RICE TUNGRO-ASSOCIATED VIRUSES AND THEIR RELATIONS TO HOST PLANTS AND VECTOR LEAFHOPPERS

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ABSTRACT

Tungro is a disease complex associated with rice tungro bacilliform (RTBV) and spherical (RTSV) viruses. RTBV and RTSV were separately purified from tungro-affected rice plants and antisera were produced. The viruses are efficiently detected from infected rice leaves in ELISA and less efficiently by latex test. The green leafhopper (GLH) *Nephotettix virescens* is the most important vector. RTBV is dependent on RTSV for its transmission by GLH. Both RTBV and RTSV are semi-persistent in GLH. GLH retained the ability to acquire RTBV longer than RTSV itself. RTSV transmission by GLH was blocked by feeding on anti-RTSV serum, while GLH retained the ability to acquire RTBV after the feeding. These facts suggest that RTSV itself may not be the bearer of the "helper function". Tungro-resistant cultivars were mostly infected with RTBV alone when exposed to GLH fed on source plants harboring RTBV and RTSV. *N. cincticeps, N. nigropictus,* and *Recilia dorsalis* also transmitted the viruses, and the transmission efficiencies showed considerable variations depending on the colonies used.

Introduction

Tungro (Ling, 1972) is the most important disease of rice in South and Southeast Asia. It has caused serious damage to rice production since the late 1960s in Bangladesh, India, Indonesia, Malaysia, Philippines and Thailand. Tungro is a disease complex associated with rice tungro bacilliform (RTBV) and rice tungro spherical (RTSV) viruses (Hibino *et al.,* 1978; Omura *et al.,* 1983). The tungro-associated viruses are transmitted by the greenleafhopper, *Nephotettix virescens* (Distant), and some other leafhopper species in a semi-persistent manner (Hibino, 1983a; Hibino, 1983b; Hibino *et al.,* 1979). Association of RTBV and RTSV with tungro has been confirmed in Bangladesh, India, Indonesia, Malaysia, Philippines, Sri Lanka and Thailand. Rice waika virus (RWV) that occurred in Kyushu, Japan in 1971 was identical with or closely related to RTSV (Saito, 1977). RTSV also spread widely as an independent disease in the Philippines (Aguiero *et al.,* 1985; Cabauatan and Hibino, 1984).

Symptomatology

Rice plants infected with both RTBV and RTSV are stunted and leaf color changes from green to light yellow or orange. Flowering is delayed and panicle exsertion is often incomplete. Panicles are often small and sterile (Ling, 1972). RTBV causes milder symptoms but mature leaves often show a yellow or orange discoloration. RTSV causes no clear symptoms or very mild stunting of plants (Hibino, 1983a; Hibino *et al.,* 1978).

The symptoms vary depending on the cultivars. Tungro-resistant cultivars were known to show milder symptoms than susceptible ones. Recent studies indicate that tungro-resistant cultivars were mostly infected with RTBV when inoculated by the leafhoppers fed on source plants harboring both viruses (Cabunagan *et al.,* 1984; Daquioag *et al.,* 1985). Milder symptoms on resistant cultivars could be explained by predominant infection with RTBV. So far, no correlation was found between resistance level of rice cultivars to tungro and symptoms on the cultivars with

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the tungro-associated viruses (Dahal and Hibino, unpublished).

The symptoms caused by RTBV infection are as severe as those by infection with both viruses on cultivars FK 135, ASD 7 and ASD 8, while very mild on Pankhari 203, Utri Merah and Utri Rajapan (Dahal and Hibino, unpublished; Hibino *et al.*, 1978). RWV causes mild stunting and occasional leaf yellowing on some japonica rice cultivars but less clear symptoms on indica cultivars.

Purification and serology

As early as 1968, Galvez purified polyhedral particles 30–33 nm in diameter from tungro-affected rice plants and indicated that the particles might be the entity responsible for tungro. Since then the particles have been referred to as "rice tungro virus." However, recent investigations clearly indicated that the polyhedral particles were not the entity reponsible for the "tungro symptoms" in Indonesia and Philippines (Hibino, 1983a; Hibino *et al.*, 1978).

In 1983, Omura *et al.*, separately purified RTBV and RTSV from tungro-affected rice plants. RTSV was distinguishable from RTBV after 3 cycles of sucrose density gradient centrifugation and CsCl equilibrium centrifugation. RTBV was purified by 3 cycles of density gradient centrifugation and by neutralization of contaminating RTSV with anti-RWV serum.

Recently, RTBV and RTSV were purified from rice plants infected with either RTBV or RTSV following simplified procedures. RTSV was isolated and purified from rice plants infected with the RTSV isolate (Hibino and Cabauatan, 1985) (Fig. 1). Rice plants were inoculated with RTBV alone by using the leafhoppers which were allowed sequential feedings on RTSV-infected plants, anti-RTSV serum, and RTBV-infected plants (Table 3). RTBV was purified from the RTBV-infected plants (Cabauatan and Hibino, unpublished) (Fig. 2).

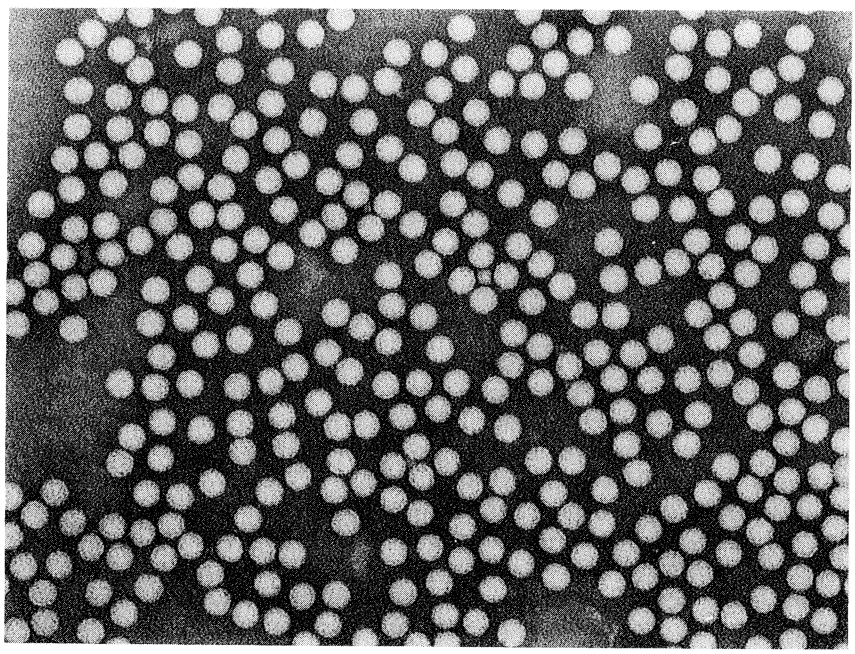

Fig. 1 Purified rice tungro spherical virus particles in neutralized 1% phosphotungstic acid. x 150,000.

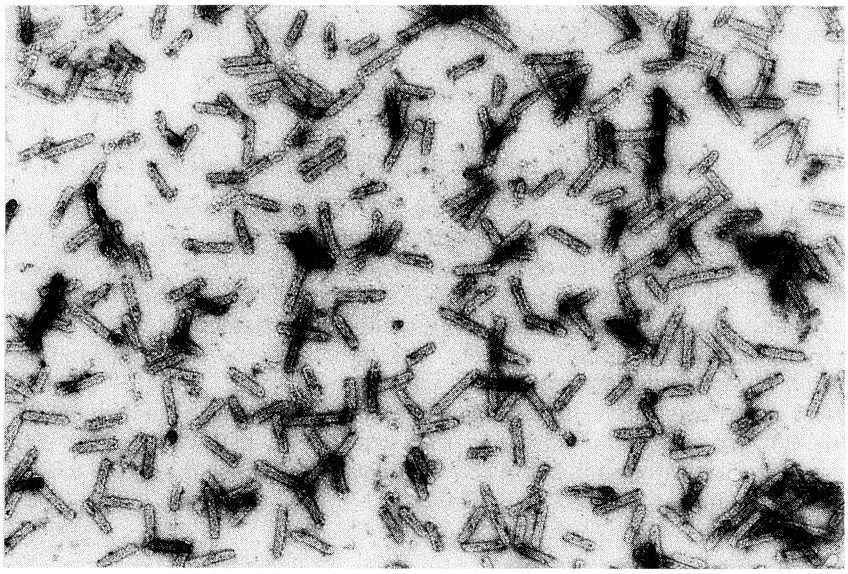

Fig. 2 Purified rice tungro bacilliform virus particles in 1% uranyl acetate. x 50,000.

So far no viruses are known to be serologically related to either RTBV or RTSV. Antisera against RTBV and RTSV did not cross-react (Omura *et al.*, 1984).

Several serological techniques have been applied to detect RTBV and RTSV from infected plants. ELISA is efficient to separately detect KTBV and RTSV from leaf extracts (Aguiero *et al.*, 1985; IRRI, 1984). Latex agglutination test is also applicable to detect the two viruses, though the efficiency is lower (Hibino *et al.*, 1983; Omura *et al.*, 1984). RTBV can be efficiently trapped on membrane-coated grids sensitized with antiserum and detected under the electron microscope, but RTSV was not trapped efficiently (Hibino, unpublished).

Transmission by leafhoppers

N. virescens is the most important vector and transmits to tungro-susceptible cultivars both RTBV and RTSV together or RTBV or RTSV alone from source plants harboring both viruses. *N. virescens* also transmits RTSV efficiently from RTSV source plants. *N. cincticeps* and *N. nigropictus* transmitted the two viruses less efficiently from source plants harboring both viruses, whereas they transmitted RTSV rather efficiently from RTSV source (Hibino, 1983a). *N. nigropictus* colonies tested in Indonesia and Japan did not transmit RTBV and RTSV together (Hibino, 1983a; Hibino *et al.*, 1979) while a colony in the Philippines was able to transmit both viruses together (Cabauatan and Hibino, unpublished). *Recilia dorsalis* colonies in Indonesia and Japan failed to transmit either viruses (Hibino, 1983a; Hibino *et al.*, 1979), while colonies in the Philippines transmitted the two viruses, though the efficiency was low (Aguiero and Hibino, unpublished). So far none of the *N. virescens, N. cincticeps, N. nigropictus* and *R. dorsalis* colonies tested transmitted RTBV from RTBV source plants. *N. parvus* and *N. malayanus* are also known to be tungro vectors but they have a weak biological relationship with rice.

RTBV is dependent on RTSV for its transmission by the leafhopper and is transmitted from RTBV source plants only when the leafhoppers that previously fed on RTSV source plants were transferred to the RTBV source for an acquisition access (Cabauatan and Hibino, 1985; Hibino,

1983b; Hibino *et al.*, 1978). Both RTBV and RTSV are semi-persistent and are retained for 4-5 days in the leafhopper (Hibino, 1983a; Hibino *et al.*, 1979). RTSV has a shorter retention period than RTBV. Both RTBV and RTSV can be acquired in a short acquisition access period and transmitted in a short inoculation access period.

Helper factor for RTBV transmission

Although the bearer of the "helper" function for RTBV transmission has not been isolated, recently accumulated evidences indicate that the hypothetical "helper factor" may not be RTSV itself but may be produced in rice cells infected with RTSV.

Effect of intervals between the first acquisition access to RTSV and the second access to RTBV on transmission by the leafhopper was examined to differentiate RTSV and the "helper factor" for RTBV transmission (Hibino, 1983b). The leafhopper retained RTSV for 3 days, while it retained the ability to acquire and transmit RTBV for 7 days.

In another experiment, individual leafhoppers fed on RTSV source plants were given a serial daily inoculation access for 3-7 days and then transferred to RTBV source plants for an acquisition access. The leafhoppers lost RTSV in 4 days but retained the ability to acquire RTBV for 7 days (Cabauatan and Hibino, 1985) (Table 1).

Table 1 Retention of RTSV and ability to acquire RTBV by *N. virescens* serially transmitted daily (P.Q. Cabauatan and H. Hibino, Phil. Phytopathol., 1985. In press)

Insect number	Viruses detected in inoculated plants[1] Transfer number										Occurrence in the colony
	1	2	3	4	5	6	7	8	9	10	(%)
1	S	S	S	▨	B	-	-	-	-	-	8.4
2	S	S	-	▨	B	-	-	-	-	-	22.4
3	S	-	-	▨	B	-	-	-	-	-	6.7
4	-	-	-	▨	B	-	-	-	-	-	3.4
5	S	S	S	S	▨	B	-	-	-	-	3.0
6	S	S	S	-	▨	B	-	-	-	-	3.0
7	S	S	-	-	▨	B	-	-	-	-	9.3
8	S	-	-	-	▨	B	-	-	-	-	12.5
9	S	S	S	S	-	X	-	▨	B	-	1.6
10	S	S	-	-	-	-	-	▨	B	-	1.6
11	S	X	-	-	-	-	-	▨	B	-	1.6

S = RTSV, B = RTBV, (-) = No transmission, X = Dead seedling, ▨ = Insect transferred to RTBV-infected plant for acquisition access. Inoculated plants were subjected to latex agglutination test 1 month after inoculation.

Interaction between the leafhopper and the two viruses was examined by blocking virus transmission by the leafhoppers through feeding immunoglobulin (IgG) to the viruses. The leafhoppers fed on anti-RTBV IgG lost RTBV and those fed on anti-RTSV IgG markedly reduced their ability to transmit RTSV (IRRI, 1984) (Table 2). Blocking the transmission of either viruses also affected the transmission of unblocked viruses. This indicates that both RTBV and RTSV are stylet-borne, adsorption of RTBV and RTSV particles to the leafhopper mouth surface is essential for their transmission, and the viruses interact with each other once adsorbed at the specific site in the mouth.

When the leafhoppers that previously fed on RTSV source plants were allowed to feed on anti-RTSV IgG and then transferred to RTBV source plants, the leafhoppers transmitted RTBV alone (Table 3 (IRRI, 1985). This result shows that RTSV need not be infective in order to aid in the transmission of RTBV or RTSV itself is not the "helper factor" for RTBV transmission. Retention period of the "helper factor" by the leafhopper ended after molting (Cabauatan and Hibino, 1985; Hibino, 1983b) (Table 4). The adsorption of RTBV to the mouth surface may be completed under the presence of the "helper factor.".

Table 2 Transmission of RTBV and RTSV by *N. virescens* that fed on different dilutions of immuno-globulin (IgG) to either RTSV or RTBV for 16 hours (IRRI Annual Report, 1984)

IgG	IgG dilution[2]	Leafhoppers transmitted[1] (No.)			
		RTBV	RTSV	RTBV+RTSV	None
RTSV	10X	13	0	2	59
	25X	97	0	6	55
	50X	71	0	3	63
RTBV	25X	0	53	0	140
	50X	1	29	1	66
Normal[3]	10X	23	8	34	31
	25X	26	1	62	13
	50X	48	3	39	35

1 Detected by latex agglutination test one month after inoculation.
2 Partially purified IgG in 0.01 M phosphate buffer (pH 7.4) containing 2% sucrose.
3 IgG partially purified from blood serum of pre-immune rabbit.

Table 3 Transmission of RTBV and RTSV by *N. virescens* that were given sequential feeding on RTSV-infected TN1 plant, anti-RTSV or normal IgG, and RTBV-infected TN1 plant (IRRI Annual Report, 1984)

IgG dilution[1]	1st (3 days)	2nd (16 hr)	3rd (8 hr)	Inoculation (24 hr)	Leafhoppers transmitted[2]			
					RTBV	RTSV	RTSV+RTBV	None
25X	RTSV	RTSV-IgG	RTBV	TN1	18	0	0	2
50X	RTSV	RTSV-IgG	RTBV	TN1	11	6	0	3
25X	RTSV	RTSV-IgG	-	TN1	0	2	0	18
50X	RTSV	RTSV-IgG	-	TN1	0	5	0	15
25X	RTSV	Normal IgG[3]	RTBV	TN1	2	0	13	5
50X	RTSV	Normal IgG	RTBV	TN1	8	1	15	0

1 Partially purified IgG in 0.01 M phosphate buffer (pH 7.4) containing 2% sucrose.
2 Detected by latex agglutination test one month after inoculation.
3 IgG partially purified from blood serum of pre-immune rabbit.

Table 4 Effect of molting on the ability of RTSV-carrying *N. virescens* nymphs to transmit RTBV (P.Q. Cabauatan and H. Hibino, Phil. Phytopathol., 1985. In press)

Insect Number[2]	Leafhoppers transmitted[2] Transfer number 1	2	3	4	Occurrence (%)
1	2		BS	-	23.8
2	S		B	-	14.3
3	(S)		-	-	38.1
4	S		-	-	23.2

1 Detected by latex test.
2 Only four out of 30 insects are represented here.
S = RTSV transmission; B = RTBV transmission.
BS = RTBV/RTSV transmission; (-) = No transmission.

 = Insect transferred to RTBV-infected leaf for acquisition access.

 = Insect transmitted RTSV but molted before transfer to RTBV-infected leaf.

 = Insects molted during access to RTBV-infected leaf.

Host range and resistance

Host range of the tungro virus agent(s) has been tested in several countries and many grass species have been reported as alternative hosts of tungro (Ling, 1972). However, the results of those tests are contradictory. It is not known whether the discrepancy is due to the presence of virus strains or vector biotypes. In the recent trial in the Philippines, none of the grasses tested were infected either with RTBV or RTSV (Daquioag and Hibino, unpublished).

Many *Oryza* species have been tested against tungro infection. All species so far tested were infected with tungro, though some of them showed a low percentage of infection (Ling, 1972).

Screening of cultivars for tungro resistance has been performed in the field or in the greenhouse and tested cultivars are scored based on percentage infection (Ling, 1972). As the leafhopper transmits the tungro-associated viruses, cultivars resistant to the leafhopper also show resistance to tungro in the field and often in the greenhouse.

IR cultivars with varying levels of resistance to the leafhopper were tested for their reactions to tungro-associated viruses in the Philippines (Hibino *et al.*, 1983; Cabunagan *et al.*, 1984). When they were inoculated by the leafhoppers fed on source plants, with both viruses, leafhopper-resistant IR50 and IR54 were mostly infected with RTBV alone, intermediate IR36 and IR42 were infected with both RTBV and RTSV or RTBV alone, and susceptible check TN1 was mostly infected with both viruses (Hibino *et al.*, 1983). When the number of the leafhoppers per plant was increased from 1 to 30 for inoculation, the percentage of infection with both viruses increased on IR36 and IR42, while only the percentage of RTBV infection increased on IR50 and IR54 (Fig. 3). When IR cultivars were exposed to the leafhoppers that fed on RTSV source plants, IR50 and IR54 also showed a fairly high percentage of infection (Cabunagan *et al.*, 1984). This indicates that they are not resistant to RTSV infection.

In Indonesia, IR50 and IR54 were resistant to tungro when they were introduced, but became susceptible after 2-3 years of intensive cultivation. IR50 and IR54 were mostly infected with both viruses in the fields in Indonesia (Hibino, unpublished). Resistance of IR50 and IR54 to tungro infection is attributed to their resistance to the leafhopper.

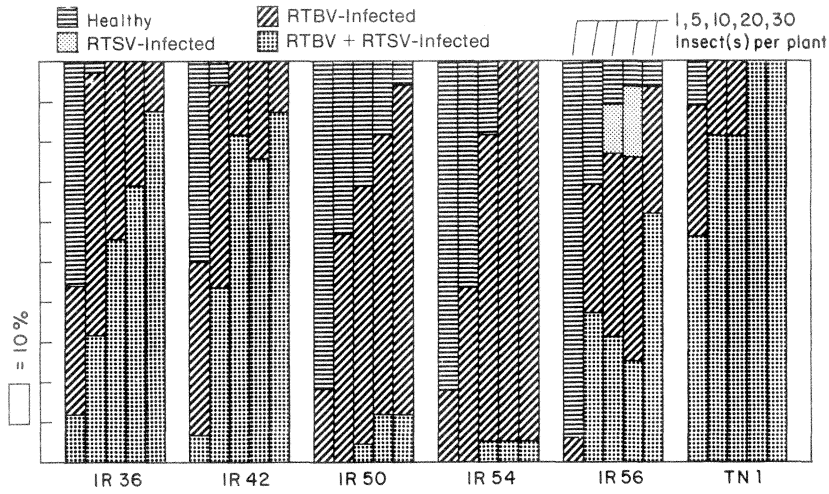

Fig. 3 Reaction of IR cultivars to tungro-associated viruses when inoculated by varying number of *N. virescens*, which were fed on source plants harboring RTBV and RSSV. Inoculated plants were subjected to latex test for the detection of the presence of the viruses.

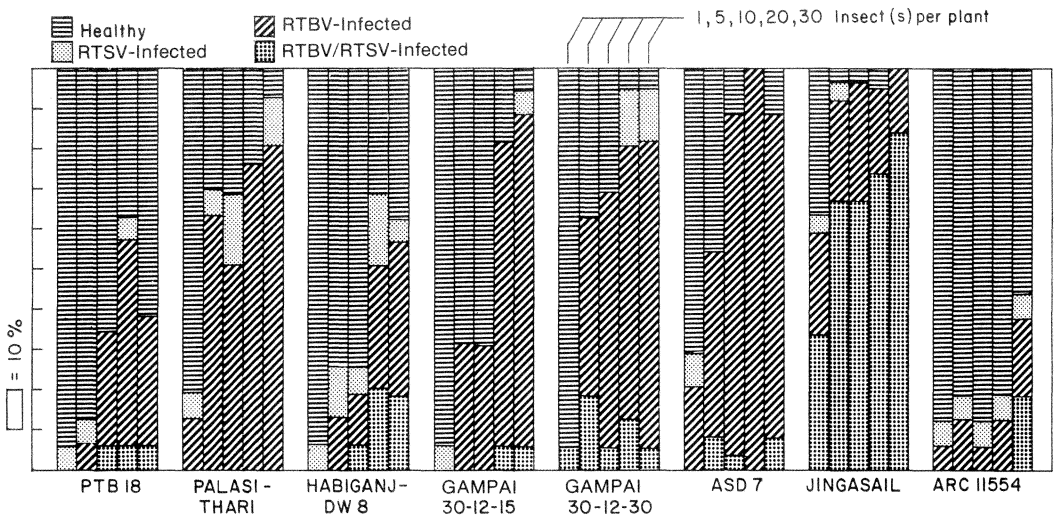

Fig. 4 Reaction of cultivars, resistant to *N. virescens* except Habiganj DW8, to tungro-associated viruses when inoculated by varying number of insects which were fed on source plants harboring RTBV and RTSV. Inoculated plants were subjected to latex test for the detection of the presence of the viruses.

All tungro-resistant cultivars so far tested in the Philippines were mostly infected with RTBV alone when they were exposed to the leafhoppers that fed on source plants with both viruses (Dahal and Hibino, 1985; Daquioag *et al.*, 1984) (Fig. 4, Table 5). Many of the resistant cultivars are resistant to the leafhopper, and three cultivars, namely Habiganj DW8, Utri Merah and Utri Rajapan, are susceptible or moderately susceptible to the leafhopper despite their strong resistance to tungro infection. The three cultivars are suspected to be resistant to the viruses. It is not known whether the leafhopper-resistant cultivars are also resistant to tungro-associated viruses.

Cultivar TKM 6 and IR cultivars with the gene from TKM 6, namely IR20, IR26, IR30 and IR40, are resistant to RTSV infection but susceptible to RTBV infection in the Philippines (Daquioag *et al.*, 1984).

Table 5 Reaction to tungro-associated viruses of cultivars with varying resistance to tungro disease (RTV) and *N. virescens* (GLH)[a]

Cultivar	Reaction to RTV[b]	Reaction to GLH[c]	Plants tested	Plants (No.) that reacted to the presence of RTBV+RTSV	Plants (No.) that reacted to the presence of RTBV	Plants (No.) that reacted to the presence of RTSV
Gampai 30-12-15	R	R	21	0	16	0
ARC 11554	R	R	11	1	9	0
Pankhari 203	R	MR	20	1	16	0
Habiganj DW8	R	MS	12	1	11	0
Utri Rajapan	R	MS	19	11	8	0
Liao-Feng	I	S	16	5	11	0
Tosidongi	I	S	12	10	2	0
Bremli	I	S	22	22	0	0
KU 115	I	S	19	19	0	0
R 21	I	S	25	25	0	0
Naylamp	S	MR	18	12	6	0
TN1	S	S	24	21	3	0
ARC 5929	S	S	8	8	0	0
63-83	S	S	20	19	0	0
Aus 100	S	—	18	18	0	0
Kuatik putih	S	MR	24	24	0	0

a Seedlings were mass-inoculated in a cage at an average 5 GLH/seedling and plants that exhibit tungro-like symptoms were tested in latex agglutination test.
b Data from IRRI Plant Pathology Department.
c Data from IRRI Entomology Department.

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Discussion

Tantera, D.M. (Indonesia): In Indonesia, among the various species of green leafhoppers that are vectors of the tungro virus complex, we have *Nephotettix malayanus, N. parvus,* in addition to *N. virescens* and *N. nigropictus.* I wonder if there are differences in the natural habitat of these leafhoppers. Indeed, *N. virescens* appears to be closely associated with rice whereas *N. nigropictus* is more related to weeds. Also there appear to be differences in the efficiency of transmission of tungro among these vectors. Did you use *N. parvus* and *N. malayanus* in your mission tests to weeds?

Answer: Such studies are presently underway.

Anjaneyulu, A. (India): Could I receive some information about the occurrence of tungro in Sri Lanka?

Answer: We were able to detect the presence of tungro virus in samples of dry leaves sent to us from Sri Lanka.

Reddy, D.V.R. (ICRISAT): 1. What is the relationship between rice tungro bacilliform virus (RTBV) and rice tungro spherical virus (RTSV) in the disease complex? 2. What is the helper factor? 3. I believe that the term "stylet-borne" should not be used as the viruses are not restricted to stylets and the term non persistent transmission may be preferable.

Answer: 1. Both RTBV and RTSV can exist either together causing severe symptoms or alone where RTBV induces mild symptoms and RTSV causes no clear symptoms. 2. RTSV acts as a "helper" for the transmission of RTBV. Actually the helper factor may not be RTSV itself but may be produced in rice cells infected with RTSV. It is difficult to isolate the helper components as in the case of tungro the infectivity cannot be detected in the sap by feeding on the membrane. 3. The term "stylet-borne" is used to indicate the location of the virus in the insect during transmission but not for the virus-vector interaction (the term transitory is used for this purpose).

Mochida, O. (IRRI): 1. Which IRRI cultivars show the highest level of resistance? 2. Are the varieties resistant to the vector or to the virus?

Answer: Most of the IRRI cultivars are resistant to the vector. The cultivars harboring the resistance genes of Gampai are also resistant to the virus under field conditions. However under heavy insect pressure and disease they tend to become susceptible. Other varieties with resistance genes from different cultivars are also resistant to the virus.

Hibino, H. (IRRI): Collaborative studies showed that in Indonesia IR50 and IR54 which harbor the Gampai genes can be infected with the two viruses. IR20 and IR30 which harbor the TKM6 genes can also be infected with the two viruses. In the Philippines TKM6 was found to be resistant to RTSV but susceptible to RTBV. Gampai is infected with RTBV alone. Based on the performance of TKM6 and Gampai, it appears that the resistance of the varieties is chiefly directed to the vector.

Anjaneyulu, A. (India): What is the relation between the resistance to the vector and the resistance to the virus?

Answer: Based on transmission studies it appears that most of the varieties are resistant to the vector. The mechanism of resistance to the virus remains unknown.

Hibino, H. (IRRI): In Indonesia we observed that after several years of cultivation varieties such as IR50 and IR54 which were once resistant to the vector became susceptible to tungro.