VECTOR SPECIFICITY OF LEAF- AND PLANTHOPPERS IN RICE VIRUS TRANSMISSION

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ABSTRACT

Six species belonging to two genera of Cicadellidae and six species in four genera of Delphacidae transmit viruses and MLO of rice in Asia. Vector specificity was found to characterize the biological relationship between plant viruses and their vector species. From the standpoint of the ecology and epidemiology of virus diseases, it is suggested that the concept of specificity should be broadened and include biological and ecological characters of vector species such as geographical distribution, seasonal prevalence, migration, dispersion and behavior as well as transmission efficiency. Most rice virus diseases, especially leafhopper-borne diseases, are found in some restricted areas within the distribution of vector species. The epidemics of green rice leafhopper-borne virus diseases of rice in Asia - such as tungro in the tropics, transitory yellowing in the subtropics, and dwarf in the temperate region - are closely associated with the predominance and seasonal prevalence of highly efficient vector species.

Introduction

Since the last international symposium on virus diseases of tropical crops organized by TARC in Tokyo, in 1976, 2 new leafhopper-borne viruses of rice have been reported: gall dwarf from Thailand (Omura *et al.,* 1980) and bunchy stunt from China (Xie and Lin, 1981). In addition, expansion of the geographical distribution has been recorded in some viruses such as grassy stunt and ragged stunt from almost all the South- and Southeast - Asian countries, transitory yellowing from Okinawa, Japan (Saito *et al.,* 1978) and dwarf from Nepal (John *et al.,* 1978; Omura *et al.,* 1982) (Table 1).

Vector specificity described in this report falls into 2 different categories, i.e. affinity of vectors for specific viruses or MLOs, and biological and ecological specificity of vectors in relation to virus transmission. The vector affinity applies to the conditions under which a given virus (or MLO) is transmitted by a colony of a species, or by a single species, or by a group of related

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Table 1 Leaf- and planthopper-borne virus and MLO diseases and their distribution in Asia

Disease	Distribution	References
Leafhopper-borne diseases		
Dwarf	Japan	Fukushi, 1934
	Korea	Park, 1966
	Nepal	John *et al.*, 1978; Omura *et al.*, 1982
	China	Xie *et al.*, 1979
Gall dwarf	Thailand	Omura *et al.*, 1980
	Malaysia	Ong and Omura, 1982
	China	Faan *et al.*, 1983
Transitory yellowing	Taiwan	Chiu *et al.*, 1965
	China	Zhu *et al.*, 1964
	Okinawa, Japan	Saito *et al.*, 1978
	Thailand	Inoue *et al.*, 1980
Tungro	Philippines	Rivera and Ou, 1965
	Malaysia	Ou *et al.*, 1965
	Thailand	Lamey *et al.*, 1967
	India	John, 1968
	Indonesia	Rivera *et al.*, 1968
	Bangladesh	Nuque and Miah, 1969
	Nepal	Omura *et al.*, 1981
Waika	Japan	Yokoyama and Sakai, 1975
Orange leaf	Thailand	Ou, 1963
	Philippines	Ou and Rivera, 1969
	India	Pathak *et al.*, 1967
	Malaysia	Ou and Rivera, 1969
	Sri Lanka	Abeygunawardena *et al.*, 1970
	Indonesia	Oka, 1977
	China	Wu *et al.*, 1980
Yellow dwarf	Taiwan	Kurosawa, 1940
	China	Hashioka, 1952
	Japan	Hashioka, 1964
	Philippines	Palomar and Rivera, 1967
	India	Raychaudhuri *et al.*, 1967
	Thailand	Wathanakul and Weerapat, 1969
	Bangladesh	Galvez and Shikata, 1969
	Sri Lanka	Abeygunawardena *et al.*, 1970
	Malaysia	Lim, 1970
	Indonesia	Satomi *et al.*, 1978
Bunchy stunt	China	Xie and Lin, 1980
Planthopper-borne diseases		
Stripe	Japan	Kuribayashi, 1931
	China	Zhu *et al.*, 1964
	Korea	Lee, 1969
	Taiwan	Chui, 1972
Black-streaked dwarf	Japan	Kuribayashi and Shinkai, 1952
	China	Zhu *et al.*, 1964
	Korea	Lee *et al.*, 1977
Grassy stunt	Philippines	Ling, 1977
	Indonesia	Tantera *et al.*, 1973
	Bangladesh	IRRI, 1978
	India	Heinrichs and Khush, 1978
	Malaysia	Hashim, 1978
	Sri Lanka	Heinrichs and Khush, 1978
	Thailand	Weerapat and Pongrasert, 1978
	China	Zhou and Ling, 1979
	Taiwan	Chen *et al.*, 1979
	Japan	Iwasaki *et al.*, 1979
Ragged stunt	Indonesia	Hibino *et al.*, 1977
	Philippines	Ling, 1977
	Bangladesh	IRRI, 1978
	India	Heinrichs and Khush, 1978
	Malaysia	Hashim, 1978
	Sri Lanka	Heinrichs and Khush, 1978
	Thailand	Weerapat and Pongrasert, 1978
	China	Zhou and Ling, 1979
	Taiwan	Chen *et al.*, 1979
	Japan	Shinkai *et al.*, 1980

species. The biological and ecological specificity of the vector is reflected in the geographical distribution, seasonal prevalence, species composition and fluctuation of predominant species, rate of population increase, life span, dispersion and migration, host plant preference, behavior and others.

Homopterous insects belonging to the families Cicadellidae and Delphacidae transmit all the known insect-borne viruses and MLOs of rice in Asia. Six species belonging to two genera of *Nephotettix* and *Recilia* leafhoppers transmit six viruses and two MLOs. Six species belonging to four genera of *Laodelphax, Unkanodes, Terthron* and *Nilaparvata* transmit four viruses.

Leafhopper-borne viruses and MLOs

1 Vector affinity for viruses and MLOs

Transmission efficiency in terms of the rate of individuals in colonies showing effective transmission differs among vector species in every virus, and, furthermore, there are marked differences in the transmission efficiency among insect colonies collected from various localities in Asia (Table 2). Based on the maximum rate of individuals transmitting the viruses, vector species can be arranged in orders within the 3 pest *Nephotettix* species for the respective viruses. The highest efficiency is achieved by *N. cincticeps* for dwarf, *N. nigropictus* for gall dwarf and transitory yellowing, and *N. virescens* for tungro and Waika, whereas there is no species difference in the transmission of yellow dwarf (Inoue, unpublished).

Virus incubation period in vector is specific to the kind viruses and MLOs: 10–15 days for dwarf, 13–16 days for gall dwarf, 8–13 days for transitory yellowing and 23–26 days for yellow dwarf. There are slight differences in the period of transmission among vector species and colonies and, furthermore, the period is inversely proportional to the transmission efficiency for transitory yellowing virus: 3 *Nephotettix* leafhoppers are involved and the males of both species can transmit the virus more efficiently than the females. Regarding the incubation period in vectors, *N. nigropictus,* a most efficient vector, has a shorter incubation period than the others and the male's period is shorter than that of the female (Inoue, 1978).

A distinctively long incubation period for yellow dwarf in every vector species (20–35 days) affects the incidence of the disease. In spite of the high efficiency of vectors in the transmission and geographically broad occurrence of the disease in every region, the epidemics of the disease have been restricted to the subtropical and southern part of temperate regions such as Japan, China and Taiwan where the vector can develop the infectivity by completion of the pathogen-incubation period during the cool season. In the tropics, it is plausible that leafhoppers which acquired the pathogen at a young nymphal stage died before they develop infectivity.

In the case of viruses with a semi-persistent transmission, the virus retention period in vectors reflects the transmission efficiency. Of the vector species tested for Waika virus, transmission efficiency is in the order of *N. virescens, N. cincticeps* and *N. nigropictus,* and the longest retention period in the vector is observed in *N. virescens* followed by *N. cincticeps* (Inoue and Hirao, 1982).

Another factor relating to the transmission efficiency is the transmission frequency expressed by the number of test rice seedlings infected with the pathogen by inoculation feeding of a single viruliferous insect within a unit period. In Waika virus tested by transferring 2 vector insect species at 1 hr intervals for 15 hr, the average frequency of transmission by *N. virescens,* the most efficient vector, is 7.4 and that by *N. cincticeps* 4.0 (Inoue and Hirao, 1981). In transitory yellowing, Chen (1979) stated that *N. nigropictus* transmitted the virus to a larger number of seedlings than *N. cincticeps.*

Transovarian transmission of virus from infective leafhoppers to their progeny has been known to be restricted to dwarf virus for *R. dorsalis* and *N. cincticeps* (Fukushi, 1934) and gall dwarf virus for *N. nigropictus* (Inoue and Omura, 1982). In the gall dwarf virus, the rate of congenitally infective progeny varied from 0 to 100% in lines of *N. nigropictus*: 57.8% for the

Table 2 Rice virus and MLO diseases, their vector species and percentage of transmitting insects

Diseases	Vector	Transmission (%)	Reference
Leafhopper-borne diseases			
Dwarf	*N. cincticeps*	0 - 65	Shinkai, 1962
	N. nigropictus	23	Nasu, 1963
	N. virescens	31	Xie and Lin, 1980
	R. dorsalis	2 - 43	Hashioka, 1964
Gall dwarf	*N. nigropictus*	2 - 95	Inoue and Omura, 1982
	N. cincticeps	1 - 42	Inoue, 1985
	N. virescens	0.1 - 0.7	Inoue, 1985
	N. malayanus	9	Inoue, 1985
	R. dorsalis	9	Morinaka *et al.,* 1982
Transitory yellowing	*N. nigropictus*	41 - 65	Chiu *et al.,* 1965
		35 - 75	Inoue, 1978
	N. cincticeps	25 - 35	Chiu *et al.,* 1965
		27 - 59	Inoue, 1978
	N. virescens	47	Hsieh *et al.,* 1970
		0 - 5	Inoue, 1978
Bunchy stunt	*N. cincticeps*	23.7	Chen *et al.,* 1978
Yellow dwarf	*N. cincticeps*	68 - 75	Inoue, 1985
	N. nigropictus	60 - 70	Inoue, 1985
	N. virescens	70 - 76	Inoue, 1985
	N. malayanus	64 - 73	Inoue, 1985
	N. parvus	63	IRRI, 1972
Orange leaf	*R. dorsalis*	7 - 14	Rivera *et al.,* 1963
Tungro	*N. virescens*	35 - 83	Rivera and Ou, 1965
	N. nigropictus	0 - 27	Ling, 1970
	N. malayanus	40	IRRI, 1973
	N. parvus	7	Rivera *et al.,* 1972
	R. dorsalis	1.1	Hino *et al.,* 1974
Waika	*N. virescens*	68 - 93	Inoue and Hirao, 1981
	N. cincticeps	25 - 40	Inoue and Hirao, 1981
	N. malayanus	42 - 63	Inoue and Hirao, 1981
	N. nigropictus	16 - 23	Inoue and Hirao, 1981
Planthopper-borne diseases			
Stripe	*L. striatellus*	14 - 54	Kuribayashi, 1931
	T. albifascia	28 - 35	Shinkai, 1967
Black-streaked dwarf	*L. striatellus*	32	Shinkai
	U. sapporonus	34	Shinkai, 1962
	T. albifascia	73	Shinkai, 1967
Grassy stunt	*N. lugens*	3 - 50	Ling, 1972
	N. muiri	33 - 69	Iwasaki *et al.,* 1980
Ragged stunt	*N. lugens*	12 - 36	Morinaka *et al.,* 1983
		19	Hibino *et al.,* 1977
	N. bakeri	5	Morinaka *et al.,* 1983

Amami colony and 31.5% for the Kagoshima colony, and 0% for the Thailand colony, on the average. Thus it appears that for a highly efficient vector, there is a higher rate of transovarian passage of virus to progeny. Such transmission is important in relation to the epidemiology and perpetuation of the virus in areas where the virus is infective.

2 Ecological and biological characters of vectors in relation to virus transmission

The population density of the respective species of the genus *Nephotettix* differs from region to region and, consequently, the species composition and relative abundance of the species differ regionally. With the exception of the temperate region where only *N. cincticeps* occurs, species composition in terms of abundance of individuals is in the order *N. nigropictus, N. cincticeps, N. virescens* and *N. malayanus* in the south-eastern subtropical area; *N. virescens, N. nigropictus, N. malayanus* and *N. parvus* in the tropical climate area; and *N. virescens, N. nigropictus, N. parvus* and *N. malayanus* in Peninsular Malaysia, Indonesia and the Philippines where an equatorial type of climate prevails. In western subtropical Asia, only *N. nigropictus* occurs.

The shift of species composition causes the outbreak of virus disease. The evidence was reported from Java, Indonesia, where the outbreak of tungro in 1980–1982 was associated with the shift of dominant species from the inefficient *N. nigropictus* to the efficient *N. virescens* during the past decade (Siwi and Roechan, 1983).

Nephotettix leafhoppers show differences in relation to their host plants. *N. virescens* is restricted to rice, *N. malayanus* to *Leersia hexandra,* and *N. parvus* to *Isachne globosa. N. cincticeps* feeds on rice (japonica varieties) and *L. japonica. N. nigropictus* has a wide range of host plants though grasses are more preferred than rice. Of the various factors concerned with the abundance of the leafhoppers, the presence of the preferred host plants and their surface area and growth stage are the most important ones.

Dispersion activity of the leafhopper is related to the spreading of the viruses with a semi-persistent type of transmission. Adult leafhoppers, *N. cincticeps* in the temperate region and *N. virescens* in the tropics, fly to paddy fields soon after rice transplanting. In both species, the adults show a high dispersion activity, as determined by catches in sticky traps and direct visual counts in contrast with the low dispersion ability of *N. nigropictus.* Those incoming adults play an important role in spreading the tungro virus in the tropics and the Waika virus in Japan, since the two viruses are transmitted in a semi-persistent manner, suggesting that the leafhoppers that fed on diseased plants develop infectivity without an incubation period. On the contrary, the progression of disease on hills in the field is slow in the case of dwarf. Consequently, the appropriate time for the prevention of the vector leafhopper to control the Waika and tungro diseases is within 1 month after rice transplanting.

Seasonal prevalence of the vector is one of the most important factors in virus epidemics. In Bangkok, about 84% of light-trapped leafhoppers were caught during the wet season. The relationship between rainfall and leafhopper population is obvious from the fact that the occurrence of leafhoppers in a high density follows early and frequent rainfalls in the wet season in India (Banergee, 1971) and in Thailand (Inoue and Ruayaree, 1977) and, consequently, tungro incidence is obvious in the wet season in Thailand. In Indonesia, however, there is no distinct difference in leafhopper populations between dry and wet season (Siwi and Roechan, 1983) as the humidity conditions do not differ appreciably between the 2 seasons.

Leafhoppers are sedentary compared with planthoppers, and thus the spread of leafhopper-borne virus to geographically distant areas is generally rare. There is one exception, namely the Waika virus outbreak in Kyushu in the south-western part of Japan, during 1969–1976 which occurred because the virus seemed to be carried by viruliferous *N. virescens,* one of the most efficient and migrative vectors among the vector species, from the tropics. Gall dwarf disease found in central Thailand (Omura *et al.,* 1980) is transmitted by *Nephotettix* leafhoppers and *Recilia dorsalis* (Inoue and Omura, 1982; Morinaka *et al.,* 1982). In spite of the wide distribution of the 2 leafhopper vectors in every region of Asia, disease incidence has been restricted to Thailand, Peninsular Malaysia (Ong and Omura, 1982) and China (Faan *et al.,* 1983). This may be due to the low migratory ability of the vector leafhoppers.

Planthopper-borne viruses

1 Vector affinity for viruses

Regarding vector specificity in virus transmission, delphacids have received less attention. In consequence, transmission of grassy stunt virus by the brown planthopper is discussed mainly in this chapter.

Reports on the proportion of active transmitters do not show distinctive differences among the vector species in the transmission of the virus, but there are marked differences in the proportion among insect colonies: 0–54% of *L. striatellus* (Kuribayashi, 19831) and 28–35% of *T. albifascia* for stripe (Shinkai, 1962), 3–50% of *N. lugens* for grassy stunt (Rivera *et al.,* 1966) and 12–76% for ragged stunt (Morinaka *et al.,* 1983).

Transmission of grassy stunt virus using 20 colonies of *N. lugens* collected from various localities of Japan and the south-eastern part of Asia was analysed by Hirao *et al.* (1985) to clarify the presence of genetic variation in the ability of virus transmission and the following results were obtained (Table 3).

Table 3 Active transmitters in colonies of *N. lugens* in rice grassy stunt transmission

Insect colony	Locality and year of insect collection	Percentage transmission	
		Females	Males
Japan (K-2)	Isahaya, 1983	17.0	14.2
Japan (C-2)	Chikugo, 1983	10.0	10.1
Japan (IG-1)	Ishigaki, 1983	15.0	11.4
China (C-2)	Canton, 1984	8.8	13.1
Philippines (1)	Los Banos	0	0
Philippines (2)	(Laboratory colony)	0	1.3
Indonesia	South Sulawesi, 1982	27.8	28.6
Thailand		11.5	16.0
Malaysia	Alor Star, 1984	5.0	9.8
East China Sea	1983	12.2	17.2

(1) There were differences in the percentage transmission among test colonies though the percentage sometimes varied markedly with the tests in the same colony.
(2) The highest percentage transmission was obtained in the Japan colony collected in Isahaya in 1982 and in the Indonesia colony collected from Sulawesi in 1982, while the lowest was recorded in the Philippine colony.
(3) The brachyperous forms showed a higher transmission efficiency than the macropterous forms in both males and females.

In the following test, selection for insect lines with a high proportion of viruliferous insects was carried out. In the first selection, in the insects which were allowed to feed on diseased rice the tested infectivity was 52.5% in the selected lines in contrast to 13.5% in the non selected lines. Furthermore, the percentage in the lines of second selection increased to 81.1% in the selected lines as compared to 17.1% in the non selected lines. However the females of the selected lines did not produce any progeny presumably due to the adverse effects of inbreeding within the selected lines.

2 Biological and ecological characters of planthoppers in relation to virus transmission

The most important characteristics of planthoppers, especially *N. lugens,* is the overseas immigration of the adults. The evidence is common in Japan in the Baiu season (rainy season) and the incidence of grassy stunt was first described by Iwasaki *et al.,* (1979). The number of immigrant planthoppers in Japan varies each year and there are local variations. The number of viruliferous planthopper immigrants was distinctly low (3 out of 2,743 individuals tested during 1979–1983 in Kyushu). The incidence is supported by the fact that the virus was carried over by viruliferous planthopper immigrants from overseas.

Feeding and mobility of the vectors affect the size of the affected area or the number of infected hills in the fields. In caged pot tests (size of pot is 0.36m^2 with 9 hills), the number of hills with grassy stunt disease transmitted by single viruliferous macropterous adults, both males and females, was 0–2 hills in a day, 0.9 hills on the average. On the other hand, as described by Hirao *et al.,* (1985), field observations indicated that the number of primarily infected hills caused by one viruliferous immigrant (macropterous form) was unexpectedly lower and the infected hills distributed in a small area (3–7 hills). This may be ascribed to the weak dispersion activity of immigrant adults in the paddy field and by their sedentary feeding behavior. The range of distribution of secondarily infected hills in terms of their numbers up to 56 hills over 6m^2 depends on the number of primarily infected hills. This is because the secondary infection is caused by nymphs or subsequently by adults which acquired the virus from primarily infected rice. And so the level of population density of the planthopper is related to the size of the affected areas in the secondary infection (Fig. 1).

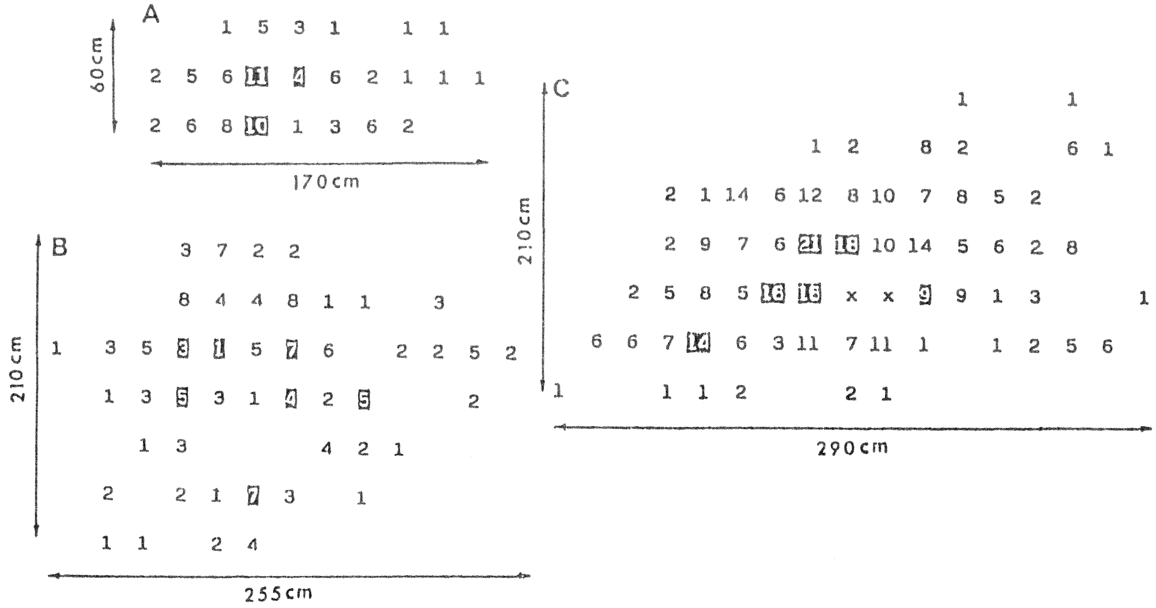

Fig. 1 Distribution of grassy stunt-infected rice hills under natural conditions in the fields in Chikugo, Southwest Japan in 1982 and 1983 (Hirao *et al.,* 1985).

Solid squares show primarily infected rice hills and figures the number of brownish heads/secondarily infected hills. Crosses: no hills.

Conclusion

Considering the geographic distribution, abundance and transmission efficiency of vector species, the epidemics of leafhopper-borne virus diseases are closely associated with the abundance of highly efficient vector species, as is the case for dwarf in the temperate region, transitory yellowing in the subtropics and tungro in the tropics. On the other hand, the epidemics of planthopper-borne virus diseases, especially grassy stunt and ragged stunt, seem to be associated with the migration of planthopper vectors which may include viruliferous individuals.

References

1) Banergee, S. N. (1971): Recent progress in rice insect research in India. *In*: Proceedings of Symposium on Rice Insects. TARC, Tokyo. p.83-90.
2) Chen, C. C. (1979): Epidemiological studies on the rice transitory yellowing with special reference to its transmission by the green rice leafhoppers. MS. Thesis of the Res. Inst. Entomol. Nat. Chung Hsing Univ. p. 1-61. (In Chinese).
3) Faan, H., Chang, S., Ho, S., Xie, S., Liu, C., Zhou, L., Liu, X. and Zhu, D. (1983): Rice gall dwarf - a new virus disease epidemic in the west of Guandong Province of south China. Guandong Ag. Sci., (1983 (1)), 44.
4) Fukushi, S. (1934): Studies on the dwarf disease of rice plant. J. Fac. Agr. Hokkaido Univ., 37, 41-164.
5) Hirao, J., Oya, S. and Inoue, H. (1985): Transmission of rice grassy stunt by the brown planthopper *Nilaparvata lugens* Stal (Hemiptera: Delphacidae). Bull. Kyushu Nat. Agric. Expt. Stn. (In press).
6) Inoue, H. (1978): Transmission efficiency of rice transitory yellowing virus by the green rice leafhopper, *Nephotettix* spp. (Hemiptera: Cicadellidae). App. Entomol. Zool., 14, 123-126.
7) Inoue, H. and Hirao, J. (1981): Transmission of rice waika virus by green leafhopper, *Nephotettix* spp. (Hemiptera: Cicadellidae). Bull. Kyushu Nat. Agr. Expt. Stn., 21, 509-552.
8) Inoue, H. and Omura, T. (1982): Transmission of rice gall dwarf virus by the green rice leafhopper. Plant Disease, 66, 57-59.
9) Iwasaki, M. and Shinkai, A. (1979): Occurrence of rice grassy stunt disease in Kyushu, Japan. Ann. Phytopath. Soc. Japan, 45, 741-744.
10) John, V. T., Heu, M. H., Manadhor, D. N. and Pradhan, R. B. (1978): Symptoms resembling those of rice dwarf disease in the Kathmandu valley, Nepal. IRRI Newsl., 3, 13-14.
11) Kuribayashi, K. (1931): On the relationship between rice stripe disease and *Delphacodes striatella* Fallen. J. Plant Prot., 18, 565-571.
12) Morinaka, T., Putta, M., Chettanachit, D., Parejarearn, A., Disthaporn, S., Omura, T. and Inoue, H. (1982): Transmission of rice gall dwarf virus by cicadellid leafhoppers *Recilia dorsalis* and *Nephotettix nigropictus* in Thailand. Plant Disease, 66, 703-704.
13) Omura, T., Inoue, H., Morinaka, T. Saito, Y., Chettanachit, D., Putta, A., Parejarearn, A. and Disthaporn, S. (1980): Rice gall dwarf, a new virus disease. Plant Disease, 64, 795-798.
14) Omura T., Inoue, H., Pradhan, R. B., Thapa, B. J. and Saito, Y. (1982): Identification of rice dwarf in Nepal. JARQ, 15, 218-220.
15) Ong, C. A. and Omura, T. (1982): Rice gall dwarf virus occurrence in Peninsular Malaysia. IRRI Newsl., 7, 7.
16) Rivera, C. T., Ou, S. H. and Pathak, M. D. (1966): Grassy stunt disease of rice and its transmission by the planthopper *Nilaparvata lugens* Stal. Plant Dis. Rep., 49, 127-131.
17) Saito, Y., Inoue, H. and Satomi, H. (1978): Occurrence of rice transitory yellowing virus in Okinawa, Japan. Ann. Phytopathol. Soc. Japan, 44, 666-669. (In Japanese, English summary).
18) Shinkai, A. (1962): Studies on insect transmission of rice viruses in Japan. Nat. Inst. Agr. Sci. Bull. Ser., C.14, 1-112. (In Japanese, English summary).

19) Siwi, S. S. and Roechan, M. (1983): Species composition and distribution of green leafhoppers, *Nephotettix* spp. and the spread of rice tungro disease in Indonesia. *In*: 1st International Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Institute of Entomology, London. p. 263-276.
20) Xie, L. H., Lin, J. Y. and Guo, J. R. (1980): Studies on bunchy stunt disease of rice, a new virus disease of rice plant. Kexue Tongbao, 25, 785-789.

Discussion

Hibino, H. (IRRI): When you tested the efficiency of colonies, did you observe any effect on virus infection of the rice varieties used to maintain the colonies?

Answer: I used only japonica varieties. There is no problem of maintaining the colonies using a large number of varieties.

Kishimoto, R. (Japan): Do you consider that local or geographical variations in efficiency can be maintained for a long period of time?

Answer: I believe that efficiency is genetically determined and can thus be maintained for many generations provided there is no mixing with other colonies.

Mochida, O. (IRRI): In field collections in light traps, it is often difficult to identify individual species of *Nephotettix* as they may be mixed or hybridization may occur. Could you comment on such aspects.

Answer: I do not consider that hybridization occurs as isolation mechanisms of species are very distinct. There may be accidental crossing. In the subtropical zone, *N. nigropictus* and *N. cincticeps* may coexist. In the tropics such problems do not occur and it is usually easy to distinguish the various species of *Nephotettix* based on their morphological characteristics.

Kiritani, K. (Japan): You mentioned that the differences in the level of transmission ability may be genetically controlled. Which factors are responsible for the maintenance of such different levels of transmission ability depending on the region?

Answer: I do not know.

Kishimoto, R. (Japan): It is generally accepted that many insect pests such as leaf- and planthoppers have the ability to change their biotypes as a reaction to insecticides or other factors. Why do you consider that the ability to transmit viruses can be maintained for many years.

Answer: This assumption is based on my personal experience.