE	0.5	NE	9	33.7	24.8	12.1
15 August	N	0.6	WNW	5	29.7	21.1	0.7
16 August	–	0	S	7	29.6	24.1	1.1
17 August	S	0.1	NW	5	29.5	23.2	0.3
18 August	SSW	1.6	SSW	8	32.5	23.3	4.8
19 August	–	0	SSW	9	28.3	23.8	11.3
20 August	S	0.1	S	7	30	22	1.1
21 August	NNE	0.5	SSW	5	32	23.8	11.8
22 August	–	0	WSW	5	33	24	0
23 August	S	0.4	WNW	5	35.5	25.7	0
24 August	N	0.6	NE	6	35	25.6	6.9
25 August	NE	0.4	S	4	30.3	22.4	2.4
26 August	–	0	N	2	31.6	24.6	12
27 August	S	0.3	S	8	28.7	24.2	49.4
28 August	–	0	NNE	5	32.2	22.8	7.3
29 August	S	0.5	S	6	32.5	24.4	0
30 August	S	2	S	8	29.2	24.5	13
31 August	–	0	WNW	6	32.6	24.2	0.7
1 September	NNE	0.5	NNW	5	29.3	24.4	31.6
2 September	S	1.8	S	7	31.9	24.1	10
3 September	SSW	0.4	S	8	32.2	24.2	13.8
4 September	S	0.8	SE	10	32.6	24.8	22.6

Table 4 continued

Date	Mean (knot ^a)		Maximum (knot ^a)		Max. temp	Min. temp	Rainfall (mm)
	Wind direction	Wind speed	Wind direction	Wind speed			
5 September	SSW	1.8	SSW	6	31.7	23.6	13.9
6 September	–	0	S	8	31	23.6	2.7
7 September	SW	0.8	SSW	7	30.7	23.8	29.5
8 September	S	1.3	NW	7	31.3	23.7	39.2
9 September	–	0	NE	6	29.5	23.1	30.8

^a 1 knot = 0.514 m/s

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