LEAFHOPPERS AND PLANTHOPPERS AS 'VIRUS' VECTORS IN JAPAN

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ABSTRACT

Four delphacids and four cicadellids have been listed as natural vectors of viruses and nine cicadellids as natural vectors of mycoplasmalike organisms (MLO's). Laodelphax striatellus, Nilaparvata lugens and Nephotettix cincticeps have been studied with particular emphasis placed on their relations to virus and MLO diseases. Population growth patterns have also been described in the above-mentioned three species and Sogatella furcifera.

NATURAL VECTORS OF PLANT VIRUSES AND MYCOPLASMALIKE ORGANISMS

The Japan archipelago stretches along the Pacific Ocean from south to north (Fig. 1), and the distribution of virus diseases and their vectors in this country is often locally restricted (Tables 1 and 2).

In Tables 1 and 2 the term 'natural vector' refers to a leafhopper or planthopper whose host range and geographical distribution overlap with those of the disease concerned, under natural conditions. The following species are not listed in Table 1 as natural vectors for the following reasons:

The delphacid, Unkanodes sapporonus (Matsumura), has been proved to transmit northern cereal mosaic virus, rice black-streaked dwarf virus and rice stripe virus in the laboratory (Shinkai 1966), but in the field these viruses do not infect any of the plants which have been recorded as host plants of the insect.

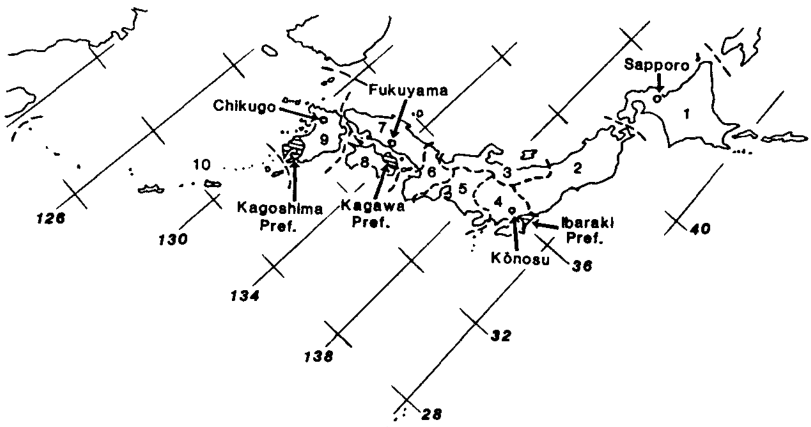

Fig. 1. Districts of Japan (figure 1: Hokkaidō, 2: Tōhoku, 3: Hokuriku, 4: Kantō-Tōsan, 5: Tōkai, 6: Kinki, 7: Chūgoku, 8: Shikoku, 9: Kyūshū, and 10: the Nansei Islands). The main island comprising districts 2-7 is called Honshū. Localities which are cited in the text are indicated on the map.

The delphacids, Nilaparvata bakeri (Muir) and N. muiri China, are capable of transmitting rice grassy stunt virus (Iwasaki et al. 1980). They reproduce on such weeds as Leersia japonica Makino but neither reproduction on rice plant nor transmission of the virus mentioned above has been observed under natural conditions.

The cicadellid, Nephotettix malayanus Ishihara et Kawase, can transmit rice waika virus under experimental conditions (Inoue 1977), but the virus has not been recorded in the Nansei Islands (district 10 in Fig. 1), where the leafhopper is distributed.

TABLE 1.

Delphacids and cicadellids as natural vectors of pathogenic agents to cereal crops in Japan

Natural vector		Virus (V) and mycoplasmalike organism (MLO)		
Species	Distribution[1]	Disease	Crop as host	Distribution[1]
Delphacidae				
Laodelphax striatellus (Fallén)	Nationwide	Northern cereal mosaic (V) [Persistent]	Wheat, oat, etc.	D1, and a part of D2
Muellerianella fairmairei (Perris)	D1 - 7	Rice black-streaked dwarf (V) [Persistent]	Rice, corn, barley, wheat, etc.	D4 - 9
Unkanodes albifascia (Matsumura)	D1 - 7, and 9	Rice stripe (V) [Persistent; transovarial]	Rice, corn, oat, etc.	D1 - 9
Nilaparvata lugens (Stål)	Nationwide	Rice grassy stunt (V) [Persistent]	Rice	D9 and 10
		Rice ragged stunt (V) [Persistent]	Rice	D9
Cicadellidae				
Nephotettix cincticeps (Uhler)	D2 - 10	Rice waika (V) [Nonpersistent]	Rice	D9
Nephotettix virescens (Distant)	D9, 10, and a part of D6	Rice dwarf (V) [Persistent; transovarial]	Rice	D4 - 9
Nephotettix nigropictus (Stål)	D9 and 10	Rice transitory yellow (V) [Persistent]	Rice	Part of D10
Recilia dorsalis (Motschulsky)	D2 - 10	Rice yellow dwarf (MLO) [Persistent]	Rice	D2 - 10

[1] D1, 2, 3 ... are the same as districts 1, 2, 3 ... in Fig. 1.

TABLE 2.

Cicadellids which have been recorded as natural vectors of mycoplasmalike organisms in Japan[1/]

Vector species	Mycoplasmalike organism		
	Disease	Host plant	Distribution[2/]
Nephotettix spp.	Rice yellow dwarf	Rice, *Alopecurus aequalis* Sobol. var. *amurensis* (Ohwi), etc.	D2 - 10
Orosius ryukyuensis (Ishihara)	Sweet potato witches' broom	Sweet potato, morning glory, etc.	D10
O. orientalis (Matsumura)	Legume witches' broom	Leguminosae, Solanaceae, Compositae, etc.	D10
Hishimonus sellatus (Uhler) *Hishimonoides sellatiformis* Ishihara	Mulberry dwarf	Mulberry, *Humulus japonicus* Sieb. et Zucc., clovers, etc.	D3 - 10
Scleroracus flavopictus (Ishihara)	Potato witches' broom	Potato, tomato, etc.	D1
	Gentiana witches' broom	Gentian, China aster, tomato, carrot, etc.	D2 and 4
	Pelargonium witches' broom	Pelargonium, sour-dock, etc.	Coastal area of the Inland Sea
	Witches' broom (A)	Japanese butterbur, pelargonium, gentian, etc.	D1
	Aster yellows (Japanese)	China aster, potato, clovers, etc.	D1
	Yellows (A)	Carrot	D1 and 9
	Yellows (B)	Tomato, lettuce, gentian, etc.	Mountainous area of D4
	Yellows (C)	Petunia	Part of D4
	Udo dwarf	*Aralia cordata* Thunb., lettuce, potato, etc.	Part of D3 and D4
Macrosteles orientalis Vilbaste	Cryptotaenia witches' broom	Japanese honewort, spinach, onion, etc.	South of D2
	Bupleurum yellows	Japanese honewort, spinach, radish, etc.	D3
	Onion yellows	Onion, Welsh onion, etc.	D7 - 9

[1/] The author is indebted for this table to M. Sugiura (personal communication). No delphacid has been known to transmit MLO.

[2/] D1, 2, 3 ... are the same as districts 1, 2, 3 ... in Fig. 1.

TABLE 3.

Overwintering populations of *L. striatellus* in 1963[1/]

A. Sapporo, Hokkaidō; collection with a suction-catcher (After Ishii 1981)

Date	Weeds along foot-paths between fallow paddy fields		Orchard grass with clover		Autumn-sown wheat	
	Nymph	Adult	Nymph	Adult	Nymph	Adult
April 26	28.1	0	18.2	0	-	-
May 8	38.0	0	19.8	0	-	-
22	41.7	17.9	19.8	0	0	0
June 7	6.6	1.0	0	0	0	4.5
18	0	0	0	0	0	0

B. Takamatsu, Kagawa Prefecture; collection by sweeping with a butterfly net (After Uehara et al. 1975)

Date	Weeds along footpaths between fal-low paddy fields		Weeds on fal-low paddy fields		Italian ryegrass		Autumn-sown wheat	
	Nymph	Adult	Nymph	Adult	Nymph	Adult	Nymph	Adult
Feb. 7	61	0	13	0	2	0	0	0
14	54	0	2	0	10	0	2	0
28	22	0	8	0	2	0	0	0
March 5	32	0	6	0	2	0	0	0
18	44	0	20	0	16	0	0	0
26	25	21	16	4	-	-	0	16
April 5	2	22	0	20	0	6	0	10
17	1	14	2	16	0	20	0	6
26	0	8	0	8	0	8	0	6

[1/] Densities of insects in A and B cannot be compared with each other because of the difference in methods of collection employed.

LAODELPHAX STRIATELLUS

Overwintering

The planthopper overwinters at the nymphal stage. Overwintering si- are weeds growing along roadsides, grassland, wheat fields, etc. Table : shows that in warm Takamatsu adults begin to appear at the end of March, while in cold Sapporo they do not appear until the end of May.

TABLE 4.

Increase in percentage of spring-sown cereal crop hills exhibiting symptoms of northern cereal mosaic virus disease in Sapporo, Hokkaidō, 1963[1/]

Date	Rye	Two-rowed barley	Barley	Oats	Wheat
June 7	31%	12%	19%	15%	40%
11	31	16	20	15	42
July 3	75	63	52	43	71
18	85	77	67	67	81

[1/] Sown on April 26 and harvested in August. (After Ishii 1981)

TABLE 5.

Annual fluctuations in acreage (100ha) of paddy transplanted early and at the usual time in relation to percentage of rice stripe virus-infected area, presence of light trap catches and percentage of viruliferous nymphs, of *L. striatellus* in Kagawa Prefecture[1/]

Year	Light trap catches[2/]	Early-season transplanting[3/]			Ordinary transplanting[3/]			Percentage of viruliferous nymphs[4/]
		A_1	B_1	B_1/A_1	A_2	B_2	B_2/A_2	
1957	626	12.0	-	- %	370	0	0 %	- %
1958	155	20.1	0.4	2.0	370	8.6	2.3	-
1959	51	14.2	2.0	14.1	370	20.1	5.4	-
1960	114	13.5	8.0	59.3	370	111.3	30.1	-
1961	2856	5.1	-	-	368	48.6	13.2	-
1962	2449	2.5	-	-	366	30.5	8.3	-
1963	2139	2.1	-	-	364	65.3	17.9	6.9
1964	62	-	-	-	360	19.6	5.4	15.6
1965	326	-	-	-	357	21.6	6.1	14.1
1966	37	-	-	-	354	6.8	1.9	11.5
1967	23	-	-	-	350	7.0	2.0	9.5
1968	73	-	-	-	348	15.7	4.5	9.2
1969	11	-	-	-	344	1.5	0.4	7.9
1970	51	-	-	-	304	6.0	2.0	8.3
1971	110	-	-	-	274	1.2	0.3	6.9

[1/] After Uehara *et al*. (1975).

[2/] First-generation adults (males and females) caught in light trap (average of 6 traps).

[3/] A: area of growing paddy; B: total area of paddy fields where more than 6% of the hills exhibited symptoms of rice stripe.

[4/] First-generation nymphs collected in wheat fields.

Transmission of northern cereal mosaic virus

It is believed that the virus remains in overwintering viruliferous nymphs and the main source of virus dissemination in the current year is represented by the macropterous adults which have developed from the viruliferous nymphs and dispersed from the overwintering site to the surroundings (Ishii 1981). In Sapporo the main period of inoculation to spring-sown wheat is from late May to the first half of June. The percentage of diseased hills becomes considerably high by the latter half of July (Table 4).

In wheat fields sown in the autumn ratoons come to grow vigorously soon after harvesting which takes place in mid-July. These ratoons and the gramineous weed, *Poa annua* Linné, play an important role in virus retention during the period from the harvesting of spring-sown cereal crops in late summer to the time of sprouting of autumn-sown wheat before winter (Ishii 1981).

The occurrence of the disease is restricted to the northern part of Japan (Table 1), although in the laboratory, *L. striatellus* originating from southwestern Japan can transmit the virus like the insects inhabiting Sapporo (Ishii 1981).

Muellerianella fairmairei and *Unkanodes albifascia* reproduce on *P. annua*. Ishii (1981) considers them as being important in promoting virus infection on the weed.

Transmission of rice stripe virus

Although some crops are listed in Table 1 as hosts of rice stripe virus, only the infection of rice is of economic importance. The virus is transmitted from the overwintered generation of *L. striatellus* to the next first generation in a transovarial way, and then viruliferous migrants invade often in large numbers the paddy fields transplanted early in the season, resulting in heavy infection of rice. Thus, in some places of Japan outbreaks of the disease have been recorded to occur as soon as the practice of early-season transplanting of rice became prevalent. In Kagawa Prefecture, for instance, the practice was abandoned due to the epidemics of the disease, soon after it was introduced there (Table 5).

Kisimoto (1968) has observed that yellow pan water traps set up in some rice plots with different dates of transplanting were useful in monitoring *L. striatellus* population, and part of the results he obtained are presented in Fig. 2.

In the 1960 s paddy was usually transplanted in the latter half of June in Kagawa Prefecture. In Kisimoto's experiment, plot E with paddy transplanted at that time was much less severely infested with *L. striatellus* than any of the plots transplanted earlier. In plots A, B and C the trend curves were similar in shape to each other, but in A the area under the curve, which indicates the intensity of catching, was significantly smaller than that in B or C. This seems to suggest that in 1965, May 10-transplanted paddy was much less attractive for alighting to the migrants than May 20- or 30-transplanted one when they came flying above the area. Differences in adult density were also observed by Ôtake (1970) between paddy transplanted on different dates in May, 1967.

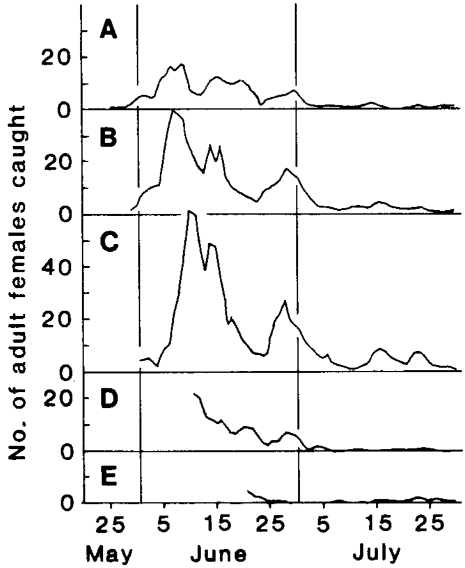

Fig. 2. Curves (3 day-smoothing) of L. striatellus adult females caught by yellow pan water traps in paddy plots transplanted on May 10 (A), May 20 (B), May 30 (C), June 9 (D) and June 19 (E), 1965. The experiment was carried out in Zentsūji, Kagawa Prefecture. (After Kisimoto 1968)

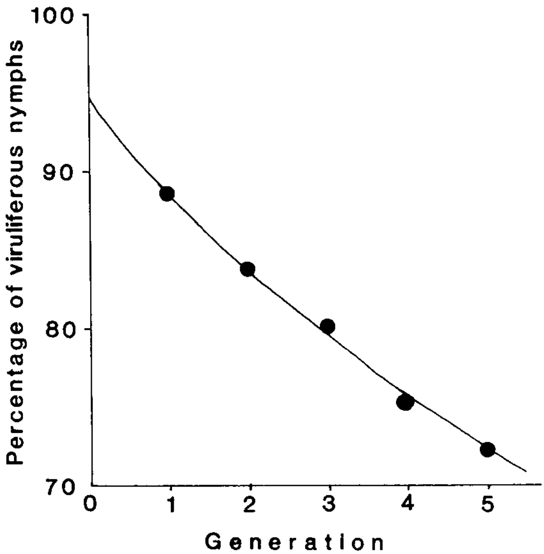

Fig. 3. Decrease in percentage of L. striatellus harbouring rice stripe virus. Generation (solid circle) and theoretical curve calculated from $P_n = P_0 r^n$. (After Kono 1966)

As shown later (Fig. 7), L. striatellus has 3-4 generations on paddy, but the growth rate of its population is usually not so high. Even when the population becomes large and a considerable number of macropterous adults are caught by light traps from mid-summer to autumn (Ôtake and Kono 1970), damage to paddy due to their sucking of juice is usually negligible.

Kono (1966) has proposed the following mathematical model concerning the relationship between the proportions, P_n and P_{n+1}, of viruliferous L. striatellus in generations n and n+1, respectively:

$$P_{n+1} = P_n r(1 - w) + w, \qquad (1)$$

where r and w are the rates of virus acquisition through transovarial transmission and through feeding on diseased plant, respectively. By putting the initial P in generation 0 as P_0 and assuming w = 0, i. e. the population has no chance of acquisition feeding,

$$P_n = P_0 r^n. \qquad (2)$$

Kono established an experimental population of L. striatellus with high virulence and reared them for 5 successive generations to observe the change in virulence under the condition w = 0, which was fulfilled by a quick exchange of food plants before the appearance of visible symptoms of the disease on plant. As seen in Fig. 3, the results of the experiment coincided well with the theoretical calculation, detecting a tendency that even when w = 0, decline in virulence was rather gradual.

In Kōnosu a rapid increase in virulence was observed from 1977 to 1980. In 1979 and 1980 the percentage of viruliferous insects reached about 20% and in spite of the light infestation of the pest, 30-50% of rice plants transplanted on June 10 became infected with the virus (Kisimoto 1981a).

Hirao (1973) treated paddy fields twice with vamidothion during the time of the occurrence of the first-generation adults and reduced the percentage of virus-infected rice stems to 1/3 as compared with untreated fields.

Transmission of rice stripe virus by Unkanodes albifascia has not been demonstrated in the field, although Hirao (1968) suggested that it may possibly occur, on the basis of his own laboratory experiments.

NILAPARVATA LUGENS

Transmission of rice grassy stunt virus and rice ragged stunt virus

In Japan the occurrence of rice grassy stunt virus disease was first recorded in Kyūshū, 1978 (Iwasaki and Shinkai 1979). Since then the disease has occurred every year in some localities of that island. As for rice ragged stunt virus disease, in contrast, there have been only a few records of its sporadic occurrence since it was first observed in Kyūshū in 1979 (Shinkai et al. 1980).

In Japan, since neither rice stubbles nor the vector, N. lugens, are able to survive winter as a matter of fact, it is reasonable to assume that the viruses mentioned above would have soon become extinct if there had not been invasion of viruliferous insects from the south to the country in the succeeding year.

Kisimoto (1976) has noticed that inflow of warm and humid air from the south, which is associated with west-to-east passage of depressions, is often accompanied with a mass immigration of N. lugens and Sogatella furcifera (Horváth) in June and July (Fig. 4). Of 38 depressions which originated in the central part of the Chinese continent and moved to the east in June and July, 1967-1972, 29 brought about planthopper immigrants to Japan.

Population growth and damage caused by N. lugens

Rice only is the host plant of N. lugens in the field (Kisimoto 1981 b). In Japan damage due to the sucking of plant juice is much more important than virus transmission. Particularly in the southwestern part of the country, the pest sometimes multiplies actively and heavy hopperburn takes place. Even in that region, however, the density is very low when immigrants invade the paddy fields. Then, in the next generation, female adults are mostly brachypterous and lay eggs vigorously without leaving the place where they grew up. Figs. 5 and 6 show typical examples of a population burst and hopperburn, respectively.

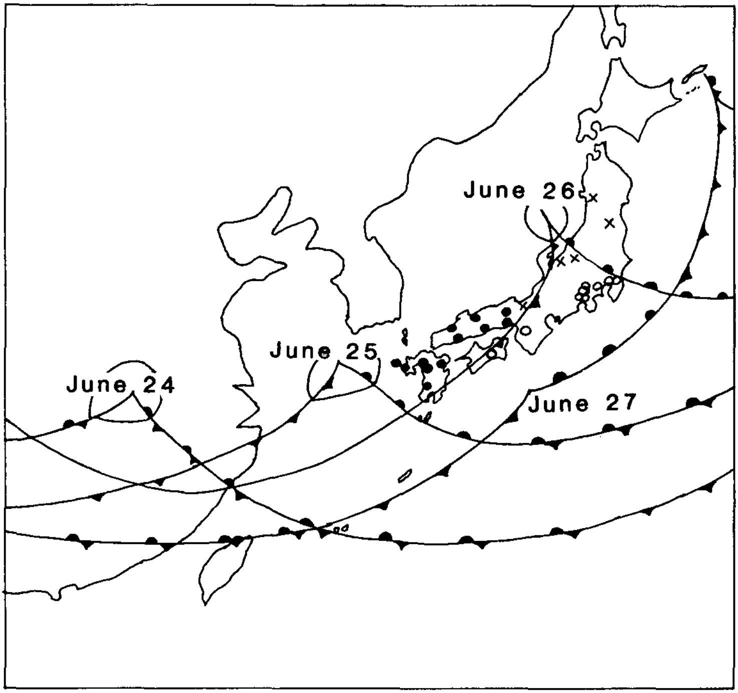

Fig. 4. Route of the depression of June No. 40, 1969 (records at 6 a. m. each day). • and o: light traps where N. lugens and S. furcifera were caught on the nights of June 25 and 26, respectively. x: light trap with no catch on either of both days. (After Kisimoto 1976)

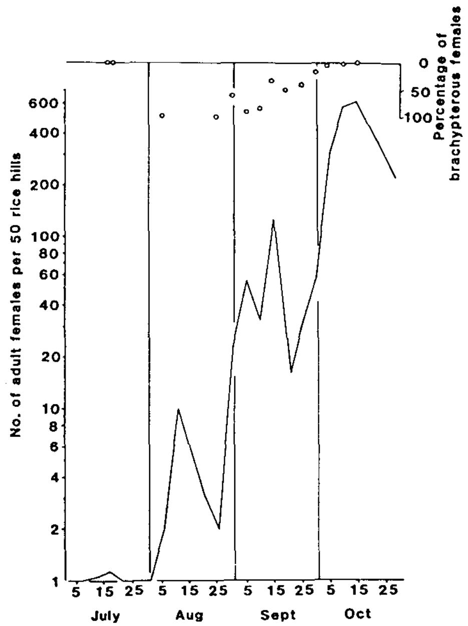

Fig. 5. Increase in the number of N. lugens adult females per 50 rice hills and fluctuation of percentage of brachypterous females, in a paddy field, Zentūji, Kagawa Prefecture, 1959. (After Kisimoto 1965; Ôtake 1978)

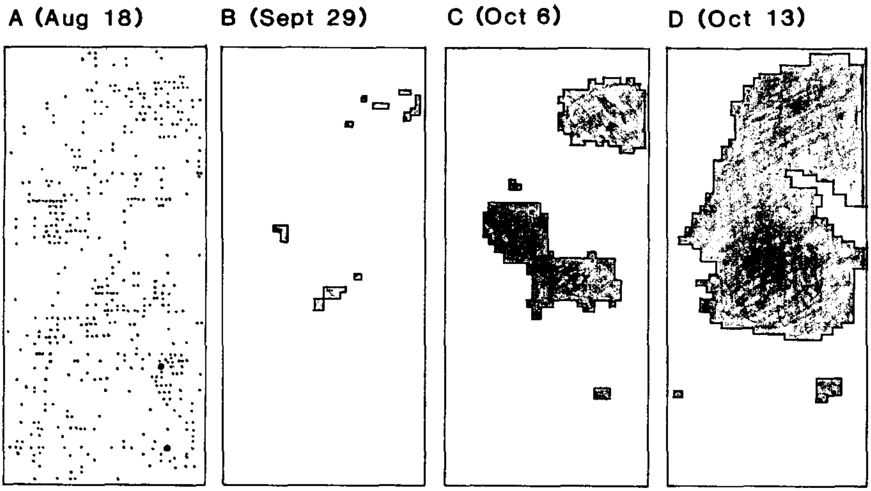

Fig. 6. Distribution of brachypterous adult females of N. lugens in August (A) and expansion of the area with complete hopperburn during September and October (dark parts in B, C and D). In A, smaller dots represent one female and larger ones a group of 4 or more females on a single rice hill. Results of successive observations of the same paddy field (27m x 8m) in Fukuyama, 1969. (After Hirao 1972)

Based on his own findings in Chikugo, Kisimoto (1975) recommends to treat paddy fields with insecticides in the last 10 days of July or the first 10 days of August whenever 50-100 N. lugens adults (males and females) are caught in a yellow pan water trap during the immigration season from the end of June to the beginning of July. Chemical treatment at the appropriate time would bring about the highest yield of rice crop (Nagata 1982).

Sogatella furcifera, which does not transmit any rice virus, also immigrates in great numbers from the south and its initial density on paddy is usually higher than that of N. lugens. In the following generations, however, it does not attain such a high level of density as N. lugens does (Fig. 7).

NEPHOTETTIX CINCTICEPS

Transmission of rice waika virus

Among the 3 species of Nephotettix listed in Table 1, N. cincticeps is the most important one because it is widely distributed and abundant everywhere.

Rice waika virus disease suddenly appeared in Kyūshū in 1971. Its causal agent belongs to the rice tungro virus group (Nishi et al. 1975; Doi et al. 1975). In 1973 the total area of infected paddy fields amounted to about 25,000 ha, but then the disease soon became endemic. Introduction of such resistant rice cultivars as Fukumasari and Saikai No. 139 is believed to have had a great influence upon the suppression of the disease (Inoue and Hirao 1981).

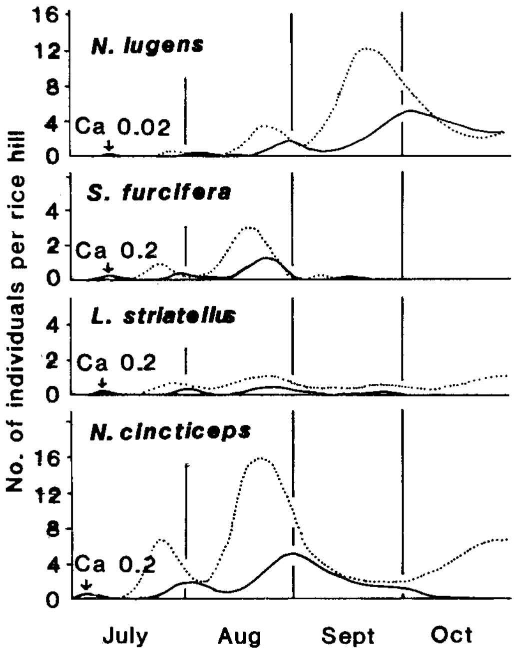

Fig. 7. Standard pattern of seasonal population trend in the main plant- and leafhoppers infesting paddy. Schematical drawings after averaging data of 6-year investigations in Chikugo. Solid and dotted lines refer to adults and 3rd-5th instar nymphs, respectively. (After Kuno 1968)

Transmission of rice dwarf virus

Around 1955 the disease started to become epidemic in areas where the practice of early-season transplanting of rice was prevalent. About 10 years later its occurrence became prominent even in areas where paddy was being transplanted at the usual time (Nakasuji and Kiritani 1976).

The overwintering population of *N. cincticeps*, in which nymphs at advanced stages of development predominate, inhabits weeds, mainly *Alopecurus aequalis* Sobol. var. *amurensis* (Ohwi), growing in the fallow paddy fields or their surroundings. When there is no rice transplanted early in the season, leafhoppers hardly find any place suitable for reproduction and the growth of the population is contained before the appearance of rice transplanted later at the usual time (Table 6). When there exists paddy transplanted earlier, on the other hand, they come there as early as May and reproduce actively (Fig. 8). It is understandable that the virus disease becomes epidemic under such conditions.

TABLE 6.

Changes in the density of *N. cincticeps* adult females in the same paddy field[1/] in Chikugo, Kyūshū

Year	No. of female adults per square metre[2/]		
	Third generation	Overwintering generation in the field in fallow	First generation (immigrants)
1968	-	5.3	3.7
1969	353.5	9.2	1.9
1970	466.5	11.7	11.0

[1/] Transplanted at the end of June and harvested in the latter half of October every year.

[2/] Estimated from the results of life-table analysis. (After Hokyo 1972)

Rice dwarf virus is harmful to *N. cincticeps* with respect to some biotic performances including fecundity (Nakasuji and Kiritani 1970). Process of transovarial transmission of this virus, therefore, cannot be expressed by such a simple model as formula 1 given for rice stripe virus. Descriptive models for the epidemiology of the disease have been presented by Nakasuji and Kiritani (1972) and Nakasuji et al. (1975).

In Kagoshima Prefecture late-autumn applications of insecticides on fallow land to control overwintering *N. cincticeps* have been recommended for preventing the occurrence of the disease in the succeeding year (Babaguchi *et al*. 1969).

Recilia dorsalis is not very important as a vector due to its low density of population. According to Shinkai (1962), the longevity of this species also decreases due to transovarial acquisition of the virus.

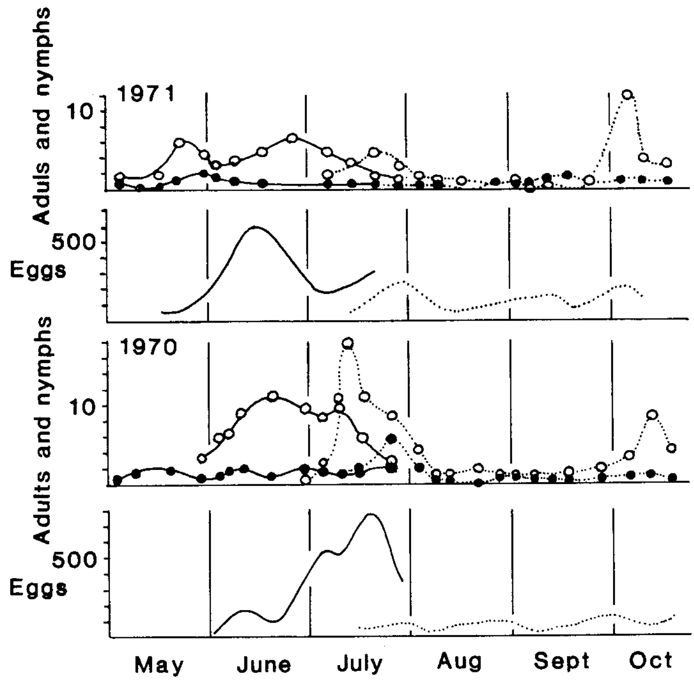

Fig. 8. Fluctuations of densities of N. cincticeps on paddy transplanted early (solid line) or at the usual time (dotted line) in Kagoshima Prefecture. ●:adults, and o: nymphs. (After Hara et al. 1975)

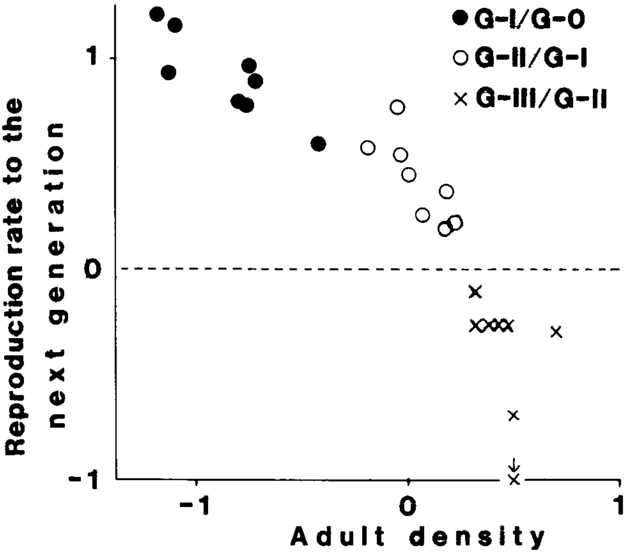

Fig. 9. Relation between reproduction rate and population density for successive 2 generations in N. cincticeps. The generation of immigrants is designated as G-0 and the following generations as G-I, G-II and G-III. (After Kuno and Hokyo 1970)

Transmission of rice yellow dwarf

This MLO disease also became prevalent after the introduction of the practice of early-season transplanting of rice. Komori *et al.* (1972) have pointed out that paddy transplanted early in the season is likely to become inoculated with the MLO, first, through transmission by *N. cincticeps* immigrants in May-June and second, through transmission by adults of the same species in August-September. In the overwintering generation nymphs become viruliferous by feeding on diseased leaves of rice ratoons in late autumn. It is also possible to consider that the MLO may overwinter in surviving rice ratoons in a warmer region.

In Ibaraki Prefecture aerial spraying of insecticides by helicopter in April was highly effective in checking the disease in the later season (Komori *et al.* 1972).

Mechanism of population stabilization

After analyzing their own field data compiled over a period of 8 years in Chikugo, Kuno and Hokyo (1970) disclosed the following characteristics of *N. cincticeps* population: (1) small variations in annual maximum density, which take place during August and September, and (2) remarkable decrease in reproduction rate with increasing population density (Fig. 9). They then suggested the existence of a density-dependent process to stabilize the population towards its peak generation. Natural enemies did not seem to be deeply involved in the process, while dispersal (emigration) of adult females by flight was largely density-dependent (Kuno and Hokyo 1970; Hokyo and Kuno 1977). Kiritani (1979) has presented an interesting table to compare some ecological characteristics between *Nephotettix* and *Nilaparvata*.

In districts 3 and 4 (Fig. 1), direct feeding damage to paddy has been suggested to be sometimes considerable (Naba 1981).

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