

Impacts of tillage practices on hoppers and predatory wolf spiders (Araneae: Lycosidae) in rice paddies

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Abstract

We investigated the effects of tillage practices on the densities of wolf spiders and planthoppers and leafhoppers in rice paddy fields. Paddies were subjected to one of two different treatments (no tillage and conventional tillage), and seasonal changes in the densities of wolf spiders and hoppers were investigated over two growing seasons (1999 and 2000). In both years, the density of wolf spiders was significantly higher and the density of hoppers tended to be lower in no-tilled paddies than in conventionally tilled paddies, although the latter difference was not statistically significant. The Iwao's omega values, which represent the degree of correlation between the spatial distributions of wolf spiders and hoppers, were higher in no-tilled than in tilled paddies during August when the hopper density decreased in no-tilled paddies.

Key words: Tillage practices; paddy fields; wolf spiders; hoppers; omega index

INTRODUCTION

Soil tillage is one of the most important agricultural practices because it is used to prepare seedbeds, mix organic material and fertilizer, and suppress weeds, diseases, and pests (Gebhardt et al., 1985). However, tillage can adversely affect arthropods and other invertebrates that inhabit the soil surface (Stinner and House, 1990). In particular, ground-dwelling predators such as spiders and carabid beetles are often harmed by tillage practices (Kawahara et al., 1974; Widiarta et al., 1991), and the densities of these predators can decrease dramatically after tilling (House and Stinner, 1983; Brust et al., 1985, 1986).

Wolf spiders (Araneae, Lycosidae) are important predators of insect pests in agroecosystems because of their abundance and high predatory potential (Riechert and Lockley, 1984; Nyffeler and Benz, 1987; Wise, 1993). Because wolf spiders are one of the most abundant predators in rice paddy fields (Kiritani et al., 1972; Kawahara et al., 1974), many entomologists have viewed them as biological control agents in rice paddies (Itô et al., 1962; Kawahara et al., 1974; Orazé et al., 1989). Kiritani et al. (1970, 1972) conducted a life-table analysis

of the green rice leafhopper, *Nephotettix cincticeps* (Uhler), in paddy fields and concluded that *Pardosa pseudoannulata* (Bös. et Str.) was the most important predator of this hopper. Sasaba et al. (1970) investigated the functional response of *P. pseudoannulata* and found that this species had high potential for predation on the green rice leafhopper. Orazé and Grigarick (1989) suggested that *Pardosa ramulosa* (McCook) was an important predator of the aster leafhopper, *Macrosteles fascifrons* Stål, in rice paddy fields in California.

Based on these findings, we expected that populations of wolf spiders would increase and prevent pest populations from expanding in no-tilled paddy fields. Hidaka (1993) reported that wolf spiders were much abundant in no-tilled paddy fields than tilled paddy fields and the peak density of planthoppers was much less abundant in no-tilled paddy fields than tilled paddy fields. However, few reports have experimentally investigated the relationships between wolf spiders and insect pests in no-tilled paddy fields. Thus, the purpose of this study was to clarify the effects of tillage practices on the population densities of wolf spiders and hoppers in paddy fields.

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MATERIALS AND METHODS

Study sites. This study was conducted in rice paddies of the Tokyo University of Agriculture and Technology in Fuchu, Tokyo, Japan, during the growing seasons of 1999 and 2000. Experimental rice paddies bordered on the west and south with other rice paddies, on the north with a road and on the east with a building and hedges (Fig. 1A). Experimental plots were subjected to two different rice-cropping systems: no tillage and conventional tillage. All fields were irrigated on 6 May 1999 and 1 May 2000; fields that were conventionally tilled were cultivated with a farm tractor on 14 May 1999 and 11 May 2000. Experimental fields were not cultivated from the harvest of 1998 to irrigation of May 1999. Rice (*Oriza sativa* L., variety Tukinohikari) seedlings were transplanted between 17–19 May 1999 and 15–19 May 2000 at a density of 16.7 hills/m². Each treatment was replicated four times (plot size: 27.5×10 m) in 1999, and three times (plot size: 27.5×11 m) in 2000. Arrangement of experimental plots in 1999 and 2000 is shown in Fig. 1B. To prevent spider's emigration and immigration, a plastic plate (25 cm high) was established on both sides of each plot and tanglefoot (Fujiyaku Industrial Co., Ltd.) was brushed on the plastic plate. However, because we often observed that the larger *P. pseudoannulata* moved to neighboring plots, the plastic plate (25 cm high) and tanglefoot could not completely prevent the movement of spiders between plots. Each plot was fertilized with 40 kg of N, P, and K per hectare several days before transplanting the rice seedlings, and with 20 kg of N, P, and K per hectare 40 days after transplantation. The herbicides Round-Up (Monsanto Co., Ltd.) and Sparkstar (Nissan Chemical Industries Ltd.) were applied to each plot three weeks before and 10 days after transplanting the seedlings, respectively. No insecticides or fungicides were applied throughout the experimental periods.

Sampling and data collection. In June of both years, the density of wolf spiders was determined, once a week in 1999 and once every ten days in 2000. Spiders were counted in 50 (1999) or 100 (2000) randomly selected quadrats (0.06 m²) within each plot. From July to September 1999 and 2000, the densities of wolf spiders and hoppers in each plot were surveyed by a modified cylinder method

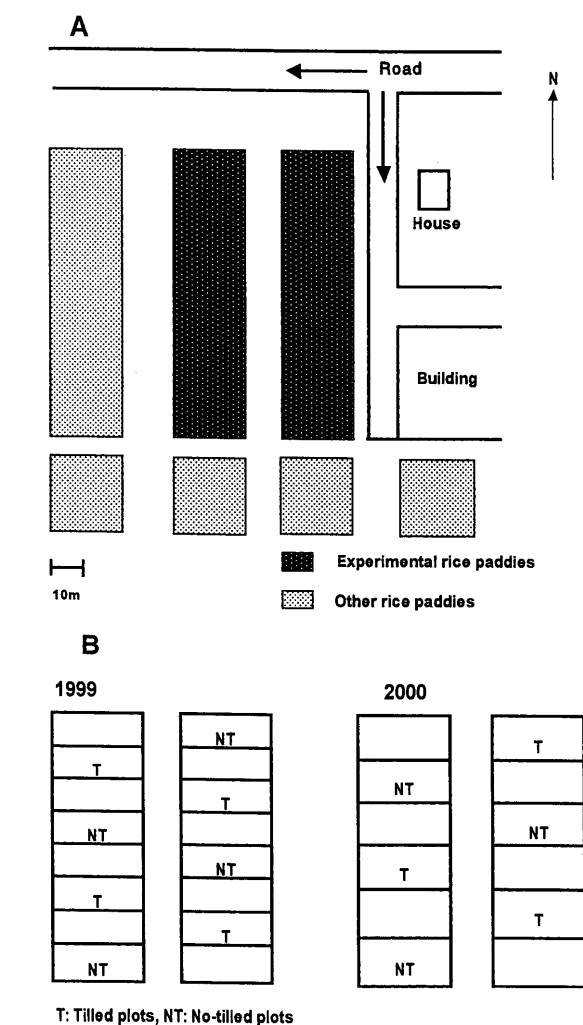


Fig. 1. A map of study site and surrounding environment (A), and the arrangement of experimental plots in 1999 and 2000 (B).

(Southwood, 1994) once every ten days. Ten hills were systematically selected in each plot, and each hill to be sampled was enclosed by forcing a plastic frame (0.3×0.4×1.2 m) into the soil. All spiders and insects within this frame were then collected with a suction apparatus. All collected specimens were transferred into a glass vial containing 70% ethanol and brought to the laboratory for identification.

Data analysis. Population data were subjected to a $(X+0.5)^{1/2}$ transformation prior to analysis. Data were analyzed with a repeated-measures analysis of variance (ANOVA). If the effect of farming type was significant or the interaction term of farming type×sampling time was significant, we analyzed population data by ANOVA with Bonferroni method every sampling time. Omega values (Iwao,

Table 1. Mean number of spiders per plot with standard errors collected in no-tilled and tilled plots in 1999 and 2000

Farming type	Spider family	July	August	September	Total
1999					
No-tillage	Lycosidae	15.5±6.8	90.0±18.6	121.3±15.6	226.8±38.0
	<i>Pardosa pseudoannulata</i>	7.0±4.0	58.8±9.9	84.0±13.8	149.8±21.1
	<i>Pirata subpiraticus</i>	8.5±6.8	31.3±17.3	37.3±21.3	77.0±45.0
	Other families	19.3±1.1	52.5±14.4	52.5±4.9	124.0±15.4
Tillage	Lycosidae	5.0±2.2	46.3±5.3	77.8±17.2	129.0±23.7
	<i>Pardosa pseudoannulata</i>	2.5±0.9	31.8±4.9	50.3±13.5	84.5±16.9
	<i>Pirata subpiraticus</i>	2.5±1.6	14.5±7.9	27.5±14.6	44.5±24.0
	Other families	21.5±6.3	50.0±12.6	78.5±16.7	150.0±34.1
2000					
No-tillage	Lycosidae	8.3±3.2	76.7±17.0	188.3±28.4	273.3±46.4
	<i>Pardosa pseudoannulata</i>	7.0±4.2	51.7±14.4	127.0±15.6	185.7±33.4
	<i>Pirata subpiraticus</i>	1.3±0.3	25.0±6.1	61.3±20.0	87.7±26.4
	Other families	35.0±8.3	67.7±16.9	132.0±15.4	234.7±36.9
Tillage	Lycosidae	6.3±2.0	36.0±13.9	70.0±18.3	112.3±30.8
	<i>Pardosa pseudoannulata</i>	4.7±1.8	26.7±11.9	48.7±13.5	80.0±24.0
	<i>Pirata subpiraticus</i>	1.7±0.3	9.3±2.0	21.3±4.9	32.3±6.8
	Other families	29.7±3.2	61.3±19.6	151.7±14.2	242.7±32.3

1977) were calculated using the number of wolf spiders and hoppers per hill collected by the modified cylinder method and were used as an index of how much the distributions of spiders and hoppers overlapped ($\omega = +1$ when distributions completely overlap, $\omega = 0$ when distributions are independent, and $\omega = -1$ when distributions are completely exclusive; Iwao, 1977).

RESULTS

Density of wolf spiders

Two species of wolf spiders, *Pardosa pseudoannulata* (Bös. et Str.) and *Pirata subpiraticus* (Bös. et Str.), were observed in no-tilled and conventionally tilled plots. The numbers of each species collected by the suction apparatus are shown in Table 1. In both years, the mean number of *P. pseudoannulata* and *P. subpiraticus* was higher in the no-tilled plots than in the conventionally tilled plots. With the exception of July 1999, *P. pseudoannulata* were more abundant than *P. subpiraticus* regardless of treatment type and sampling period. The mean number of spiders other than lycosids was not significantly different between no-tilled plots and the conventionally tilled plots ($p > 0.05$).

Seasonal changes in the density of wolf spiders showed the same trends in 1999 and 2000 (Fig. 2). Just after transplantation of the seedlings in June,

the density of wolf spiders was higher in no-tilled plots than in tilled plots, and was nearly stable in all plots. At that time, because the rice plants were still short, the wolf spiders were rarely observed on the rice plants in any of the plots. In no-tilled plots the wolf spiders inhabited withered weeds above the water surface. In July, we observed no differences in spider density between the two treatments, although overall density began to increase. In August, the density of wolf spiders increased rapidly in no-tilled plots and increased slowly in the tilled plots, resulting in a difference in the density of wolf spiders between no-tilled and tilled plots in August. In September, the density of wolf spiders stopped increasing in both plots. To examine the effects of tillage practices on the density of wolf spiders, we performed a repeated-measures ANOVA and found a significant effect of treatment on the density of wolf spiders in 1999 and 2000 (Table 2). Thus we analyzed population data by ANOVA with Bonferroni method every sampling time. No significant effect was observed in 1999 but a significant effect of treatment was detected on data collected on 5 and 15 September in 2000 ($p < 0.05$).

To estimate the reproductive time of *P. pseudoannulata*, we investigated the size distribution of this species by measuring the carapace width of individuals collected with the suction ap-

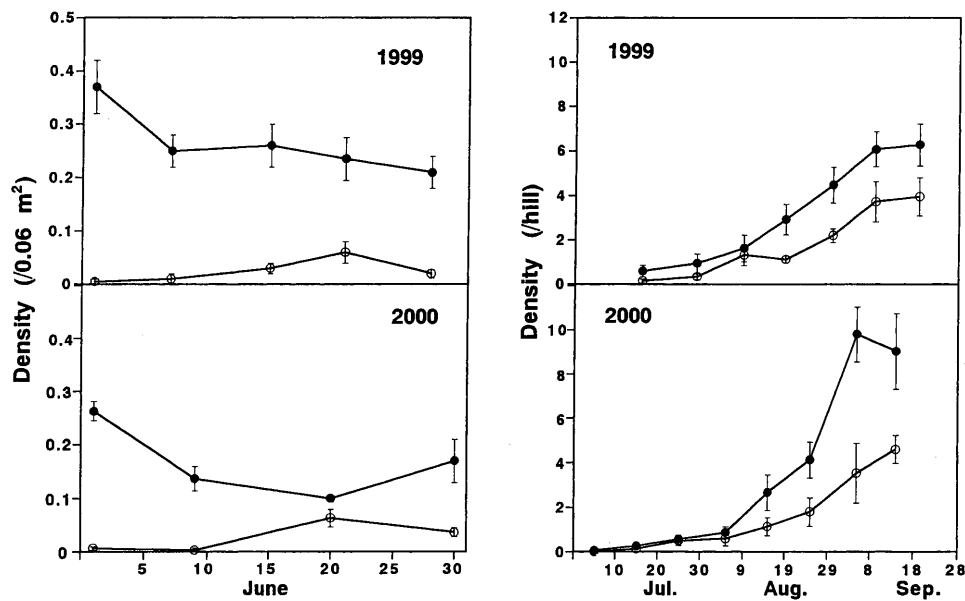


Fig. 2. Seasonal changes in the mean density of wolf spiders per plot in no-tilled and conventionally tilled paddy fields in 1999 and 2000. Open and closed circles indicate tilled and no-tilled plots, respectively. Vertical lines indicate standard errors.

Table 2. Results of a repeated-measures ANOVA to assess differences in the density of wolf spider among sampling times and treatments in 1999 and 2000

Source	1999			2000		
	F	d.f.	p	F	d.f.	p
Farming type	8.52	1	0.03	7.73	1	0.049
Sampling time	59.82	11	<0.01	71.84	11	<0.01
Farming type × Sampling time	1.73	11	0.09	5.47	11	<0.01

The number of wolf spiders was transformed to $(X+0.5)^{1/2}$ before analysis.

paratus (Fig. 3). The size of *P. pseudoannulata* was categorized into three classes based on carapace width: small (=1.0 mm; included many spiderlings), medium (1.0–2.0 mm), and large (>2.0 mm; included many subadults and adults). Although all three size classes of *P. pseudoannulata* were collected in no-tilled plots throughout the sampling period, the peak frequency of the large class was observed in late July of both years. In the tilled plots, the large class of *P. pseudoannulata* was not collected in late July and the peak frequency of the large class was observed in mid-August.

Density of hoppers

Two species of leafhoppers, *Nephotettix cincticeps* (Uhler) and *Inazuma dorsalis* (Motschulsky), and two species of planthoppers (Delphacidae),

Laodelphax stratella (Fallén) and *Sogatella furcifera* (Horváth) were observed in no-tilled and conventionally tilled plots. The numbers of each species collected by the suction apparatus are shown in Table 3. Since the two planthopper species were not discriminated from each other during nymphal stages, the data are shown as the number of Delphacidae. In both years, the mean number of *N. cincticeps*, *I. dorsalis*, and Delphacidae per plot was lower in the no-tilled plots than in the conventionally tilled plots except Delphacidae in 2000. *Nephotettix cincticeps* was the most abundant regardless of treatment type and sampling period with the exception of September 2000 in no-tilled plots.

The density of hoppers tended to be lower in no-tilled plots than in tilled plots during the growing

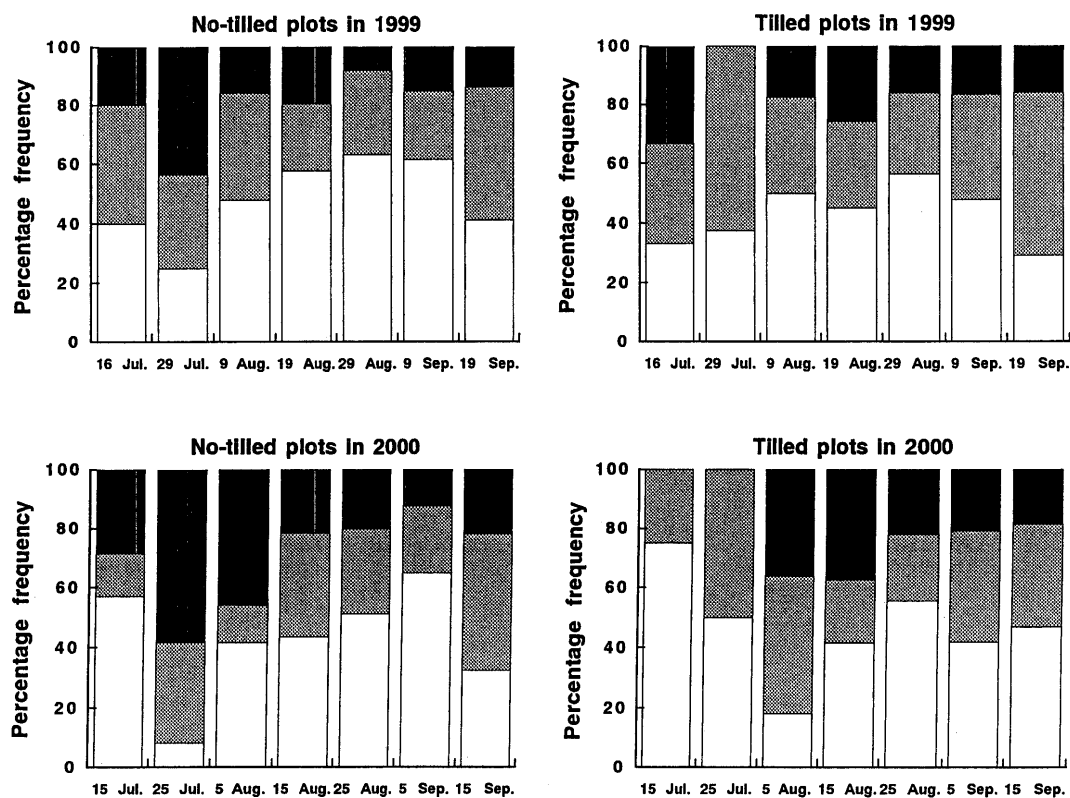


Fig. 3. Seasonal changes in the proportion of small, intermediate, and large size classes of *Pardosa pseudoannulata* collected at each census in no-tilled and tilled paddy fields in 1999 and 2000. The open, dotted, and closed histograms show small ($=1.0\text{ mm}$), intermediate ($1.0\text{--}2.0\text{ mm}$), and large ($>2.0\text{ mm}$) size classes, respectively, based on carapace width.

Table 3. Mean number of hoppers per plot with standard errors collected in no-tilled and tilled plots in 1999 and 2000

Farming type	Species or family of hoppers	July	August	September	Total
1999					
No-tillage	<i>Nephotettix cincticepes</i>	130.8 \pm 24.8	206.3 \pm 25.9	43.8 \pm 13.7	380.8 \pm 46.6
	<i>Inazuma dorsalis</i>	1.3 \pm 0.8	4.5 \pm 0.3	16.8 \pm 2.7	22.5 \pm 3.4
	Delphacidae ^a	10.5 \pm 2.1	18.5 \pm 5.4	31.3 \pm 11.3	60.3 \pm 18.0
Tillage	<i>Nephotettix cincticepes</i>	207.8 \pm 24.5	277.5 \pm 48.5	74.5 \pm 8.5	559.8 \pm 56.6
	<i>Inazuma dorsalis</i>	3.0 \pm 0.7	17.0 \pm 3.8	16.3 \pm 6.5	36.3 \pm 8.9
	Delphacidae ^a	16.3 \pm 4.1	30.3 \pm 8.3	32.8 \pm 13.8	79.3 \pm 16.7
2000					
No-tillage	<i>Nephotettix cincticepes</i>	295.0 \pm 15.3	325.0 \pm 67.1	80.0 \pm 22.3	700.0 \pm 101.6
	<i>Inazuma dorsalis</i>	1.3 \pm 0.3	15.0 \pm 6.1	31.0 \pm 5.7	47.3 \pm 11.3
	Delphacidae ^a	35.3 \pm 8.0	325.0 \pm 67.1	87.3 \pm 9.4	447.7 \pm 77.0
Tillage	<i>Nephotettix cincticepes</i>	658.7 \pm 84.0	338.7 \pm 46.5	145.0 \pm 21.4	1,142.3 \pm 146.4
	<i>Inazuma dorsalis</i>	10.0 \pm 1.2	27.3 \pm 8.2	52.0 \pm 4.2	89.3 \pm 12.6
	Delphacidae ^a	45.0 \pm 14.0	49.7 \pm 3.7	76.3 \pm 17.5	700.0 \pm 101.6

^a Delphacidae includes *Laodelphax stratella* and *Sogatella furcifera*.

seasons of 1999 and 2000 (Fig. 4). In 1999, seasonal changes in the density of hoppers showed the same trends in both treatments. The mean density of hoppers was always lower in no-tilled than in tilled plots. In 2000, the patterns of seasonal

changes in hopper density differed between treatments. The density of hoppers was lower in no-tilled plots than in tilled plots on 5 July and 15 July, and decreased rapidly on 25 July. In August, the density of hoppers did not differ between treat-

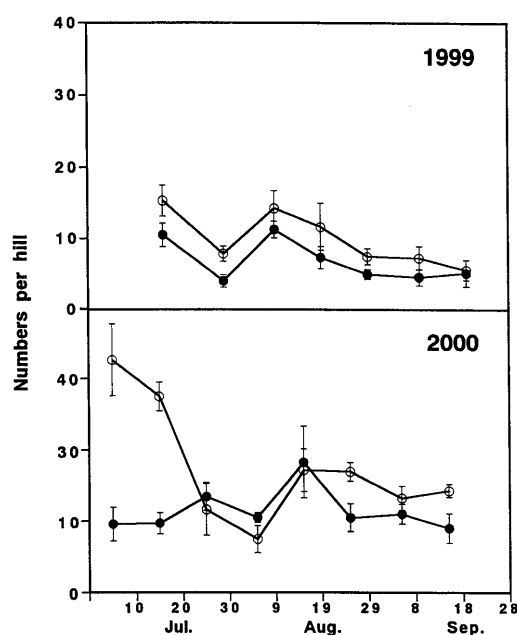


Fig. 4. Seasonal changes in the mean density of hoppers per plot in no-tilled and conventionally tilled paddy fields in 1999 and 2000. Open and closed circles indicate tilled and no-tilled plots, respectively. Vertical lines indicate standard errors.

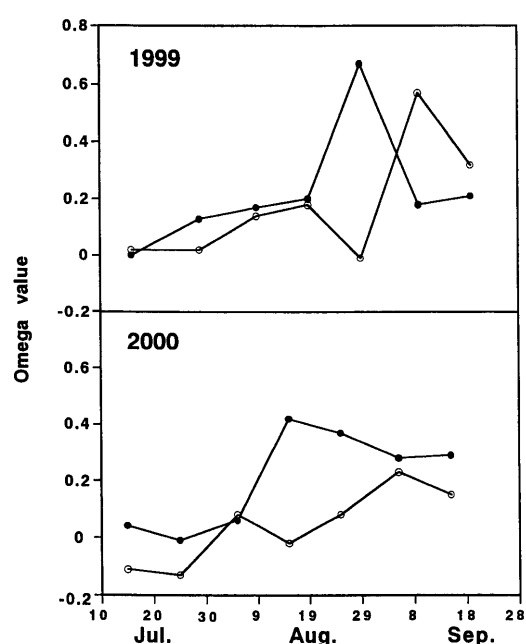


Fig. 5. Seasonal changes in the Iwao's omega value as an index of overlapping distributions between spiders and hoppers in 1999 and 2000. Open and closed circles indicate tilled and no-tilled plots, respectively.

Table 4. Results of a repeated-measures ANOVA to assess differences in the density of hoppers among sampling times and treatments in 1999 and 2000

Source	1999			2000		
	<i>F</i>	d.f.	<i>p</i>	<i>F</i>	d.f.	<i>p</i>
Farming type	4.17	1	0.09	4.35	1	0.11
Sampling time	11.51	6	<0.01	8.05	7	<0.01
Farming type×Sampling time	0.39	6	0.88	11.44	7	<0.01

The number of hoppers was transformed to $(X+0.5)^{1/2}$ before analysis.

ments. At the end of August, the density of hoppers in the no-tilled plots decreased suddenly, and this decrease resulted in a difference in the density of hoppers between the two treatments in September. To examine the effects of tillage practice on the density of hoppers, we performed a repeated-measures ANOVA. As a result, we found no significant effects of tillage practice on the density of hoppers in 1999 and 2000 but found significant interaction between farming type and sampling time in 2000 (Table 4). Thus we analyzed population data by ANOVA with Bonferroni method at every sampling time in 2000 and a significant effect of treatment was detected on data collected on 5 and 15 July ($p < 0.05$).

Distribution overlap between spiders and hoppers

To analyze the interactions between wolf spiders and hoppers, we calculated the omega value as an index of overlapping distributions in each plot on each sampling date (Fig. 5). In 1999, omega values were < 0.2 on most sampling dates for both treatments, indicating independent distributions of wolf spiders and hoppers. However, high omega values were obtained on 29 August and 9 September in 1999 in no-tilled and tilled plots, respectively, indicating that wolf spiders and hoppers were positively associated with each other. In 2000, omega values were < 0.2 throughout the survey period in the tilled plots, indicating that wolf spiders and hoppers were distributed independently. On the

other hand, omega values in no-tilled plots were <0.1 from 15 July to 5 August and exceeded 0.3 afterward, indicating positive associations from mid-August to mid-September.

DISCUSSION

In 1999 and 2000, the density of wolf spiders was significantly higher in no-tilled plots than in tilled plots (Table 2). In June, just after the rice seedlings were transplanted, we observed a large difference in the density of wolf spiders between no-tilled and tilled plots. At that time rice plants were still small, therefore wolf spiders could not inhabit the rice plants in either plot. However, since there were complex structures such as withered weeds in the no-tilled plots, the wolf spiders in no-tilled plots could inhabit these complex structures. These results suggest that tilling destroys wolf spider habitat, resulting in a greatly reduced density of spiders in tilled plots. Previous studies have reported that the density of spiders is closely tied to the structural complexity of local environments (Andow, 1991; Rypstra et al., 1999). Several researchers have also reported that generalist predators including spiders were successfully increased when shelters, e.g., unharvested crops, mulch and crates, were placed in crop fields (Nentwig, 1988; Heidger and Nentwig, 1989; Riechert and Bishop, 1990; Carter and Rypstra, 1995). Thus, physical structures may provide a shelter and a refuge for spiders shortly after planting, when crops are still small and the structural complexity of the field is low.

Moreover, the density of wolf spiders did not differ between no-tilled and tilled plots from July to early August, but was significantly higher in no-tilled plots from mid August to September. This difference in spider density between the two treatments may be due to the differences in the population growth of wolf spiders between the two treatments. The size distribution of *P. pseudoannulata* showed that individuals in no-tilled plots grew more rapidly than those in tilled plots, and the peak frequency of the large size class of *P. pseudoannulata* including female adults with egg sac occurred in late July and in mid-August in no-tilled and tilled plots, respectively. The egg stage of *P. pseudoannulata* lasts 19–21 days at 25°C (Kawahara et al., 1974); thus spiderlings should appear in

the fields about three weeks after oviposition. This was confirmed, because in mid-August, spiderlings accounted for most of the population of *P. pseudoannulata* in no-tilled plots. On the other hand, the density of wolf spiders in tilled plots increased from August. This increase in density might be due to the immigration of spiders from surrounding areas. Orazé et al. (1989) suggested that the increase in the density of wolf spiders in rice paddies was due to immigration of spiders from the levees in California. In conclusion, the high density of wolf spiders in no-tilled plots may be due to their early establishment and reproduction.

Although the density of hoppers was not significantly lower in no-tilled plots than in tilled plots in 1999 and 2000 (Table 4), the interaction between the farming type and the sampling time was significant in 2000. Thus, we analyzed population data by ANOVA with Bonferroni method every sampling time and found significant effects of tillage practice on the density of hoppers on 5 and 15 July in 2000. During this period, the growth of rice plants in no-tilled plots was retarded compared to tilled plots (Motobayashi et al., 2001). In general, rice plants cannot grow rapidly during the initial growth stages in no-tilled systems (Andow et al., 1998). Slow growth of rice plants may help prevent colonization by planthoppers (Hidaka, 1993; Kajimura et al., 1995). Therefore, changes in the growth patterns of rice plants may result in the differences in hopper density between no-tilled and tilled plots observed in early and mid-July. The density of hoppers tended to be lower in no-tilled plots than in tilled plots in late August 1999 and 2000 but this difference was not significant. During this period, the omega value was higher in no-tilled plots than in tilled plots. We also observed that hoppers accounted for $>60\%$ of the diet of wolf spiders in no-tilled plots in August of 1999 and 2000 (Ishijima et al., unpublished). Judging from these observations, wolf spiders may play a role in suppressing hopper populations in no-tilled plots between mid-August and late August but further studies are necessary to confirm this hypothesis.

Habitat management practices, including no tillage, are aimed at favoring natural enemies and enhancing biological control in agricultural systems (Landis et al., 2000). It is important to know whether the natural enemies that are conserved by

habitat management actually suppress pest populations. This study showed that the absence of tillage resulted in increased populations of wolf spiders, which tended to control pest populations. Therefore, no tillage seems to be an efficient method for controlling pests in paddy fields.

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REFERENCES

- Andow, D. A. (1991) Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* 36: 561–586.
- Andow, H., C. Kominami, H. Fujii and K. Okada (1998) Growth analysis of no-tillage and conventional tillage rice plants. *Jpn. J. Soil Sci. Plant Nutr.* 69: 618–625 (in Japanese with English summary).
- Brust, G. E., B. R. Stinner and D. A. McCartney (1985) Tillage and soil insecticide effects on predator-black cutworm (Lepidoptera: Noctuidae) interactions in corn agroecosystems. *J. Econ. Entomol.* 78: 1389–1392.
- Brust, G. E., B. R. Stinner and D. A. McCartney (1986) Predator activity and predation in corn agroecosystems. *Environ. Entomol.* 15: 1017–1021.
- Carter, P. E. and A. L. Rypstra (1995) Top-down effects in soybean agroecosystems: spider density affects herbivore damage. *Oikos* 72: 433–439.
- Gebhardt, M. R., T. C. Daniel, E. E. Schweizer and R. R. Allmaras (1985) Conservation tillage. *Science* 230: 625–630.
- Heidger, C. and W. Nentwig (1989) Augmentation of beneficial arthropods by strip-management. 3. Artificial introduction of a spider species which preys on wheat pest insects. *Entomophaga* 34: 511–522.
- Hidaka, K. (1993) Farming systems for rice cultivation which promote the regulation of pest populations by natural enemies: planthopper management in traditional, intensive farming and LISA rice cultivation in Japan. *FFTC Extension Bulletin* 374: 1–15.
- House, G. J. and B. R. Stinner (1983) Arthropods in no-tillage soybean agroecosystems: Community composition and ecosystem interactions. *Environ. Manag.* 7: 23–28.
- Itô, Y., K. Miyashita and K. Sekiguchi (1962) Studies on the predators of the rice crop insect pests, using the insecticidal check method. *Jpn. J. Ecol.* 12: 1–12.
- Iwao, S. (1977) Analysis of spatial association between two species based on the interspecies mean crowding. *Res. Popul. Ecol.* 18: 243–260.
- Kajimura, T., K. Fujisaki and F. Nakasuji (1995) Effect of organic rice farming on leafhoppers and planthoppers 2. Amino acid content in the rice phloem sap and survival rate of planthoppers. *Appl. Entomol. Zool.* 30: 17–22.
- Kawahara, S., K. Kiritani and N. Kakiya (1974) Population biology of *Lycosa pseudoannulata* (Bös. et Str.). *Bull. Kochi Inst. Agric. For. Sci.* 6: 7–22 (in Japanese with English summary).
- Kiritani, K., N. Hokyo, T. Sasaba and F. Nakasuji (1970) Studies on population dynamics of green rice leafhopper, *Nephotettix cincticeps* Uhler: Regulatory mechanism of the population density. *Res. Popul. Ecol.* 12: 137–153.
- Kiritani, K., S. Kawahara, T. Sasaba and F. Nakasuji (1972) Quantitative evaluation of predation by spiders on the green rice leafhopper, *Nephotettix cincticeps* Uhler, by a sight-count method. *Res. Popul. Ecol.* 13: 187–200.
- Landis, D. A., S. D. Wratten and G. M. Gurr (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- Motobayashi, T., Y. Naruoka and H. Wada (2001) Growth and yield characteristics of rice plants on no-tillage paddy field compared with plants in the conventional-tillage paddy field. *Jpn. J. Crop Sci.* 70 (Extra issue 1): 18–19 (in Japanese).
- Nentwig, W. (1988) Augmentation of beneficial arthropods by strip-management. I. Succession of predacious arthropods and long-term change in the ratio of phytophagous and predacious arthropods in a meadow. *Oecologia* 76: 597–606.
- Nyffeler, M. and G. Benz (1987) Spiders in natural pest control: A review. *J. Appl. Entomol.* 103: 321–339.
- Oraze, M. J. and A. A. Grigarick (1989) Biological control of aster leafhopper (Homoptera: Cicadellidae) and midges (Diptera: Chironomidae) by *Pardosa ramulosa* (Araneae: Lycosidae) in California rice fields. *J. Econ. Entomol.* 82: 745–749.
- Oraze, M. J., A. A. Grigarick and K. A. Smith (1989) Population ecology of *Pardosa ramulosa* (Araneae, Lycosidae) in flooded rice fields of northern California. *J. Arachnol.* 17: 163–170.
- Riechert, S. E. and L. Bishop (1990) Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology* 71: 1441–1450.
- Riechert, S. E. and T. Lockley (1984) Spiders as biological control agents. *Annu. Rev. Entomol.* 29: 299–320.
- Rypstra, A. L., P. E. Carter, R. A. Balfour and S. D. Marshall (1999) Architectural features of agricultural habitats and their impact on the spider inhabitants. *J. Arachnol.* 27: 371–377.
- Sasaba, T., K. Kiritani and S. Kawahara (1970) Assessment of the predatory ability of spiders for comparative purposes. *Jpn. J. Appl. Entomol. Zool.* 14: 144–146 (in Japanese).
- Southwood, T. R. E. (1994) *Ecological Methods*. Chapman and Hall, London. 524 pp.
- Stinner, B. R. and G. J. House (1990) Arthropods and other invertebrates in conservation-tillage agriculture. *Annu. Rev. Entomol.* 35: 299–318.
- Widiarta, I. N., K. Fujisaki and F. Nakasuji (1991) Life tables and population parameters of the green leafhopper, *Nephotettix cincticeps* (Uhler), in the southwestern district of Japan with special reference to the first generation on foxtail grass. *Res. Popul. Ecol.* 33: 257–267.
- Wise, D. H. (1993) *Spiders in Ecological Webs*. Cambridge University Press, Cambridge. 328 pp.