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# Rice viruses transmitted by the brown planthopper *Nilaparvata lugens* Stål

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The brown planthopper (BPH) *Nilaparvata lugens* transmits both rice grassy stunt (RGSV) and rice ragged stunt (RRSV) viruses in a persistent manner without transovarial passage. RGSV-infected rice plants show severe stunting and profuse tillering. The leaves are stiff and narrow and show occasional interveinal chlorosis and bronzing. RGSV is a member of the *Tenuivirus* group. RRSV-infected plants show stunting, abnormal leaves with serrated edges and/or twisted tips, and vein swelling or galls on the underside of the leaf blades and outer surface of the leaf sheaths. RRSV is a member of the *Oryzavirus* group of the family Reoviridae. In South Vietnam, the two viruses infect the rice plant together and cause the rice yellowing syndrome.

Virus diseases of rice spread by insect vectors have been considered to be of minor importance worldwide, being estimated to cause average actual crop losses of less than 1.5%. However, sporadic epidemics of rice virus diseases could cause devastating damage in a particular region or country (Ramasamy and Jatileksono 1996). For instance, the areas where rice tungro virus disease is epidemic are small in relation to the total rice production of the region or country, but affected fields may suffer a total yield loss. Such damages have a significant impact on the livelihood of farmers in Asia, who generally depend on the crops produced on relatively small farms (Azzam and Chancellor 2002).

The brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), is a serious insect pest of rice, especially in tropical Asia, where rice crops are continuously cultivated. Both nymphs and adults of BPH damage rice plants through extensive feeding on them. BPH also transmits viruses such as rice ragged stunt (RRSV) and rice grassy stunt (RGSV) (Hibino 1989, 1996). Thus, increased levels of BPH occasionally accompany substantial losses of rice crops by the virus diseases. From 2005 to 2006, more than 485,000 ha of rice production area in southern Vietnam were severely affected by viral diseases seemingly spread by BPH, resulting in the loss of 828,000 tons of rice valued at US$120 million (Du et al 2007). The rice virus disease widely observed in southern Vietnam has been called "yellowing syndrome" from the characteristic symptom of leaf yellowing. Rice yellowing syndrome was later found

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highly associated with infection with RGSV or co-infection of RGSV with RRSV, both transmitted by BPH, although the symptoms vary depending on varieties and virus species, and the timing and sequence of infection (Du et al 2007).

## Rice ragged stunt virus

Rice ragged stunt virus disease was first recognized in 1976 in Indonesia (Hibino et al 1977, Hibino 1979). Later, the disease was reported in Malaysia, the Philippines, Thailand, China, India, Sri Lanka, Taiwan (Hibino 1989, Chen et al 1979), and Japan (Shinkai et al 1980). High levels of RRSV were observed in Indonesia and the Philippines between 1977 and 1981, and in Thailand between 1980 and 1982, and again between 1989 and 1990 (Hibino 1996). Major outbreaks of RRSV incidences had not been reported in other countries until high levels of RRSV were observed in southern Vietnam in 2006 (Du et al 2007).

Rice plants infected with RRSV show stunting, dark-colored leaves with serrated edges or twisted tips, and vein swelling or galls on the underside of leaf blades and outer surface of the leaf sheaths (Fig. 1). The gall results from hyperplasia and hypertrophy of the phloem tissue. Plants infected with RRSV at the seedling stage develop new leaves with distinct symptoms such as twisting and serration 2 weeks after inoculation and thereafter develop leaves showing milder or no definite symptoms. At the flowering stage, the upper leaves and flag leaves may show twisting symptoms. Panicles of infected plants are fully exserted. Electron microscopic observation of diseased tissue revealed that RRSV is localized in the phloem and gall tissues. Inclusion bodies consisting of a viroplasmic matrix and numerous virus particles were observed in infected cells (Hibino 1989, 1996, Ling et al 1978).

RRSV is a member of the family *Reoviridae* and the type species of the genus *Oryzavirus* (Boccardo and Milne 1984, Holmes et al 1994, Nuss and Dall 1990). The virus particles are icosahedral of about 50 nm in diameter (Boccardo and Milne 1984). The virus genome is composed of 10 double-stranded RNA segments each having the genus-specific conserved terminal nucleotide sequences of 5′-GAUAAA---GUGC-3′ (Yan et al 1992). RRSV particles are composed of five major, highly immunoreactive structural proteins with estimated molecular weights of 33, 39, 43, 70, and 120 kDa and at least five minor structural proteins (49, 60, 76, 90, and 94 kDa). Three nonstructural proteins (31, 63, and 88 kDa) were also identified from in vitro translation of the RRSV genome (Lu et al 1988, 1990). The nucleotide sequences of RRSV genome segments S5, S8, and S9 have been determined. The genome segments S5, S8, and S9 apparently encode, respectively, a 90-kDa minor structural protein (Li et al 1996), a 67-kDa major structural protein, which appears to correspond to the 70-kDa protein reported by Lu et al (1988 and 1990) and Upadhyaya et al (1996), and a 38-kDa major structural protein, which appears to correspond to the 39-kDa protein reported by Lu et al (1988, 1990), Upadhyaya et al (1995), and Uyeda et al (1995). The 67-kDa protein is further proteolytically processed to 46-, 43-, and 26-kDa proteins (Upadhyaya et al 1996). Upadhyaya et al (1997) reported that the RRSV genome segments S7 and S10 encode nonstructural proteins of 68 and 32 kDa, respectively.

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**Fig. 1. Symptoms on rice plants caused by RRSV, RTSV, and RGSV. Variety Taichung Native 1 was inoculated with RGSV, RRSV, or RTSV through insect transmission. (A) Leaf yellowing and stunted growth caused by RGSV and RRSV. (B) Serrated leaf tissue caused by RRSV infection. (C) Twisted leaf tip caused by RRSV infection.**

## Rice grassy stunt virus

Rice grassy stunt virus disease was first reported in the Philippines in 1963 (Rivera et al 1966). It was also reported in China, Japan, Taiwan, and other countries in South and Southeast Asia (Hibino 1989). High levels of RGSV incidences were reported in Indonesia (1970 to 1977), the Philippines (1973 to 1977 and 1982 to 1983) (Hibino 1989, Hibino et al 1985), India (1972 to 1984) (Kulshreshtha et al 1974, Mariappan et al 1984), and Kyushu, Japan (1978) (Iwasaki and Shinkai 1979).

Rice plants infected with RGSV show pronounced stunting and proliferation of short, erect, and narrow leaves that are pale green or pale yellow in color and infected leaves may show mottling symptoms on young emerging leaves and rusty spots on older leaves (Fig. 1).

Severe strains of RGSV that cause yellow-orange leaf discoloration and premature death of plants were reported in Taiwan (Chen and Chiu 1982), the Philippines, Thailand (Hibino et al 1985), and India (Mariappan et al 1984). The severe strain in the Philippines was designated as RGSV 2 (Cabauatan et al 1985), while the severe strain in Taiwan was called rice wilted stunt virus (Chen and Chiu 1982). Rice cultivars with a gene with resistance to RGSV introduced from a wild rice species, *Oryza nivara* (Khush and Ling 1974), have been widely used. However, the severe strain of RGSV (RGSV 2) in the Philippines was highly pathogenic to the resistant cultivars (Cabauatan et al 1985, Hibino et al 1985).

RGSV-infected rice cells contain masses of fibrils in the nuclei and cytoplasm, and membrane-bound bodies with fibrils in the cytoplasm. Tubules associated with isometric particles of 18 to 25 nm in diameter can be observed in the sieve tubes (Hibino 1986a,b).

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RGSV is a member of the genus *Tenuivirus*, which consists of six members with rice stripe virus (RSV) as the type species (Hibino 1986, Toriyama 1995, Falk and Tsai 1998, Mayo et al 2000). RGSV is serologically distantly related to RSV (Hibino et al 1985). Tenuiviruses other than RGSV have four single-stranded, ambisense RNA genome segments, while RGSV possesses six RNA segments (Miranda et al 2000, Toriyama et al 1997, 1998). RNA segments 1, 2, 5, and 6 of RGSV are equivalent to RNA segments 1, 2, 3, and 4 of RSV, respectively. RGSV RNA segments 3 and 4 are unique in this genus. RNA 1 of tenuiviruses except RGSV is negative sense and encodes RNA-dependent RNA polymerase (RdRp) on the complementary strand (cRNA 1), while RNA 1 of RGSV is ambisense and contains a small open reading frame on the viral strand (vRNA 1) (Miranda et al 2000, Toriyama et al 1998). Thus, the tenuivirus genome appeared to encode at least seven proteins, one on cRNA 1 and two each on three other ambisense RNA segments, although the expression and the function of most of them are yet to be investigated. Among the proteins encoded in the RGSV genome, only the functions of the 339-kDa RdRp encoded on cRNA 1 and the 35–36-kDa nucleocapsid protein (N) encoded on cRNA 3 (cRNA 5 in the case of RGSV) are known. The virions are thin filamentous ribonucleoprotein particles of 3–10 nm in diameter consisting of vRNA, cRNA, N proteins, and a few molecules per particle of RdRp (Mayo et al 2000). A 94-kDa protein encoded on cRNA 2 is hypothesized to be a membrane protein (Estabrook et al 1996). No enveloped virions have been observed in tenuivirus-infected plants or insects by electron microscopy (Falk and Tsai 1998). A 21-kDa p6 protein encoded on RGSV vRNA 6 and a 20-kDa protein encoded on vRNA 4 of maize stripe virus (MSpV) were shown to be expressed in infected plants and to form cytoplasmic inclusion bodies, but they have not been detected in the vector insects (Falk et al 1987, Miranda and Koganezawa 1995).

## Relationships among BPH, BPH-transmitted viruses, and host plants

RRSV and RGSV are transmitted in a persistent manner by BPH and other species of *Nilaparvata* (Hibino 1986b, 1989, Milne and Ling 1982). The viruses multiply in the vectors. Once the vectors acquire the viruses, they retain the viruses throughout their lifespan even after molting but cannot transmit the viruses through the eggs. BPH carrying RGSV has a shorter lifespan and lower fecundity than virus-free BPH (Hirao et al 1987, Ling 1977). The ability of BPH to transmit the viruses appeared to be inheritable. Populations of BPH with low virus transmission ability can be selected by mating nonviruliferous BPH (Iwasaki et al 1982). RRSV particles were found aggregated in or around the viroplasmic inclusions or arranged in tubules in the cytoplasm of cells of BPH carrying RRSV. Isometric particles of RGSV were found in crystalline arrays in the fat body and tracheas of BPH carrying RGSV (Shikata et al 1980).

RRSV and RGSV can infect other graminaceous plants by artificial inoculation using BPH. However, natural infection of weeds and cereals other than rice is rare, as BPH survive and reproduce mainly in rice (Hibino 1979, 1989, Milne and Ling 1982). Infected rice plants, stubbles, and viruliferous BPH serve as the sources of the virus to spread. The outbreaks of RRSV and RGSV in some countries may have occurred

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when the levels of the viruses present in fields reached epidemic proportions due to the increased population density of BPH (Ling et al 1978, Dyck and Thomas 1979). Another probable factor associated with outbreaks of RGSV and RRSV is the long-distance flight of BPH (Hirao et al 1984, Iwasaki et al 1985, Kishimoto 1976). BPH flies from fields affected with the viruses to newly planted rice fields in distant areas and disperses the viruses. BPH and BPH-transmitted viruses are often endemic in tropical Asia. In temperate countries, BPH can migrate annually during the monsoon season from the endemic areas (Cheng et al 1982, Kishimoto 1976, Lee and Park 1977).

Rice cultivars resistant to BPH have been used in many countries of Asia to control BPH and BPH-transmitted viruses. In many cases, the incidences of RGSV in the resistant cultivars initially appeared to be very low; however, biotypes of BPH that can overcome the resistance became prevalent a few or several years after the release of the cultivars (Hibino 1996, Claridge and Den Hollander 1980). Once populations of BPH that can colonize resistant cultivars develop, the cultivars may become a major source of virus spread in fields.

## Resurgence of BPH-transmitted viruses in the Mekong Delta

Rice plants showing symptoms suspected to be of viral infection such as leaf yellowing had been reported as early as the 1960s in southern Vietnam and given names such as "yellow stunt," "chlorotic stunt," or "bushy stunt" (Toan 1969). Widespread occurrence of diseases in rice plants suspected to be caused by viruses was also observed in the northern part of Vietnam during 1964 to 1970, affecting virtually all varieties planted on about 50,000 ha (Du 1988). The viral nature of the diseases was not confirmed, but, because of the presence of high populations of green leafhoppers (GLH, *Nephotettix virescens* Distant) in the affected areas, the disease in northern Vietnam was suspected to be caused either by tungro viruses or by yellow dwarf mycoplasma. Rice tungro disease was reported in central Vietnam, but not in the Mekong Delta (Vien et al 1994, 1996). Another occasion of rice disease epidemic in the Mekong Delta supposedly caused by viruses was also recorded during 1978 to 1980 after the outbreak of BPH. The outbreak resulted in more than 90% losses of the rice crops. Rice plants in the affected areas showed typical symptoms of RRSV such as serrated leaves, twisted and malformed leaves, vein swelling on leaf sheaths and blades, leaf curling, and stunted growth (Trung 1985). Other studies also reported the occurrence of RRSV in Vietnam (Vu and Nguyen 1979, Luong and Nguyen 1995).

The rice disease called yellowing syndrome was observed in the Mekong Delta in 1989 but it became more evident after 1994 (Fig. 2). In 1997, the incidence of yellowing syndrome was estimated at 5–10% in many varieties grown in the region, and close to 50% in some fields that received high nitrogen fertilizer. Diseased tillers showed interveinal chlorosis to yellowish color, stunting, and no further growth. The disease was later called "benh vang lun," which means "stunting and yellowing syndrome" in Vietnamese. Based on the epidemiological characteristics, the symptoms, and abundance of BPH in the affected fields, it was suggested that the yellowing

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**Fig. 2. Rice plants affected by the yellowing syndrome in southern Vietnam, August 2006.**

syndrome of rice was associated with "benh lua co dong 2" or "RGSV 2" (Du et al 2005).

The epidemiological characteristics of the yellowing syndrome in the Mekong Delta indicated the involvement of viruses and insect vectors; however, the exact causes of the disease had not been previously well understood. In order to elucidate viruses associated with the yellowing syndrome, samples were collected from rice plants showing symptoms of virus infection such as leaf yellowing and bronzing, and stunting (Fig. 3), in the Mekong Delta between 2005 and 2006, and the presence of viruses was examined. Virus infection in the plants was examined by enzyme-linked immunosorbent assay (ELISA) using antibodies to RRSV, RGSV, rice tungro spherical virus (RTSV), and rice tungro bacilliform virus (RTBV). Some of the results by ELISA were confirmed by reverse transcriptase-polymerase chain reaction (RT-PCR) for viral genome sequences.

The results indicated that in 2005 only a small proportion (19%) of plants showing the symptoms collected from one of the two sites were infected with RGSV, while no RRSV, RTSV, and RTBV infection was detected at either site (Table 1). In 2006, however, the levels of RGSV and RRSV infection were evidently higher than in 2005. RGSV was detected in at least 60% of plants showing symptoms collected from various sites. In addition, substantial portions of plants with the symptoms were found mix-infected with RGSV and RRSV. Only one plant among those examined during 2006 was found infected with RTSV, and RTBV was not detected in any of the plants. Thus, the yellowing syndrome was likely associated with the infection by RGSV or the mixed infection by RGSV and RRSV.

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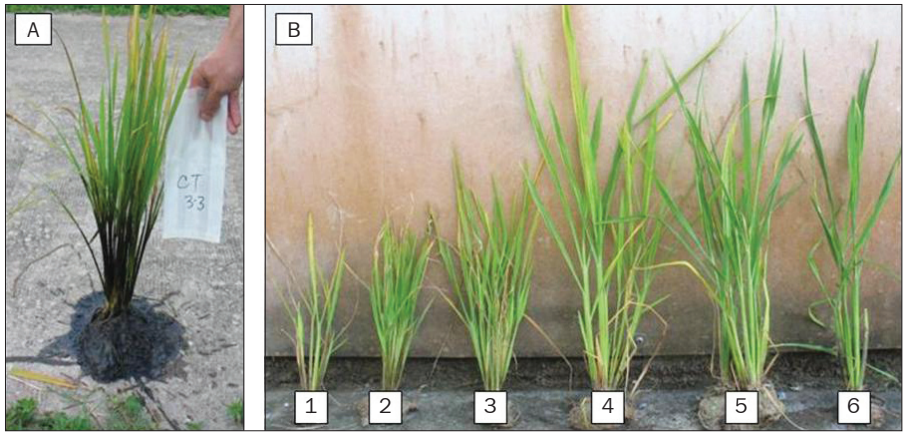


**Fig. 3. Various symptoms in rice plants caused by mixed infection with RGSV and RRSV. (A) Characteristic symptoms of yellowing syndrome showing leaf yellowing and bronzing, and profuse tillering. (B) Various symptoms caused by RGSV and RRSV observed in a single field in southern Vietnam, October 2006. See text for the description of symptoms.**

Types and severity of disease symptoms varied among plants mix-infected with RGSV and RRSV (Fig. 3). Some plants showed only yellowing, bronzing, and stunting but no profuse tillering (plant 1 of Fig. 3), while other plants showed profuse tillering typical of grassy stunt (plants 2 and 3 of Fig. 3). There were also plants exhibiting yellowing and serrated and twisted leaves without profuse tillering (plants 5 and 6 of Fig. 3). The variation in symptoms might be caused by the difference in the timing and sequence of infection with RGSV and RRSV in the field.

RGSV and RRSV were also detected from 49% and 74% of BPH collected at various sites of the Mekong Delta in 2006 (Table 1). The proportion of BPH from which both viruses were detected was 8%. The proportions of BPH carrying one of or both RGSV and RRSV varied depending on the time and the site of collection. During the surveys in 28 provinces of southern Vietnam in 2007, the proportion of RGSV-carrying BPH was higher than 50% in 8 provinces, and the proportion of BPH carrying both RGSV and RRSV was higher than 30% in 9 provinces.

The incidences similar to the yellowing syndrome observed in the Mekong Delta of Vietnam were also reported in central and northern regions of Vietnam and areas of Cambodia adjacent to Vietnam. In 2007, surveys for the distribution of rice viruses were conducted in those regions. Plants with leaf yellowing but not those with profuse tillering and leaf bronzing were also observed in central and northern regions of Vietnam. The plants showing yellowing were found infected with RRSV. No RGSV, RTSV, or RTBV was detected in the plants collected from the regions. Meanwhile, plants with leaf yellowing and bronzing were often observed in the areas of Cambodia adjacent to Vietnam. The plants collected in Cambodia were found infected with RGSV.

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**Table 1. Detection of RRSV and RGSV in rice leaf and BPH samples collected from areas in southern Vietnam from January 2005 to October 2006.**

| Time of sampling | Site of sampling | Type of sample | Number of samples | Percentage of viruses detected in samples | | |
|---|---|---|---|---|---|---|
| | | | | RRSV | RGSV | RRSV + RGSV |
| Jan 2005 | Can Tho | Rice leaves | 37 | 0 | 19 | 0 |
| | An Giang | Rice leaves | 15 | 0 | 0 | 0 |
| Mar 2006 | An Giang | Rice leaves | 18 | 50 | 94 | 50 |
| | Tien Giang | Rice leaves | 12 | 83 | 83 | 66 |
| Aug 2006 | Ho Chi Minh | Rice leaves | 119 | 39 | 63 | 35 |
| | Long An | Rice leaves | 82 | 42 | 64 | 32 |
| | Tien Giang | Rice leaves | 20 | 65 | 90 | 60 |
| | Binh Phuoc | Rice leaves | 204 | 59 | 84 | 54 |
| | Tra Vinh | Rice leaves | 5 | 20 | 100 | 20 |
| | Dong Nai | Rice leaves | 1 | 100 | 100 | 100 |
| | Various sites | BPH | 35 | 41 | 66 | 8 |
| Oct 2006 | Tien Giang | Rice leaves | 90 | 18 | 94 | 18 |

## Concluding remarks

Viruses transmitted by BPH have been an occasional but persistent problem for rice production in tropical Asia. Management of BPH populations should reduce the risk of damage by BPH-transmitted viruses in fields. However, the recent outbreaks of BPH-transmitted virus diseases also indicate the necessity for control of the viruses to minimize damage in case of BPH outbreaks. Eradication of virus sources in fields and the deployment of virus-resistant varieties are effective in preventing further spread of virus diseases. Regular monitoring of viruses in fields by economical diagnostic tools would facilitate the eradication and escape procedures for virus diseases. The effectual range of virus resistance in plants is often limited. Preliminary analysis of virus genomes indicated that the isolates of RGSV in the Mekong Delta appeared to be divergent from the isolates previously reported. Although it became evident that RGSV and RRSV transmitted by BPH are associated with the devastating disease in the Mekong Delta, the possible involvement of other viral agents in the disease cannot be eliminated. Thus, understanding of biological characteristics of host-vector-virus interrelationships is crucial for the development of durable resistance to viruses, and effective management of virus diseases spread by BPH.

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## Notes

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