Epidemiological Study on Rice Dwarf Virus Transmitted by the Green Rice Leafhopper *Nephotettix cincticeps*

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Rice dwarf virus (RDV) is a pathogen transmissible by the green rice leafhopper *Nephotettix cincticeps* and two other kinds of leafhoppers. This virus can multiply in the body of a vector and can be transmitted from a mother insect to her progeny by means of transvarial transmission[2], and the virus multiplicated in the vector affects seriously the physiological conditions of the vector[17,21].

The natural population of *N. cincticeps* is strictly controlled through density dependent processes[1,11,15]. The systems analyses on the changing process of this vector's population density and on the transmission process of RDV by the vector have been studied by mathematical models[20,24].

In spite of such abundant accumulation of pathological and ecological knowledge, the detailed analytical study on the prevalence factor of RDV has been scarcely performed.

The author would like to investigate factors which are responsible for the recent prevalence of this disease, with special reference to the ecological factors.

Actual circumstances of RDV prevalence

Some abrupt outbreaks of rice dwarf disease, which were discovered at first in Shiga Prefecture in 1883, prevailed in Kyoto, Okayama, Hyogo, Shiga, Nagano, Shizuoka, Yamanashi, Hiroshima, Ibaragi, Gunma and Miyazaki districts during the period from 1889 to 1930[1]. The characteristics of these outbreaks were the mosaic pattern of infected areas without regional continuity and these outbreaks lasted only for one or two years.

But after World War II, around 1955, this disease began to prevail in the Kyushu district and the southern area of Shikoku extending progressively to the coastal regions of the Pacific and Seto Inland Sea. The characteristics of the epidemics were the continuity in time and space over an extended area. For example, it was reported that the infected areas of about 210,000 ha covered 22 prefectures in 1971.

Cause of the recent epidemics

1) Increasing early planted rice cultivation

After World War II, the early cultivation of rice became possible because of the widespread use of protected semi-irrigated rice nursery by the utilization of polyfilm, and it spread rapidly in western Japan to avoid the damage inflicted by typhoon.

Fig. 1 shows the annual changes of the areas cultivated with early planted rice and of the areas infected by rice dwarf disease in Kochi Prefecture. The areas cultivated with early planted rice began to increase gradually immediately after World War II and attained to 5,000 ha in 1955 and 10,000 ha in 1960. Such increase of early planted rice cultivation might have caused the prevalence of RDV because of the following two reasons:

The first reason is that the introduction of early planted rice cultivation into the middle-

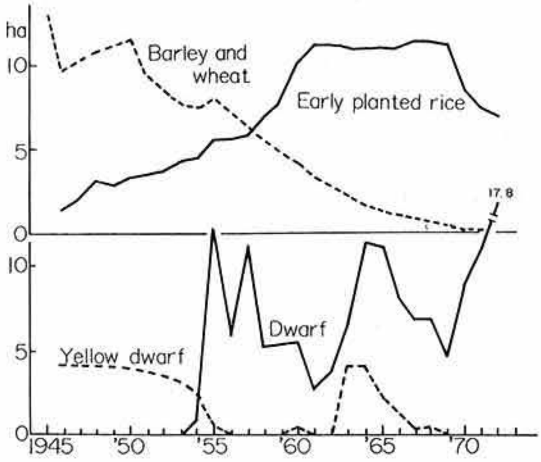

Fig. 1. Changes in acreage of the early planted rice and that of barley and wheat cultivated in the paddy fallow in Kochi (Top)
Fluctuations in infested acreage of paddy fields by rice yellow dwarf disease and rice dwarf disease in Kochi (Bottom)

season cultivation areas of rice results in mixed cropping which changes the abundance and pattern of the occurrence of the green rice leafhopper.

In the camparison with annual catches of *N. cincticeps* by light traps for three to five years between the mixed cropping area and the single cropping area of middle-season rice in Kochi Prefecture, the former attained about five times as much as the latter.

Hara (1967)[3] also reported that, in the comparison with the pattern of occurrence of *N. cincticeps* between the period from 1941 to 1951 and that from 1958 to 1965 in the early planting area of rice which had been established around 1952 in Kagoshima Prefecture, *N. cincticeps* of the first generatin (five generations emerge during a year) increased apparently in abundance owing to the introduction of the early planted rice.

When the early planted rice does not exist, the first generation of *N. cincticeps* develops mainly on a gramineous weed *Alopecurus aequalis* in fallow fields, and the rate of increase in this generation is 1 or less[4], while it attains 20 to 100 times as much when the insect develops on the early-planted rice[11]. These changes in abundance and in the pattern of occurrence of *N. cincticeps* caused by the introduction of early planted rice result in the prevalence of RDV.

The second reason is that the pattern of the inter-generation variation in respect to the percentage of RDV infected insects among the population of *N. cincticeps* is changed by existence of early-planted rice[19] and its level rises[6].

Fig. 2 shows the pattern of inter-generation variation of the percentage of infected insects in the early planted rice area (Nangoku) and in the single cropping area of middle-season rice (Ino) in Kochi Prefecture.

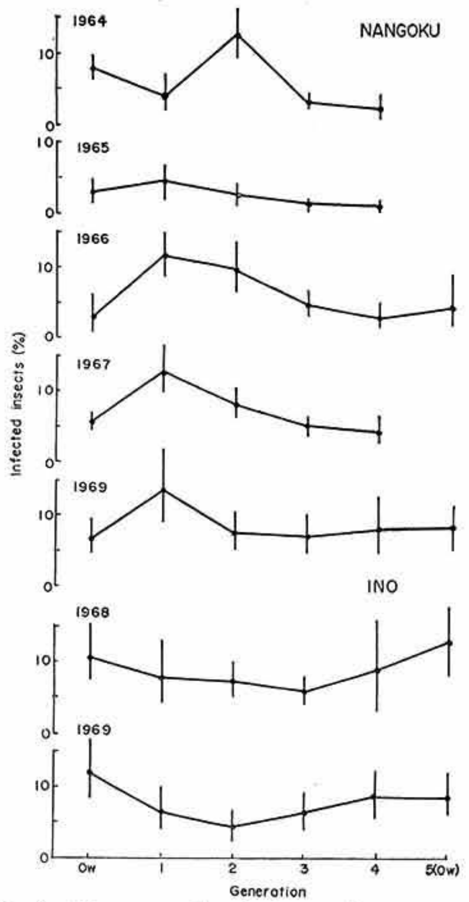

Fig. 2. Inter-generational changes in percentage of RDV-infected insects in Nangoku where early and late rice crops are cultivated, and Ino where single crop of middle-season rice is cultivated[19]

In the early-planted rice area, the adult insects of overwintering generation transmit RDV to the seedlings in the nursery of early-season rice and cause disease of rice plants at the nymphal period of their offspring, and the nymphs became infected by sucking the juice of these infected plants, and the percentage of infected insects increases rapidly. In summer, the percentage of infected insects decreases because of the death rate increased by the physiological adverse effect of RDV[17].

On the other hand in the middle-season rice area, the percentage of infected insects of first generation does not increase because of the feeding on weeds which scarcely infected by RDV. The percentage of infected insects increased in the fourth and the fifth generation (Fig. 2). This was caused by the tillers developed on the infected stubbles as an extraordinary sucking source of virus because the paddy fields of this area were ill-drained.

Therefore, this is rather a peculiar condition[18),19)]. Generally speaking, however, the high percentage of infected insects seems not to be maintained because the percentage in the first generation does not increase but continues to decline in the middle-season rice area except the ill-drained paddy field.

The percentage of infected rice hills, which was investigated on 86 selected places in Kochi Prefecture between 1970 and 1972, was classified into four classes and plotted against the ratio of early-planted rice area to the total area of the paddy fields in that region as shown in Fig. 3 where × marks indicate ill-drained areas. It can be clearly recognized that the introduction of early-season rice increases the occurrence of rice dwarf disease.

But when the area became a complete single cropping area of early-season rice, the prevalence of RDV does not occur any more owing to the remarkable decrease in the abundance of the green rice leafhopper because of the want of rice plant for the insects of the fourth and fifth generatins. It was also proved that RDV does not occur in the single cropping area of middle-season rice except ill-drained area.

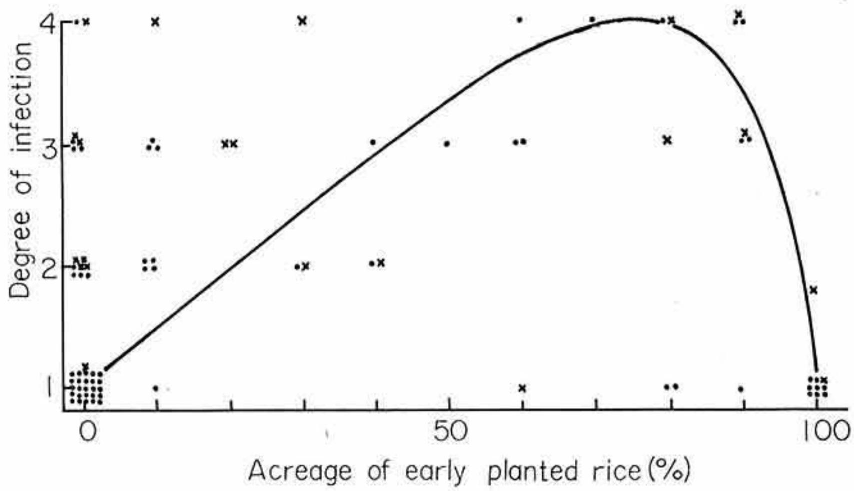

Fig. 3. Relationship between the percentage acreage of early planted rice in the paddy fields and the degree of infection of RDV. ● indicates well drained paddy fields. × indicates area of poor drained paddy fields

Weighed degree of infection	Percentage of infected rice hills
1	0— 4.9
2	5— 9.9
3	10—19.9
4	20—

It is reported that, in Ibaragi Prefecture where the introduction of early-season rice began from 1957, the percentage of infected insects of second generation increased up to 15% in 1959 and 1960 while it was only 0 to 1.2% in 1957[6].

2) Utilization of synthetic insecticides

There must exist other cause of RDV prevalence besides the introduction of early-season rice cultivation because there are some areas affected with RDV prevalence, nevertheless no early-season rice was introduced.

The year, around 1955, when RDV began to prevail corresponds to the time when the utilization of BHC or parathion started in the paddy field. The light-trap records of many regions manifested that the abundance of *N. cincticeps* increased remarkably in every region from this period without any respect to the change of rice cropping[10].

Kobayashi (1961)[14] considered that *N. cincticeps* increased because BHC applied to control rice stem borer *chilo suppressalis* also killed the spiders which are the important natural enemy of the leafhopper. The insecticidal check method confirmed his conception afterward[7,12].

Furthermore, Kiritani et al. (1972)[13] investigated the predation of spiders and presumed that 4.4–100% of nymphs and 9.0–100% of adults of *N. cincticeps* were preyed upon by spiders. It is known that BHC can kill one-half of spiders with its concentration of 2 to 4% of the LC_{50} for *N. cincticeps*[8].

The simulation by the systems model demonstrated that the population density of *N. cincticeps* could be decreased to one-half by increasing the number of spiders from one to four per rice hill. Such phenomenon was also actually recognized when no insecticide had been applied to the paddy field for six years[10,23]. Such increased incidence of *N. cincticeps* owing to the application of synthetic insecticides may be also important as one of the causes which make RDV break out enormously and make its prevalence constant.

3) Increase of fallow paddy field owing to the decrease of winter cropping (barley and wheat) on drained paddy field

Fig. 1 shows the relation of annual change in acreage between the winter cropping of paddy field (barley and wheat) and the occurrence of rice dwarf disease after World War II.

Since about 1950, the acreage of barley and wheat decreased continuously. This decrease was caused because the winter cropping (barley and wheat) became impossible owing to the introduction of early-season rice cultivation and to the imcompetence for the competition in price with imported barley and wheat.

As a result, a vast area of paddy field has been left as fallow paddy field where gramineous weeds such as *Alopecurus aequalis* grow and develop overwintering nymphs of *N. cincticeps* up to the first generation.

Hokyo (1972)[4] estimated the density of adult population of overwintering generation in such fallow paddy field at 7 to 38 per m^2. Muramatsu et al. (1970)[16] reported that the estimated adult density is 32 per 1 m^2 by the marking-recapture method. This may be a far higher value than that when barely or wheat was cultivated on the paddy field instead of weeds.

An idea to control RDV by eliminating weeds from fallow paddy fields has been proposed[4,6] but it is not yet practiced actually. But the role of the fallow paddy field on the prevalence of RDV is presumable from the example of large scale chemical control of the pests in the fallow paddy field.

There are two periods in which the acreage affected by rice dwarf disease decreased greatly (Fig. 1). These are the periods when cooperative pest control or aerial application was carried out on vast fallow paddy field. These controlling methods were abandoned afterward because the opposition of inhabitants against the drift of insecticides was increased. These methods are also likely to accelerate the development of insecticidal resistance of *N. Cincticeps*. But if these prob-

Table 1. System model of RDV epidemiology[20)]

Parameter	Symbol	Generation* of *N. cincticeps* (variety of rice)	Submodel	Equation number	Model 1	Model 2
Egg density/hill in *n*th generation	$N_{E(n)}$	1st to 3rd (*E.*) 4th to 5th (*L.*)	$N_{E(n+1)}=89.34N_{E(n)}^{0.300}$	(6)	—	
		3rd to 4th (*E.*→*L.*)	$N_{E(4)}=335800N_{E(3)}^{-1.346}$	(7)	—	
Adult density/hill	$N_{A(n-1)}$	*ow.* to 4th (*E.* & *L.*)	$N_{A(n-1)}=\frac{N_{E(n)}}{F_{M(n-1)}}$	(8)	—	
Men fecundity/female	$F_{M(n-1)}$					
Density of 1st-instar nymphs/hill	$N_{L-1(n)}$	1st to 5th (*E.* & *L.*)	$N_{L-1(n)}=0.549N_{E(n)}^{0.881}$	(9)	—	
Proportion of newly infected rice hills						
by immigrated adults	$A_{T(I)}$	*ow.* (*E.*), 3rd (*L.*)	$A_{T(I)}=0.113\log N_AP+0.491$	(10)	—	—
by ensuing progeny	$A_{T(II)}$	1st (*E.*),	$A_{T(II)}=0.098\log N_{L-1}P+0.255$	(11)	—	—
Proportion of infected rice hills	A_I	1st (*E.*), 4th (*L.*)	$A_I=A_{T(I)}$	(1)	—	—
	A_{II}	2nd, 3rd (*E.*), 5th (*L.*)	$A_{II}=A_{T(I)}+A_{T(II)}-A_{T(I)}A_{T(II)}$	(1) & (2)	—	—
Loss in yield of unpolished rice by RDV-infection	L_I		$L_I=0.800A_{T(I)}$	(4)	—	—
	L_{II}		$L_{II}=0.333A_{T(II)}$	(5)	—	—
Index of infected rice plants	I_v	1st to 5th (*E.* & *L.*)	$I_v=\frac{bA}{(1-A)+aA+bA'}$ $(A=A_I$ or $A_{II})$	(3)	—	—
Proportion of infected individuals	$P_{(n)}$	1st to 5th (*E.* & *L.*)	$P_{(n)}=1.278I_{v(n)}^{0.727}$	(12)	—	—
			$P_{(n+1)}=P_{(n)(n)}(\alpha r)_{(n+1)}(1-W_{(n+1)})+W_{(n+1)}$	(13)		—
Proportion of individual acquired RDV orally	$W_{(n)}$	1st to 5th (*E.* & *L.*)	$W_{(n)}=1-e^{-2.355}I_{v(n)}$	(15)		—
Relative rate of increase of infected insects to non-infected ones	$_{(n)}(\alpha r)_{(n+1)}$	1st to 5th (*E.* & *L.*)	$_{(n)}(\alpha r)_{(n+1)}=-0.029T_{(n+1)}+0.938$	(14)		—
Mean temperature	$T_{(n+1)}$					

* *E.*: Early planted rice, *L.*: Late planted rice, *ow.*: Overwintering generation

lems could be managed adequately by some other means, the prevalence of RDV might be decreased.

4) Other factors

As for the other factors which are related to the prevalence of RDV, the heavy manuring culture of rice, change in varietal resistance of rice against RDV and variation of acquisitive abilities of RDV by the vector or the virulence of the virus might be listed.

The use of chemical fertilizer started around 1955, and the cultivation of high yielding varieties became possible by the use of chemical fertilizer and synthetic insecticides in spite of their weak resistance against disease and insects.

Studies on the varietal resistance to RDV revealed that many resistant varieties are involved in the indica type rice[22),24)], while no resistant variety of japonica type rice has been found except Ozawabana No. 1[5)].

Therefore, it is difficult to connect the change of varieties and chemical fertilizer directly with the recent prevalence of RDV. But it seems to be possible that the heavy manuring cultivation of rice increased the rate of reproduction of *N. cincticeps*[6)].

Nothing has been found about the variation of the virulence of RDV. Shinkai (1962)[25)] and Kimura (1962)[9)] reported on the acquisitive ability of *N. cincticeps* against RDV. They reported that the *N. cincticeps* in prevalent area of RDV is higher in acquisitive ability than that in non-prevalent area. The relation between such variability of vector in terms of the acquisitive ability of the virus and the prevalence of RDV is a vital problem which should be studied in the future.

Simulation of prevalence by means of the systems model of RDV-epidemiology

Nakasuji and Kiritani (1972)[20)] invented a systems model for the descripition of the transmission process of RDV (Table 1), and they simulated the change in percentage of infected rice plants and that of loss in yield of brown rice by changing the population density of *N. cincticeps* and the percentage of infected insects by means of this model. (Table 2).

It was presumed, as the result, that the population density of the vector in the overwintering generation must be decreased to less than about one-tenth or the transmission of RDV by the vector of that generation to the nursery of early-season rice should be decreased to less than one-third to reduce the percentage of loss in yield to less than ten percent[20)].

On the other hand, the trend of the prevalence of RDV after ten years was simulated changing three parameters as the influential factors on the prevalence, that is, the density of vector, efficiency of feeding acquisition of RDV of vector, and efficiency of transmission of RDV by vector on rice plant (Nakasuji et al. unpublished).

The model of the population change of *N. cincticeps* reported by Sasaba et al. (unpublished) was used for the calculation in this simulation, and as the result, the percentages of infetced insects and of the loss in yield of brown rice were obtained reducing each value of the parameters to one-half of the standard value in Kochi Prefecture (Table 3).

This simulation indicated that the present population density of vector must be decreased to less than one-tenth to reduce the percentage of loss in yield to below ten percent, and that the most influential parameter is the efficiency of transmission.

Though the use of synthetic insecticides and the increase of fallow paddy field raise the population density of vector, the introduction of early-season rice, which may provoke not only the increase of vector density but also the remarkable increase of the percentage of infected insects, might have performed a special important role on the prevalence of RDV.

Table 2. Evaluation of the effectiveness of different control methods by the simulation using the RDV-leafhopper-plant system

Simulation 1 refers to the case where no treatment against RDV-infestation is conducted. Next, the efficiency of the control is evaluated assuming that either of the proportion (P_{ow}) of infected individuals or the density (N_{Aow}) of the adults of overwintering generation is reduced one—third of those of the untreated population (simulations 2 and 3). In Simulations 4 and 5, we reduced the population (P_1) of the 1st generation to one—third that of the untreated population. This can be practically realized either by reducing the amount of the virus sources for the feeding acquisition by 1st generation insects (Simulation 4) or by decimating the density of the overwintering population as low as 8 percent of the untreated population (Simulation 5)[20]

Simulation	Treatment		Expected percentage of infected rice hills in early planted rice		Expected percentage loss in yield of unpolished rice (L_I+L_{II})	Control measures available
	Proportion of infected individuals (P_n)	Density of *N. cincticeps* (N_{An})	Tillering stage (A_I)	Shooting stage (A_{II})		
1	1	1	13.3	29.9	16.8	No treatment
2	1/3 (ow. gen.)[1]	1	7.8	22.6	11.6	Unknown
3	1	1/3 (ow. gen.)	7.8	19.6	10.4	Repeated sprays of an insecticide in the nursery bed (a conventional control method)
4	1/3 (1st gen.)	1	3.2	16.9	7.2	Covering the nursery bed with nylon gauze
5	1/3 (1st gen.)	0.08 (ow. gen.)[2]	3.2	4.3	3.0	Aerial application of an insecticide or control of overwintering nymphs in the fallows by a selective insecticide to encourage the activity of natual enemies.

1) ow. gen. refers to overwintering generation

2) Decimation of overwintering population to 8 percent of the untreated population will result in two-thirds decrease of the proportion of infected individuals in the 1st generation

Table 3. Relative importance of various factors in determination of the degree of occurrence of RDV

Parameters	Expected percentage when the value of each parameter is reduced to ½		Suggested control measures
	Infected insects (%)	Reduction in yield of brown rice (%)	
Density of the vector	6.2	18.1	Insecticidal treatment
Efficiency of the feeding acquisition of RDV	3.0	16.9	Genetic manipulation
Efficiency of the transmission of RDV	3.0	8.5	Resistant variety or physical exclusion of sucking by e.g. nylon cloth

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References

1) Fukushi, T.: Studies on dwarf disease of rice plant. *J. Fac. Agr. Hokkaido Imp. Univ.*, 37, 41–164 (1934).

2) Fukushi, T.: Further studies on dwarf disease of rice plant. *J. Fac. Agr. Hokkaido Imp. Univ.*, 45, 83–154 (1940).

3) Hara, K.: Occurrence and control of rice

dwarf virus (RDV) in Kagoshima Prefecture. *Shokubutsu-boeki*, 21, 55–59 (1967). [In Japanese]

4) Hokyo, N.: Studies on the life history and the population dynamics of the green rice leafhopper, *Nephotettix cincticeps* Uhler. *Bull. Kyushu Agr. Exp. Sta.*, 16, 282–382 (1972). [In Japanese with English summary]
5) Ishii, M., Yasuo, S. & Yamaguchi, T.: Testing methods and analysis of the varietal resistance to rice dwarf disease. *J. Cent. Agr. Exp. Sta.*, No. 13, 23–44 (1969). [In Japanese with English summary]
6) Ishii, M., Yasuo, S. & Yamaguchi, T.: Epidemiological studies on rice dwarf disease in Kanto-Tosan district, Japan. *J. Cent. Agr. Exp. Sta.*, No. 14, 1–115 (1970). [In Japanese with English summary]
7) Ito, Y., Miyashita, K. & Sekiguchi, K.: Studies on predators of rice crop insect pests, using the insecticidal check method. *Jap. J. Ecol.* 12, 1–11 (1962).
8) Kawahara, S., Kiritani, K. & Sasaba, T.: Selective activity of rice-pest insecticides against green rice leafhopper and spiders. *Botyu-kagaku*, 36, 121–128 (1971). [In Japanese with English summary]
9) Kimura, I.: Further studies on rice dwarf virus-I. *Ann. Phytopathol. Soc. Japan*, 27, 197–203 (1962). [In Japanese with English summary]
10) Kiritani, K.: Strategy in integrated control of rice pest. *Rev. Plant Protec. Res.*, 5, 76–104 (1972).
11) Kiritani, K. et al.: Studies on population dynamics of green rice leafhopper, *Nephotettix cincticeps* Uhler: Regulatory mechanism of the population density. *Res. Popul. Ecol.*, 12, 137–152 (1970).
12) Kiritani, K. et al.: An attempt of rice pest control by integration of pesticides and natural enemies. *Ginsei*, 22, 19–23 (1971). [In Japanese with English summary]
13) Kiritani, K. et al.: Quantitative evaluation of predation by spiders on green rice leafhopper, *Nephotettix cincticeps*, by sight-count method. *Res. Popul. Ecol.*, 13, 187–200 (1972).
14) Kobayashi, T.: Effect of insecticidal applications to the rice stem borer on leafhopper population. Special Rep. on prediction of pests, Ministry of Agr. & Forest., No. 13, 126 (1961). [In Japanese with English summary]
15) Kuno, E.: Studies on population dynamics of rice leafhoppers in paddy field. *Bull. Kyushu Agr. Exp. Sta.*, 14, 131–246 (1968). [In Japanese with English summary]
16) Muramatsu, Y., Sugino, T. & Nakamura, K.: Sampling effciency of methods to estimate the number of *Nephotettix cincticeps* Uhler in the resting paddy field. *Jap. J. Appl. Entomol. Zool.*, 14, 19–24 (1970). [In Japanese with English summary]
17) Nakasuji, F. & Kiritani, K.: Ill-effects of rice dwarf virus upon its vector, *Nephotettix cincticeps* Uhler (Hemiptera: Deltocephalidae), and its significance for changes in relative abundance of infected individuals among vector populations. *Appl. Entomol. Zool.*, 5, 1–12 (1970).
18) Nakasuji, F. & Kiritani, K.: Rates of feeding acquisition of rice dwarf virus (RDV) by the green rice leafhopper, *Nephotettix cincticeps*. *Proc. Ass. Plant Protection, Shikoku*, No. 5, 1–9 (1970). [In Japanese]
19) Nakasuji, F. & Kiritani, K.: Inter-generation changes in relative abundance of insects infected with rice dwarf virus in populations of *Nephotettix cincticeps* Uhler (Hemiptera: Deltocephalidae). *Appl. Entomol. Zool.*, 6, 75–83 (1971).
20) Nakasuji, F. & Kiritani, K.: Descriptive models for the system of the natural spread of infection of rice dwarf virus (RDV) by the green rice leafhopper, *Nephotettix cincticeps* Uhler (Hemiptera: Deltocephalidae). *Res. Pop. Ecol.*, 14, 18–35 (1972).
21) Nasu, S.: Studies on some leafhoppers and planthoppers which transmit virus diseases of rice plant in Japan. *Bull. Kyushu Agr. Exp. Sta.*, 8, 153–345. [In Japanese with English summary]
22) Sakurai, Y.: Varietal resistance to stripe, dwarf, yellow dwarf and black-streaked dwarf. "The virus diseases of rice plant" IRRI Johns Hopkins Press, 257–275 (1969).
23) Sasaba, T. & Kiritani, K.: Evaluation of mortality factors with special reference to parasitism of the green rice leafhopper, *Nephotettix cincticeps* Uhler (Hemiptera: Deltocephalidae). *Appl. Entomol. Zool.*, 7, 83–93 (1972).
24) Sasaba, T., Kiritani, K. & Urabe, T.: A preliminary model to simulate the effect of insecticides on a spider-leafhopper system in the paddy field. *Res. Pop. Ecol.*, 15, 44–57 (1973).
25) Shinkai, A.: Studies on insect transmissions of rice virus disease in Japan. *Bull. Nat. Inst. Agr. Sci.* Ser. C, No. 14, 1–112 (1962). [In Japanese with English summary]