INSECT VECTORS OF RICE VIRUS AND MLO-ASSOCIATED DISEASES

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ABSTRACT

Homopterous insects belonging to the families Cicadellidae (leafhoppers) and Delphacidae (planthoppers) transmit all known rice viruses and mycoplasma-like organisms (MLOs) in the world except the soil-borne necrosis mosaic virus in Japan, beetle-borne yellow mottle virus in Africa, and in Europe the aphid-borne giallume virus that has been considered a strain of barley yellow dwarf virus. Six species belonging to two genera of cicadellids transmit six rice viruses and two MLOs in transitory and persistent manners with or without transovarial passage. Nine species in five genera of delphacids transmit in a persistent manner five rice viruses that are either nontransovarial and transovarial. These homopterous insects also cause direct rice crop damage known as hopperburn. The geographic distribution of the insects could be the main reason for the restriction in the occurrence of some rice virus and MLO-associated diseases to a region. Nevertheless, the diseases pose a continuing threat to rice production.

INTRODUCTION

More than 80% of the arthropod vectors of phytopathogenic agents belong to the order Homoptera. This order is divided into two suborders, Auchenorrhyncha and Sternorrhyncha. The former includes the important vectors of rice viruses and mycoplasma-like organisms (MLOs), the cicadellids (Cicadoidea: Cicadellidae) and the delphacids (Fulgoroidea: Delphacidae). The major portion of this paper discusses the two important families of homopterous vectors in relation to rice virus transmission and the other insect vectors incriminated only in a limited scope.

Historical Background

Written accounts of suspected rice virus diseases appeared as early as 1859 when De Vriese made the first scientific report on "mentek" disease in Indonesia (Ou 1965). "Penyakit merah" appears to have been first mentioned by Coleman-Doscas in Malaysia in 1934 (Singh 1969). However, these early reports did not mention transmission tests and both disorders were first considered physiological in nature.

The first report of insect involvement in a plant disease cycle was made as early as 1883 when rice dwarf was recorded in Japan (Fukushi 1934, Katsura 1936).

Insect transmission of rice virus diseases in the Philippines was reported in 1941. The rice virus diseases known in different names as "stunt" or "dwarf" transmitted by *Nephotettix bipunctatus* Fabr. (Agati et al 1941) and "accep na pula" or "stunt" transmitted by *N. bipunctatus cincticeps* Uhler (Serrano 1957), were all considered similar to tungro

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(Ling 1972). In other words, before 1950 reports on rice virus transmissions were available only in Japan and the Philippines.

A number of historical milestones in plant virology were indicated in the studies of some rice viruses. Rice dwarf virus (RDV) was the first plant virus known to be insect transmitted, transovarially transmitted (Fukushi 1934), propagative in its insect vector (Fukushi 1939, 1940), and localized in the vector cells by electron microscopy (Fukushi et al 1960). The rice tungro virus was the first cicadellid-borne virus demonstrated not to persist in its vector (Ling 1966). In addition, one of the earliest plant diseases associated with MLO is rice yellow dwarf. Nasu et al (1967) first demonstrated the presence of MLOs in infected rice plants and in the midgut and salivary glands of *N. nigropictus* and *N. cincticeps*.

Rice Virus and MLO-associated Diseases

At the First International Congress on Rice Virus Diseases held at the International Rice Research Institute, Philippines, in 1967, 10 rice virus diseases were discussed, including those suspected to be of viral nature. Thereafter, the number of rice virus diseases whose transmission and causative agent are well demonstrated increased to 14 (Table 1). Two diseases of rice are associated with MLOs (Table 2): the rice yellow dwarf (Nasu et al 1967) and rice orange leaf (Saito et al 1976). However, the fulfillment of Koch's postulates for MLOs as pathogenic agent of rice diseases has not been claimed.

Rice mosaic and wilted stunt were formerly considered as distinct rice virus diseases (Committee Report 1969, Ling 1972, 1981). However, there is no information that rice mosaic, mechanically transmissible to maize seedlings (Martinez et al 1960), is transmissible from maize to rice or rice to rice. Wilted stunt in Taiwan (Chen et al 1978) seems to be similar to grassy stunt in virus-vector interaction, with symptoms varying in season and in severity depending on the cultivar infected (Chen & Chiu 1982).

Some rice virus and MLO-associated diseases are known under different names. Tungro is "cella pance" and "penyakit habang" in Indonesia, leaf yellowing in India, "penyakit merah" in Malaysia, and yellow-orange leaf in Thailand. Yellow dwarf is "padi jantan" in Malaysia. The yellow stunt in China (Chen et al 1979) and rice rosette in the Philippines (Bergonia et al 1966) are similar to transitory yellowing and grassy stunt respectively, based on symptomatology, vector species, and virus-vector interaction (Ling 1981, Ling & Tiongco 1980).

Leaf gall disease of rice and maize reported in Australia (Grylls 1979) appears very similar to the rice and maize leaf gall disease in the Philippines (Agati & Calica 1949). The cause of the Philippine leaf gall was attributed to insect toxin (Maramorosch et al 1961). However, the Australian leaf gall, transmitted by *Cicadulina bimaculata* (Evans), contained spherical particles 45-50 nm that were not distinguishable from maize wallaby ear virus (MWEV). The virus also reacted in serological tests with antisera to MWEV and antisera to maize rough dwarf virus (Grylls 1979).

Table 1. Known rice virus diseases and their distribution.

Disease	Distribution	References
Black-streaked dwarf	China	Zhu et al 1964
	Japan	Kuribayashi & Shinkai 1952
	Korea	Lee et al 1977
Bunchy stunt	China	Xie & Lin 1980
Dwarf	China	Xie et al 1979
	Japan	Fukushi 1934
	Korea	Park 1966
	Nepal	John et al 1978
Gall dwarf	Thailand	Omura et al 1980
Giallume	Italy	Osler et al 1974
Grassy stunt	India	Anjaneyulu 1974
	Indonesia	Tantera et al 1973
	Japan	Iwasaki & Shinkai 1979
	Malaysia	Ou & Rivera 1969
	Philippines	Rivera et al 1966
	Sri Lanka	Abeygunawardena et al 1970
	Taiwan	Hsieh & Chiu 1970
	Thailand	Wathanakul et al 1968
Hoja blanca	The Americas	Everett & Lamey 1969
Necrosis mosaic	Japan	Fujii 1967
	India	Ghosh 1979
Ragged stunt	Bangladesh	IRRI 1978
	China	Zhou & Ling 1979
	India	Heinrichs & Khush 1978
	Indonesia	Hibino et al 1977
	Malaysia	Hashim 1978
	Philippines	Ling 1977
	Sri Lanka	Heinrichs & Khush 1978
	Taiwan	Chen et al 1979
	Thailand	Weerapat & Pongprasert 1978
Stripe	China	Zhu et al 1964
	Japan	Iida 1969
	Korea	Lee 1969
	Taiwan	Chui 1972
	U.S.S.R.	Pinsker & Reifman 1975
Transitory yellowing	China	Zhejiang AAS 1974
	Okinawa, Japan	Saito et al 1978
	Taiwan	Chiu et al 1965
	Thailand	Inoue et al 1980
Tungro	Bangladesh	Nuque & Miah 1969
	India	John 1968
	Indonesia	Rivera et al 1968
	Malaysia	Ou et al 1965
	Nepal	John et al 1979
	Philippines	Rivera & Ou 1965
	Thailand	Lamey et al 1967
Waika	Japan	Furuta 1977
Yellow mottle	Kenya	Bakker 1970
	Ivory Coast	Fauquet & Thouvenel 1978

Table 2. MLO-associated diseases of rice and their distribution.

Disease	Distribution	References
Orange leaf	China	Wu et al 1980
	India	Pathak et al 1967
	Indonesia	Oka 1977
	Malaysia	Ou & Rivera 1969
	Philippines	Rivera et al 1963
	Sri Lanka	Abeygunawardena et al 1970
	Thailand	Ou 1963
Yellow dwarf	Bangladesh	Galvez & Shikata 1969
	China	Hashioka 1952
	India	Raychaudhuri et al 1967
	Indonesia	Satomi et al 1978
	Japan	Hashioka 1964
	Malaysia	Lim 1970
	Okinawa, Japan	Shinkai et al 1963
	Philippines	Palomar & Rivera 1967
	Sri Lanka	Abeygunawardena et al 1970
	Taiwan	Kurosawa 1940
	Thailand	Wathanakul & Weerapat 1969

Two viruses are presently suspected or considered strains of other viruses. The rice giallume virus occurring in Italy and transmitted by the aphid *Rhopalosiphum padi* (Osler et al 1974) is now recognized as a strain of barley yellow dwarf virus (Amici et al 1978, Faoro et al 1978). The rice black-streaked dwarf virus in temperate Asia transmitted by three species of delphacids is suspected to be a strain of maize rough dwarf virus (Shikata & Kitagawa 1977).

A new disease, rice chlorotic streak, was reported in India. It is transmitted by the rice mealybug *Heterococcus rehi* (Anjaneyulu et al 1980). This disease will be included in the list as soon as the nature and morphological features of the causal agent are established.

Transmission

Rice viruses and MLOs are transmitted by mechanical means, through soil (probably by a fungus), or by insect vectors. Transmission of necrosis mosaic through seeds at the rate of less than 10% was reported by Fujikawa et al (1971). In contrast, Fujii and Okamoto (1969) reported the absence of transmission in 16,000 rice seeds tested. No seed transmission was recorded in the other rice virus diseases from a total of more than 53,000 seeds tested by various investigators (Ling 1981).

Mechanically transmitted rice viruses are necrosis mosaic (Fujikawa et al 1969) and yellow mottle (Bakker 1970). The latter is also transmitted by a number of beetles and a species of grasshopper (Bakker 1970, 1971, 1974).

Soil transmission also observed in necrosis mosaic, was first reported by Fujii et al (1968) and confirmed by Fujikawa et al (1969). However, the virus is probably transmitted by the fungus *Polymyxa graminis* (Inouye and Fujii 1977).

The other rice viruses and MLOs are transmitted either by cicadellids or delphacids. Cicadellids transmit six viruses and two MLOs, while the delphacids transmit five rice viruses. Only rice giallume is known to be transmitted by an aphid.

INSECT VECTORS AND RICE VIRUSES AND MLOs

Except for the soil-borne rice necrosis mosaic virus, the beetle-borne rice yellow mottle virus and the aphid-borne rice giallume, all known rice viruses and MLOs are transmitted by homopterous insects belonging to the families Cicadellidae and Delphacidae (Table 3).

The feeding behavior of homopterous insects may explain in part their success as virus vectors. Their mouthparts are highly adapted for piercing plant tissues. The insects can selectively feed in the mesophyll, phloem, or xylem making them ideal vectors of pathogens multiplying in those tissues (Forbes & MacCarthy 1969). The transmission mechanism of these insects is described in a number of literatures (Harris 1977, 1979, 1980, 1981, Harris & Childress 1980, Harris et al 1981, Pirone & Harris 1977).

The names of insect vectors of rice viruses have undergone changes. Ling (1973) compiled synonymies of insect vectors of rice viruses, in which previous names and sequence of changes in insect name were listed. Nielson (1979) published the taxonomy and phylogeny of cicadellid vectors as well as a list of the vector species and the pathogens they transmit.

Cicadellid-borne Viruses and MLOs

Five species of the genus *Nephotettix* are known vectors of rice viruses and MLOs: *N. cincticeps* (Uhler), *N. malayanus* Ishihara & Kawase, *N. nigropictus* (Stål), *N. parvus* Ishihara & Kawase, and *N. virescens* (Distant). The genus *Nephotettix* Matsumura was revised by Ishihara (1964, 1969) and later by Ghauri (1971). Significant nomenclatural changes were made by Ghauri favoring the use of *nigropictus* (Stål) rather than *apicalis* (Motschulsky) and *virescens* (Distant) rather than *impicticeps* Ishihara. Besides the five *Nephotettix* species, *R. dorsalis* (Motschulsky) is also a vector. This is the only known vector species in the genus *Recilia* Edwards, formerly *Inazuma*.

Six rice viruses are transmitted by cicadellids -- two are transitory in their vectors, two are persistent without transovarial passage, and two have transovarial passage.

Rice tungro virus (RTV) is transmitted by *N. malayanus* (IRRI 1973), *N. nigropictus* (Ling 1970, Rivera & Ling 1968), *N. parvus* (Rivera et al 1972), *N. virescens* (Ling 1966, Rivera & Ou 1965), and *R. dorsalis* (Rivera et al 1969). As far as the insect population in the field and the efficiency of transmission are concerned, *N. virescens* is the most important vector of the virus. The active transmitters vary among vector species - 42% for *N. malayanus*, 0 to 27% for *N. nigropictus*, 8% for *N. parvus*, 83% for *N. virescens*, and 4 to 8% for *R. dorsalis*. The nymphs usually transmit RTV as efficiently as adult, but lose their infectivity after molting. Insect infectivity decreased by about 40 to 50%, 24 hours after acquisition feeding. The minimum acquisition and inoculation feeding periods are 30 and 5 minutes. The longest retention period obtained for *N. virescens* is 6 days at 32° and 22 days at 13°C (Ling & Tiongco 1979), 3 days for *N. nigropictus*, and 4 days for *R. dorsalis*. The virus seems to have no deleterious effect on *N. virescens*.

Table 3. The cicadellid and delphacid vectors of rice viruses and MLOs.

	Vector	Diseases	Reference
I.	Fam. Cicadellidae		
	Nephotettix cincticeps	Bunchy stunt	Xie & Lin 1980
		Gall dwarf	Inoue & Omura 1982
		Dwarf	Fukushi 1934
		Transitory yellowing	Chiu et al 1968
		Waika	Hirao et al 1974
		Yellow dwarf	Iida & Shinkai 1950
	N. malayanus	Gall dwarf	Inoue & Omura 1982
		Tungro	IRRI 1973
		Waika	Inoue 1977
		Yellow dwarf	IRRI 1975
	N. nigropictus	Dwarf	Nasu 1963
		Gall dwarf	Omura et al 1980
		Transitory yellowing	Chiu et al 1965
		Tungro	Rivera & Ling 1968
		Waika	Satomi et al 1975
		Yellow dwarf	IRRI 1963
	N. parvus	Tungro	Rivera et al 1972
		Yellow dwarf	Rivera et al 1972
	N. virescens	Bunchy stunt	Xie & Lin 1980
		Dwarf	Xie et al 1981
		Gall dwarf	Inoue & Omura 1982
		Transitory yellowing	Hsieh et al 1970
		Tungro	Rivera & Ou 1965
		Waika	Kimura et al 1975
		Yellow dwarf	Shinkai 1959
	Recilia dorsalis	Dwarf	Fukushi 1937
		Gall dwarf	Putta et al 1980
		Orange leaf	Rivera et al 1963
		Tungro	Rivera et al 1969
II.	Fam. Delphacidae		
	Laodelphax striatellus	Black-streaked dwarf	Kuribayashi & Shinkai 1952
		Stripe	Kuribayashi 1931
	Nilaparvata bakeri	Grassy stunt	Iwasaki et al 1980
		Ragged stunt	Morinaka et al 1981
	N. lugens	Grassy stunt	Rivera et al 1966
		Ragged stunt	Hibino et al 1977
			Ling et al 1977
	N. muiri	Grassy stunt	Iwasaki et al 1980
	Sogatodes cubanus	Hoja blanca	Galvez et al 1960
	S. orizicola	Hoja blanca	Galvez 1968
	Terthron albovittatus	Stripe	Shinkai 1970
	Unkanodes albifascia	Black-streaked dwarf	Shinkai 1967
		Stripe	Hirao 1968
	U. sapporonus	Black-streaked dwarf	Shinkai 1966
		Stripe	Shinkai 1966

Rice waika was reported as a new disease in Japan in 1973. The rice waika virus (RWV) is spherical, 30 nm in diameter (Doi et al 1975, Nishi et al 1975) and is serologically related to RTV (Saito et al 1976). The virus is transmitted nonpersistently by *N. cincticeps* and *N. virescens* (Nishi et al 1975), *N. nigropictus* (Satomi et al 1975), and *N. malayanus* (Inoue & Hirao 1981). The active transmitters vary according to species: 81% in *N. virescens*, 53% in *N. malayanus*, 35% in *N. cincticeps*, and 17% in *N. nigropictus* (Inoue & Hirao 1981). The first-instar nymphs of *N. cincticeps* were only slightly less efficient than the second to the last instars. Third- and fifth-instar nymphs and adult females had equal efficiency (Inoue & Hirao 1981).

Rice bunchy stunt was reported in Fujian, China in 1973. The rice bunchy stunt virus (RBSV) is transmitted by *N. cincticeps* and *N. virescens*. The symptoms are closely similar to RDV, but no transovarial transmission was obtained and *R. dorsalis* was not a vector. In addition, no transmission was obtained from cicadellid *Empoasca subrufa*, delphacid *N. lugens*, and aphid *R. padi*. Although RBSV and RDV are morphologically similar, no cross-protection and apparently no immunological relation exist between them (Xie & Lin 1980).

Rice transitory yellowing was first reported from Taiwan in 1965 and transmitted by *N. nigropictus* (Chiu et al 1965). Later, *N. cincticeps* (Chiu et al 1968) and *N. virescens* (Hsieh et al 1970) were identified as vectors of the virus in a persistent manner. No congenital transmission in *N. nigropictus* was detected. The cicadellids *R. dorsalis* and *Cicadulina bipunctella* and the delphacid *N. lugens* did not transmit RTYV (Chiu et al 1968). The percentages of transmitters were 20-34% and 9-13% when susceptible and resistant cultivars were used as virus sources (Chen & Chiu 1980). The green leafhoppers showed a negative preference for RTYV-diseased plants as 7, 18, and 75% of the test insects preferred RTYV-diseased plants, healthy plants, and rice yellow dwarf-diseased plants, respectively. Nymphs of *N. cincticeps* were more efficient than the adults in transmitting the virus, and the males slightly more efficient than the females. No sex difference in efficiency was observed in *N. nigropictus* (Chen & Chiu 1980). Hsieh (1969) demonstrated multiplication of the virus in the vector. No transmission of RTYV was obtained from 78 *N. malayanus* tested in Japan, even with 2-day acquisition feeding (Inoue 1979).

A rice disease called yellow stunt occurred in Kwangtung, China, in 1964. The disease is similar to rice transitory yellowing in symptomatology, host range, transmission, insect vectors, and virus particles morphology (Chen et al 1979, Chung & Pui 1980).

Dwarf not only is the first virus disease of rice identified but also contributed to classical knowledge of plant virology. There are accounts of the history of transmission of rice dwarf (Fukushi 1934, 1969; Nielson 1968; Ling 1972; Harris 1979). Virus transmission by *R. dorsalis*, first reported by Takata in 1895 and 1896, was confirmed by Fukushi (1937); by *N. cincticeps* as mentioned in the report of Shiga Agricultural Experiment Station (Fukushi 1934, Iida 1969); and by *N. nigropictus* (Nasu 1963). Shinkai (1962) did not succeed in transmitting RDV by *N. virescens* but Xie et al (1981) reported success. The percentage of active transmitters is about 23% for *N. nigropictus* (Nasu 1963), 0 to 69% for *N. cincticeps* (Shinkai 1962), and 2 to 43%

for *R. dorsalis* (Hashioka 1964). The virus is persistent and is congenitally transmitted to the offspring from infective females, but not from infective males (Fukushi 1934). Thirty two to 100% of the offspring of an infective *N. cincticeps* females and 0 to 64% in *R. dorsalis* are congenitally infective (Shinkai 1965). A single infective female can produce infective progenies up to six succeeding generations. For *R. dorsalis*, the percentage of congenitally infective insects decreases remarkably as the insect generations pass; the fourth generation insects often are not infective.

Another cicadellid-borne rice virus with transovarial passage is gall dwarf reported in Thailand in 1979. The virus is transmitted by *R. dorsalis* and *N. nigropictus* (Morinaka et al 1980, Omura et al 1980, Putta et al 1980) and *N. cincticeps*, *N. malayanus*, and *N. virescens* (Inoue & Omura 1982). Transmission efficiency was highest in *N. nigropictus*, followed by that in *N. cincticeps* and *N. malayanus*. *N. virescens* was an inefficient vector. Transovarian transmission on *N. nigropictus* was recorded (Inoue & Omura 1982). No transmission was obtained with *N. lugens* and *L. striatellus* (Inoue & Omura 1982).

Two rice diseases associated with MLOs are transmitted by cicadellids in a persistent manner without transovarial passage.

Rice orange leaf disease was first observed in Thailand (Ou 1963). The pathogen is transmitted by *R. dorsalis* (Rivera et al 1963, Wathanakul et al 1968, Abeygunawardena et al 1970, Singh 1971). The proportion of active transmitters varies from 7 to 14%. The shortest acquisition feeding period is 5 hours. The incubation period in the insect is 2 to 6 days (Rivera et al 1963). Tests have failed to show its transmission by *Macrosteles fascifrons*, *Nisia atrovenosa*, *Peregrinus maidis*, *Sogata paludum*, *Tettigella spectra* (Rivera et al 1963); *Nephotettix* sp. (Wathanakul et al 1968); and *N. nigropictus*, *N. virescens*, and *N. lugens* (Rivera et al 1963, Abeygunawardena et al 1970, Singh 1971).

Yellow dwarf was first reported in Japan in 1919 and its presence in tropical Asia has been recognized only in the sixties. Yellow dwarf pathogen is transmitted by *N. cincticeps* (Iida & Shinkai 1950); *N. virescens* (Shinkai 1959, Abeygunawardena et al 1970; Palomar & Rivera 1967); *N. nigropictus* (IRRI 1963, Ouchi & Suenaga 1963); *N. malayanus* (IRRI 1973); and *N. parvus* (Rivera et al 1972). Palomar & Rivera (1967) reported 69% active transmitters for *N. nigropictus* and 83% for *N. virescens*; Shinkai (1962) reported 88% to 96% for *N. cincticeps* and 94% for *N. virescens*. Infective insects sometimes retained their infectivity the rest of their life. Transstadial passage occurs but there is no evidence of transovarial passage. Several insects did not transmit the pathogen. Shinkai (1962) reported *Inemadara oryzae*, *L. striatellus*, *M. fascifrons*, *M. quadrimaculatus*, *N. lugens*, *Nisia atrovenosa*, *R. dorsalis*, *Sogatella furcifera*, and *Tettigella viridis*; and Lim (1969) *Tettigoniella spectra* and *Scotinophara coarctata*.

Delphacid-borne viruses

As vectors of plant virus diseases, delphacids have received less attention than cicadellids. Delphacid vectors of rice viruses include nine species belonging to genera *Laodelphax*, *Nilaparvata*, *Sogatodes*, *Terthron*, and *Unkanodes* (Table 3). For a number of years, only one species of *Nilaparvata*, *N. lugens* (Stål), was known to transmit rice viruses. However, two other species -- *N. bakeri* (Muir) and *N. muiri* China -- were recently reported to transmit rice grassy stunt virus (RGSV) and rice ragged stunt virus (RRSV) under experimental conditions (Iwasaki et al 1980, Morinaka et al 1981). These vectors may be responsible for transmitting viruses in the field. No delphacid vectors was incriminated with MLO-diseases of rice.

Five rice viruses are transmitted by delphacids, all in a persistent manner. Three are without transovarial passage and two with transovarial passage.

Rice black-streaked dwarf virus (RBSDV) is transmitted by *Laodelphax striatellus* (Kuribayashi & Shinkai 1952), *Unkanodes sapporonus* (Shinkai 1966) and *U. albifascia* (Shinkai 1967, Hirao 1968). Negative transmission was obtained from *Sogatella furcifera* and *N. lugens* (Shinkai 1962). *U. sapporonus* favors maize, wheat, and barley because rice is not its natural host. The proportion of active transmitters is 32% for *L. striatellus* (Shinkai 1962), 34% for *U. sapporonus* (Shinkai 1966), and 50% (Hirao 1968) to 73% (Shinkai 1967) for *U. albifascia*. Most active individuals of *L. striatellus* can acquire the virus during 1-day feeding, but its shortest acquisition feeding period is 30 minutes; and 15 minutes for *U. albifascia* (Hirao 1968). The incubation period in *L. striatellus* is 4 to 35 days (Iida & Shinkai 1969), but often 7 to 21 days (Shinkai 1965). In *U. albifascia* the incubation period is 7 to 25 days, or an average of 13 (Hirao 1968). The shortest inoculation feeding period is 5 minutes for *L. striatellus* (Shinkai 1962) and 15 minutes for *U. albifascia* (Hirao 1968). Most insects remain infective until they become old. The longest retention period obtained is 58 days for *L. striatellus* (Shinkai 1962) and 49 days for *U. albifascia* (Hirao 1968). Transstadial passage occurs but there is no evidence of transovarial passage.

Rice grassy stunt was previously reported to be transmitted only by *Nilaparvata lugens* (Rivera et al 1966). Recently, *N. bakeri* and *N. muiri* were demonstrated to be vectors too (Iwasaki et al 1980). The proportion of active transmitters in field populations of *N. lugens* varies from 3 to 50%, usually 20 to 40%. The shortest acquisition access time for positive transmission by *N. lugens* is 15 minutes, and the proportion of the infective insects increases as the acquisition access time lenghtened (Rivera et al 1966). After an incubation period of 5 to 28 days, usually 10-11 days, the insect transmitted the virus at a low rate after 5 to 15 minutes inoculation feeding. Transmission reached a maximum at 24 hours. Viruliferous insects remain inoculative for life. Transmission by *N. cincticeps*, *N. nigropictus*, *N. virescens*, *R. dorsalis*, *S. furcifera*, and *L. striatellus* failed (Hsieh & Chiu 1970). The three biotypes of *N. lugens* identified in the Philippines have similar ability to transmit the rice grassy stunt virus (Aguiero & Ling 1977).

Before Morinaka et al (1981) reported transmission of rice ragged stunt by *N. bakeri*, only *N. lugens* was known as the vector of rice ragged stunt virus (RRSV)(Hibino et al 1977, Ling et al 1978). Based on several reports, the average percentage of active transmitters varied from 12 to 40% (Hibino et al 1977, Kartaatmadja 1979, Ling et al 1978, Senboku et al 1978). In a single test with a small number of insects, however, 14 to 26% of the insects were active transmitters. The shortest acquisition access time reported to effect positive transmission was 3 hours (Chetanachit et al 1978). The latent period ranged from 3 to 33 days and averaged 9 days (Hibino et al 1977, Ling et al 1978). The minimum inoculation access time for successful transmission was 10 minutes (Kartaatmadja 1979) and 60 minutes as reported by Hibino et al (1977) and Chetanachit et al (1978). The insects that fed on ragged stunt-diseased plants retained their infectivity from 3 to 35 days, averaging 15 days (Ling et al 1978). The daily transmission pattern of the insects was intermittent and the insects retained their infectivity after molting and even until death. No transovarial transmission was obtained. Three biotypes of *N. lugens* differing in their ability to infect rice cultivars did not differ in their ability to transmit RRSV (Ling et al 1978).

Rice stripe virus is transmitted by *Laodelphax striatellus* (Kuribayashi 1931), *Terthron albovittatus* (Shinkai 1970), *U. albifascia* (Shinkai 1967, Hirao 1968) and *U. sapporonus* (Shinkai 1966). *L. striatellus* seems to be the principal vector. The proportion of active transmitters is 14 to 54% for *L. striatellus* (Kuribayashi 1931) and 28 to 35% for *U. albifascia* (Shinkai 1967). The shortest acquisition feeding period is 3 minutes for *L. striatellus* (Yamada & Yamamoto 1955) and less than 30 minutes for *U. albifascia* (Hirao 1968). The incubation period of the virus in *L. striatellus* is 5 to 21 days, often 5 to 10 days (Shinkai 1962); it is 5 to 26 days in *U. albifascia* with an average of 12 (Hirao 1968). The longest retention period of *L. striatellus* is 47 days (Shinkai 1962). Transstadial and transovarial passage occur (Shinkai 1962, 1966, 1967; Hirao 1968).

Sogatodes cubanus and *S. orizicola* are known to transmit rice hoja blanca virus (Galvez et al 1960, Galvez 1968). *S. orizicola* is the major vector of rice hoja blanca because it prefers rice. In a natural population of *S. orizicola*, the active transmitters are about 5 to 15%, but can be increased by selective breeding (Galvez 1968, 1969). Using a highly active colony, Galvez (1968) demonstrated an incubation period of 30-36 days, with an acquisition threshold period of 15 minutes. The shortest inoculation feeding period is 30 minutes. Galvez (1968) demonstrated a high percentage of transovarial transmission, about 96% of 500 eggs after 10 generations. Showers & Everett (1967) reported that the life span of adult insects from an infective female is significantly shorter than that of progeny of an infective male. Viruliferous insects lay one-third as many eggs and hatch fewer nymphs than do virus-free insects (Jennings & Pineda 1971). The percentage of nymphs reaching adult stage and the insects' life span are also reduced.

Other vectors

The following are rice viruses that are vectored by insects other than cicadellids and delphacids and probably by a fungus.

Rice giallume, recognized as a strain of barley yellow dwarf virus, is transmitted by the aphid *R. padi* (Osler et al 1974), but not by the aphid *Sigpha glyceriae* (Osler & Longoni 1975).

Rice yellow mottle virus is readily mechanically transmissible to rice. The virus was recovered from sap of infected rice plants, their guttation fluid, and from standing irrigation water in a field with ratoon rice. Insects with chewing mouthparts, mainly chrysomelid beetles common in and around the rice fields, transmit the virus. The following insects were able to transmit rice yellow mottle virus --

Coleoptera, Chrysomelidae: *Apophylia* sp., *Chaetocnema abyssinica*, *C. kenyensis*, *C. pulla*, *Chaetocnema* sp., *Crytocephalus* sp., *Dactylispa bayoni*, *Dicladispa (Chrysispa) paucispina*, *D. (C.) viridicyanea*, *Monolepta flaveola*, *M. haematura*, *Oulema dunbrodiensis* f. *nigripennis*, *Sesselia pusilla*, *Trichispa sericea*; Orthoptera, Tettigonidae: *Conocephalus merumontanus* (Bakker 1970, 1971, 1974). Insects belonging to the genus *Apophylia* and *S. pusilla* are the most efficient vectors, while the *Chaetocnema* spp., and *T. sericea* generally caused lower percentages of infection. *S. pusilla*, *C. pulla*, and *T. sericea* are able to acquire the virus when left for 15 minutes on diseased rice. Although the insects are able to infect seedlings in 15 minutes, in general the beetles appear to acquire the virus faster than they are able to infect a plant. *S. pusilla* and *C. pulla* are able to retain the virus for 8 and 5 days, respectively, often causing infection of the rice plants on several consecutive days, while *T. sericea* retain the virus for one day only (Bakker 1971, 1974).

Rice necrosis mosaic can be transmitted by mechanical means and through soil (Fujikawa et al 1969, Fuji et al 1968). Soil transmission from one plant to another might be due to *P. graminis* as rice roots harbor that fungal population to a great extent (Inouye 1977).

VECTOR-VIRUS RELATIONSHIP

A biological relationship between plant viruses and their insect vectors exists. Watson and Roberts (1939, 1940) initiated the concept of grouping insect-borne viruses into persistent and nonpersistent based on their virus-vector interactions. Since then, several groupings have been proposed (Sylvester 1956, Kennedy et al 1962, Ling & Tiongco 1979, Harris 1977).

The biological relationship between cicadellid-borne rice viruses and their vectors was formerly thought to be persistent. But with the demonstration of nonpersistence of rice tungro virus in the green leafhopper (Ling 1966), the cicadellid-borne viruses have now been categorized into transitory and persistent (Ling & Tiongco 1979). The transitory characteristic was also observed in maize chlorotic dwarf virus (Nault et al 1973) and rice waika virus (Nishi et al 1975). The transmission is characterized by the absence of detectable latent period, a decline in vector infectivity, and nonstadial transmission.

Delphacids are known to transmit rice viruses in the persistent manner.

The rice viruses in the persistent group can be further classified into nontransovarial and transovarial. The former describes viruses that are not transmitted to the progeny through the egg; in the latter, the viruses are transmitted to the progeny through the egg.

VECTOR SPECIFICITY

Vector specificity is a specific relationship existing between the insect vector and the pathogen it transmits. This condition is present in the vectors transmitting rice viruses and MLOs. Some pathogens are transmitted only by one major taxon and in one instance by only one vector species.

Genus specificity, where two or more species are known to be vectors, is frequently encountered in cicadellid transmission. Rice yellow dwarf is transmitted by five species of *Nephotettix*. Members of this genus are also responsible for vectoring rice transitory yellowing and rice waika viruses. This specificity also exists between the delphacids *Sogatodes* and *Nilaparvata*, which transmit hoja blanca and grassy stunt and ragged stunt viruses, respectively.

Species specificity is exemplified by transmission of orange leaf (MLO) by *R. dorsalis*, where this species is the only vector of that pathogen, although it is capable of transmitting dwarf, gall dwarf, and tungro.

Notwithstanding the specificity exhibited by cicadellids, considerable diversity of transmission efficiencies and abilities could be observed. The three species of *Nephotettix* -- *N. cincticeps*, *N. nigropictus*, and *N. virescens* -- and *R. dorsalis* are capable of transmitting both persistent (transovarial and nontransovarial) and transitory types of viruses. Except for *N. parvus*, four vector species of *Nephotettix* can transmit different shapes and sizes of virus particles. *N. virescens*, for example, can transmit large spherical bunchy stunt and dwarf viruses; small spherical waika virus; bullet-shaped transitory yellowing virus, and complex particles of tungro virus. Diversity not only in transmitting different size and shapes of virus particles but also different kinds of pathogen are encountered. Besides transmitting virus particles, all the cicadellid vector species also transmit MLOs.

VECTOR DISTRIBUTION AND DISEASE OCCURRENCE

The occurrence of most rice virus diseases in a region seems to have geographic restriction. Since there is no unequivocal evidence of transmission of rice viruses through seeds, the limiting factor may be the geographic distribution of vector insects because most rice viruses are transmitted only by insects.

Insect-transmitted rice virus diseases, their vector insects, and the host plants of the vector insects and viruses seem to have specific interactions among them. Some virus diseases are found in limited areas where their specific vector insects are distributed. For instance, *S. orizicola* and *S. cubanus* are prevalent in the Americas (CIE Map Nos. 202, 224) where hoja blanca disease occurs. *L. striatellus*, the vector of black-streaked dwarf and stripe viruses, is prevalent and widely distributed in temperate region (CIE Map No. 201). Of the *Nephotettix* spp., *N. nigropictus* and *N. virescens* are dominant in subtropical and tropical Asia (CIE Map Nos. 286, 287). *N. malayanus* and *N. parvus* are distributed in tropical Asian countries but are relatively scarce. *N. cincticeps* is distributed mainly in temperate Asia, China, Japan, and Korea. Whereas tungro is found in wide areas, dwarf disease is seen in some limited regions.

DIRECT INSECT DAMAGE

The development of high yielding rice cultivars and changes in cultural practices are some reasons for the increase in importance of *Nephotettix* spp. and *N. lugens* in Asia.

N. lugens has recently become a serious threat to rice production because it not only transmits pathogens but also causes direct damage by feeding on the rice crop, thus reducing its yield potential. If pest density is high, the plant dies and a condition known as hopperburn results. Appearance of damage varies according to the population density, stage of insect, feeding duration, cultivar, stage of rice plant, and probably the presence or absence of water in the rice field (Mochida et al 1978, Mochida & Okada 1979, Sogawa & Cheng 1979).

CONTROL

Knowledge of the relationship between vector density and disease incidence is useful in forecasting damage and applying control measures. This has been demonstrated in the epidemiological studies of rice tungro (Ling et al 1982). The use of insecticides and the planting of varieties resistant to the insect and to the virus have been the two control methods against rice tungro and grassy stunt diseases. Cultural methods and biological control agents may be important in the integrated control of rice viruses.

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