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Transmission characteristics of Southern rice black-streaked dwarf virus by rice planthoppers

Lingling Pu, Guohua Xie, Chunyan Ji, Bing Ling, Maoxin Zhang, Donglin Xu, Guohui Zhou*

College of Natural Resources and Environment, South China Agricultural University, Wushan, Tianhe District, Guangzhou, Guangdong 510642, China

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ABSTRACT

Southern rice black-streaked dwarf virus (SRBSDV) is a recently proposed distinct species in the genus *Fijivirus*, family Reoviridae. During the past decade, SRBSDV has spread throughout southern China and northern Vietnam, and has become one of the greatest threats to rice production in these regions. We evaluated three common planthopper species affecting rice: white-backed planthopper (WBPH, *Sogatella furcifera*), brown planthopper (BPH, *Nilaparvata lugens*) and small brown planthopper (SBPH, *Laodelphax striatellus*) to determine their virus transmission abilities. It was confirmed that WBPH was an efficient persistent-transmitting vector for SRBSDV. Neither BPH nor SBPH were viral vectors, although a small proportion (3.7%) of tested SBPH acquired the virus from diseased rice. We characterized the virus transmission properties of WBPH. 83% of the tested insects fed on virus-infected rice plants became viruliferous. The minimum virus acquisition and inoculation access periods were 5 and 30 min, respectively, for both WBPH nymphs and adults. The circulative transmission periods of the virus in WBPH ranged from 6 to 14 days, and most viruliferous individuals transmitted the virus in intermittent periods ranging from 2 to 6 days. A single individual of WBPH could infect 8–25 rice plants with the virus in a 5-day period. WBPH could transmit SRBSDV from rice to maize seedlings, but it was barely able to acquire the virus from infected maize. These results improve our understanding of the epidemiology of SRBSDV, and will be useful for development of disease control strategies.

1. Introduction

A new rice dwarf disease caused by Southern rice black-streaked dwarf virus (SRBSDV), a recently proposed novel species in the genus *Fijivirus*, family Reoviridae, was first discovered in Guangdong Province, China, in 2001 (Zhang et al., 2008; Zhou et al., 2008; Wang et al., 2010a). In the past decade, the disease has rapidly spread throughout southern China and northern Vietnam, and SRBSDV has become one of the most important rice pathogens in these regions (Guo et al., 2010; Hoang et al., 2011). The virus infects a group of Poaceae species including rice, maize, Chinese sorghum (*Coix lacryma-jobi*), *Echinochloa crusgalli*, and *Pennisetum flaccidum* (Zhou et al., 2008). In 2009, it was estimated that up to 315,000 ha of rice growing in nine Chinese provinces were infected, and more than 6500 ha of rice crops were completely destroyed. In 2010, SRBSDV infection had spread to 13 provinces in southern China, 28 in northern Vietnam and one in central Vietnam, with 1,601,600 ha of rice infected (Guo et al., 2010). Recently, the virus has been detected in Japan and Korea (Heong K.L., International Rice Research Institute, personal communication). According to our previous study (Zhou et al., 2008), SRBSDV can be transmitted efficiently by white-backed planthopper (WBPH, *Sogatella furcifera*). The small brown planthopper (SBPH, *Laodelphax striatellus*) transmits SRBSDV only under experimental conditions with a relatively low efficiency. However, few studies have been conducted on the transmission properties of the virus by rice planthoppers. A better understanding of the vector–SRBSDV–host interaction system is important for control of the disease.

The genus *Fijivirus* includes eight recognized species: *Fiji disease virus* (FDV), *Oat sterile dwarf virus* (OSDV), *Garlic dwarf virus* (GDV), *Nilaparvata lugens reovirus* (NLRV), *Mal de Rio Cuarto virus* (MRCV), *Pangola stunt virus* (PaSV), *Maize rough dwarf virus* (MRDV), and *Rice black-streaked dwarf virus* (RBSDV). Except for GDV, whose vector is still unknown, all fijiviruses propagate *in vivo* in their hopper vectors in a persistent manner (Milne et al., 2005). These viruses move from the gut lumen to hemolymph or other organs in their vectors, and finally enter the salivary glands, from which they are inoculated into plant hosts by the vectors during feeding (Gray and Banerjee, 1999). The planthopper vectors of fijiviruses belong to several genera in the Delphacidae family: the genus *Perkinsiella* for FDV, *Javesella* for OSDV, *Delphacodes* for MRCV, *Laodelphax* for

* Corresponding author. Tel.: +86 20 85280306.
E-mail address: ghzhou@scau.edu.cn (G. Zhou).

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RBSDV and MRDV and *Sogatella* for PaSV. Under experimental conditions, fijiviruses can be transmitted by some other planthoppers at low efficiency (Milne et al., 2005). NLRV propagates in brown planthopper (BPH, *Nilaparvata lugens*) but not in rice, the only host plant of BPH, and only NLRV among the fijiviruses can be transmitted via eggs (Nakashima and Noda, 1995). Previous data have revealed that SRBSDV is transmitted by WBPH at a high rate and by SBPH at a relatively low rate. The virus does not appear to be transmitted by BPH or seeds (Zhou et al., 2008; Wang et al., 2010b).

In this study, we investigated the transmission of SRBSDV by three potential vectors, WBPH, BPH and SBPH under artificial conditions. We determined the transmission characteristics of SRBSDV by WBPH in rice and maize. The results improve our understanding of the epidemiology of SRBSDV, and will ultimately be useful for development of disease control strategies.

2. Materials and methods

2.1. Tested host plants and planthopper species

The seeds of rice (cultivar "Qiuyou 998") and maize (cultivar "super sweet") were purchased from the Guangdong Academy of Agricultural Sciences, China, and sown in pots. The plants were maintained in insect-proof cages under greenhouse conditions at 20–28 °C. Non-viruliferous individuals of WBPH and BPH were collected from rice fields in Guangzhou, Guangdong Province, China, and SBPH was kindly provided by Dr. Yijun Zhou (Jiangsu Academy of Agricultural Sciences, Nanjing, Jiangsu Province, China). The three species of planthoppers were separately maintained in insect-proof cages at 26–28 °C and relative humidity of 60–75%. Adult male or female hoppers were transferred to new cages with healthy rice seedlings when the plants they fed came to late growth stage, and the insects were allowed to propagate for 2–3 generations before being used.

2.2. Virus resource

SRBSDV was obtained from infected rice field samples in Guangzhou, Guangdong Province, China, and confirmed by reverse transcription polymerase chain reaction (RT-PCR). The virus was transmitted by WBPH to, and maintained on, rice plants (cultivar "Qiuyou 998") grown in insect-proof greenhouses.

2.3. RT-PCR detection of SRBSDV

We used a one-step dual RT-PCR method as described by Wang et al. (2012) to detect SRBSDV in plants or planthoppers. Briefly, total RNA prepared from leaf tissue or an individual planthopper was amplified by RT-PCR using One Step RNA PCR kit (AMV) (TaKaRa Biotech. Co. Ltd, Dalian, China) following the manufacturer's protocol. We used two sets of primers S5-F1/S5-R2, (5′-ttacaactggagaagcattaacacg-3′/5′-atgaggtattgcgtaactgagcc-3′) and S10-oF/S10-oR, (5′-cgcgtcatctcaaactacag-3′/5′-tttgtcagcatctaaagcgc-3′) to produce two expected DNA fragments of 819 bp and 682 bp from SRBSDV-positive samples.

2.4. Virus acquisition ability of three rice planthopper species

WBPH, BPH and SBPH were allowed to feed on diseased rice plants during the tillering period in the greenhouse for one month. Then, the second-generation nymphs at late-stage and adults were collected from the plants and the presence of the virus in each individual insect was detected by RT-PCR. The rates of viruliferous planthoppers were calculated from the PCR results.

2.5. Acquisition access period (AAP) of WBPH

The 3rd–4th instar WBPH nymphs were collected from infected rice plants and transferred to virus-free rice seedlings at the 2–3-leaf stage (two or three insects per plant) in glass culture tubes. The insects were killed 24 h later. RT-PCR detection was conducted at 10 days post inoculation (dpi), and the seedlings positive with the virus were used for the following tests.

The non-viruliferous 3rd–4th instar WBPH nymphs starved for 1–2 h were transferred to the SRBSDV-infected rice seedlings. The nymphs fed for 5, 10, or 30 min or 3 or 24 h were respectively transferred to virus-free rice seedlings at the 3-leaf stage in glass culture tubes (one insect per tube). The seedlings inoculated with nymphs were maintained for 15 days at 27 °C, relative humidity of 60–75%, under a 16-h light/8-h dark photoperiod.

The insects still alive at 15 dpi were collected and tested for the presence of the virus by RT-PCR. The AAP of WBPH was calculated from the RT-PCR results.

2.6. Inoculation access period (IAP) of WBPH

The second-generation WBPH nymphs of 3rd–4th instar or adults propagated on infected rice plants were collected and starved for 2 h, then transferred to the virus-free rice seedlings at 2–3-leaf stage. The insects were allowed to feed on the seedlings for 5, 10 and 30 min and 3, 12 and 24 h respectively, and individually detected by RT-PCR to confirm whether they were viruliferous or not. The seedlings inoculated with confirmed viruliferous WBPH were grown for 15 days under the conditions described above. The IAP of WBPH was determined from the results of RT-PCR detection of the tested plants at 15 dpi.

2.7. Circulative transmission period of SRBSDV in WBPH

Thirty nymphs at the 3rd–4th instar stage were fed on infected rice plants for 24 h and transferred to virus-free rice seedlings in glass culture tubes (one plant per tube). The tested plants were replaced by healthy ones every two days until the insects died. All tested plants were grown in an insect-proof greenhouse and RT-PCR was conducted 15 days later. The circulative transmission period of SRBSDV in WBPH was calculated from the RT-PCR results.

2.8. Transmission rate of SRBSDV by individual WBPH

Rice seedlings (at the 2-leaf stage) cultivated from seeds sown in a 2-L glass beaker (60 seeds per beaker) were inoculated with a second-generation individual WBPH adult propagated on infected rice plants. The test was conducted more than 30 replicates. The insects were collected and detected by RT-PCR at 5 dpi. The plants inoculated with confirmed viruliferous WBPH were subjected to RT-PCR detection 10 days later. The transmission rate of SRBSDV by WBPH was calculated according to the RT-PCR results from the tested plants.

2.9. Ability of WBPH to transmit SRBSDV to maize

WBPH nymphs at 3rd–4th instar stage propagated on infected rice plants were inoculated onto "Super sweet 268" maize seedlings at 2–3 leaf stage (two or three insects per seedling). The insects were killed 48 h after inoculation. Their ability to transmit SRBSDV was evaluated by RT-PCR detection of the tested plants at 10–15 dpi.

2.10. Ability of WBPH to acquire SRBSDV from maize

Non-viruliferous WBPH nymphs at late growth stage or adults were fed on SRBSDV-infected maize plants at the 5–6 leaf stage for 48 h and then on healthy rice plants for 10 days. RT-PCR detection was conducted to determine the rate of viruliferous WBPH.

2.11. Ability of SBPH to transmit SRBSDV

RT-PCR detection was conducted on 600 second-generation SBPH nymphs at the 3rd–4th instar stage that had been propagated on SRBSDV-infected rice plants. The virus acquisition rate was calculated according to the RT-PCR results. Then 1,200 SRBSDV-fed individuals of SBPH (equally divided into 12 groups) were inoculated onto healthy rice seedlings at the 2–3-leaf stage (10 seedlings per group) and RT-PCR detection was carried out to detect the virus in the insects and the inoculated plants at 15 dpi. The virus inoculation rate of SBPH was calculated according to the RT-PCR detection results.

3. Results

3.1. Virus acquisition ability of three rice planthopper species

During April to July, 2010 and April to June, 2011, 600 individual nymphs (100 in each of six experiments) of BPH, WBPH and SBPH at late growth stage were collected from the second-generation populations raised on SRBSDV-infected rice plants at the tillering stage. No individuals of BPH was found positive with SRBSDV in RT-PCR detection, whereas 83% (498/600) of WBPH and 3.7% (22/600) of SBPH become viruliferous. In the six respective experiments, with 100 inscects in each, the number of individuals tested as positive with the virus were 76, 92, 78, 82, 86 and 84 for WBPH, and 5, 6, 0, 5, 4 and 2 for SBPH. Our results indicated that BPH cannot acquire the virus, and that WBPH has a greater frequency of virus acquisition from SRBSDV-infected rice plants than SBPH does.

3.2. AAP and SRBSDV acquisition efficiency of WBPH

One or two WBPH individuals obtained SRBSDV after 5 min virus feeding and a few of them (8.3% nymphs and 7.1% adults) became viruliferous after 3 h. The virus-positive rates of nymphs and adults increased to 50.0% and 25.9% respectively after 24 h virus feeding (Table 1).

3.3. IAP and SRBSDV inoculation efficiency of WBPH

Neither the nymphs nor adults of virus-fed WBPH could transmit SRBSDV to the tested plants within 10 min, but they successfully established infection in 11.5 and 13.3% of tested plants, respectively, after 30 min feeding. Infection rates of the tested plants were stable as 26.0–26.2% and 22.4–22.6% when the inoculation period varied between 3 and 12 h, and approximately doubled with an inoculation period of 24 h (Table 2).

Table 1
Acquisition access period and Southern rice black-streaked dwarf virus-positive rate of white-backed planthopper (WBPH).

Feeding time	Nymph			Adult		
	Total	Viruliferous	Positive rate (%)	Total	Viruliferous	Positive rate (%)
5 min	55	2	3.8	24	1	4.2
10 min	76	3	3.9	58	2	3.4
30 min	50	2	4	72	3	4.2
3 h	60	5	8.3	42	3	7.1
24 h	34	17	50	54	14	25.9

3.4. Circulative transmission period of SRBSDV in WBPH and intermittent transmission

Of the 30 tested insects, 17 were viruliferous as detected by RT-PCR. Incubation of the virus in these 17 vector individuals was examined by virus transmission assays (Table 3). The maximum circulative transmission period of SRBSDV in WBPH was 14 days (in insect individual no. 17) and the minimum period was 6 days (in insect individual no. 4). For most individuals, the circulative transmission period ranged from 8 to 12 days. The circulative transmission period significantly differed among individuals. Some of the tested individuals (nos. 4, 5, 10 and 11) could continuously transmit SRBSDV throughout their lifespan, but most of them (nos. 6–9, 12, 13 and 15–17) intermittently transmitted the virus at intervals of 2–6 days. Three tested individuals (nos. 1–3) could not transmit the virus at any time during their lifespan.

3.5. Transmission efficiency of SRBSDV by individual WBPH

We tested 10 female and 12 male viruliferous WBPH adults. Individuals could infect 8–25 plants within five days, with an average of 17.6 plants per female and 15.3 plants per male WBPH (Table 4).

3.6. Virus inoculation and acquisition ability of WBPH on maize

In the experiments to test SRBSDV transmission from rice to maize, 79.2% (42/53) of maize seedlings at 2–3 leaf stage became SRBSDV-infected via the inoculation of WPBH nymphs within 48 h. Whereas, in the experiments to test SRBSDV acquisition from maize, all of the tested 120 WBPH nymphs died and 75 WBPH adults were alive after 48 h of feeding on diseased maize seedlings at the 5–6 leaf stage. These 75 adults were allowed to feed for 7 days on healthy rice plants, and 61 of them were still alive at the end of the 7-day period. RT-PCR detection showed that only 3.3% (2/61) of them were viruliferous. These results indicate that WBPH can transmit SRBSDV from rice to maize, but only a small percentage of them acquire the virus from infected maize.

3.7. Transmissibility of SRBSDV by SBPH

Only 3.7% (22/600) of the second-generation SBPH nymphs propagated on diseased rice plants were virus-positive, as determined by RT-PCR. In the other test, there were 2–5 viruliferous insects in each of the 12 groups; however, none of the inoculated rice plants in any group became infected. This indicates that a few SBPH individuals can acquire SRBSDV from diseased rice, but they cannot transmit the virus to healthy plants.

4. Discussion and conclusions

SRBSDV is a novel virus species in the genus *Fijivirus*, first recognized in 2008 (Zhang et al., 2008; Zhou et al., 2008). The biological properties of this virus are poorly understood at present, although its entire genomic sequence has been determined (Wang et al., 2010a). The characteristics of its transmission by planthoppers, as revealed in this study, will increase our understanding of the disease cycle, and will ultimately be useful for development of disease control strategies. We confirmed that SRBSDV was transmitted by WBPH in a persistent manner among rice plants, and from diseased rice to maize seedlings. However, only a small percentage of WBPH individuals acquired the virus from infected maize. Neither BPH nor SBPH was transmission vector of SRBSDV, although a few SBPH individuals were able to acquire the virus from infected rice.

Table 2
Inoculation access period of white-backed planthopper (WBPH) and Southern rice black-streaked dwarf virus transmission rate.

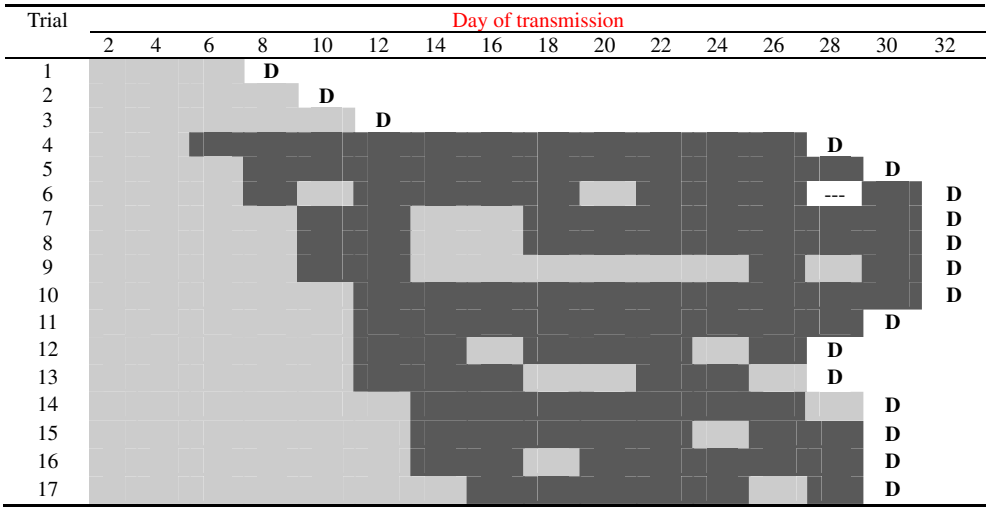
Feeding time	Nymph			Adult		
	No. of rice seedlings tested	No. of rice seedlings infected	Transmission rate (%)	No. of rice seedlings tested	No. of rice seedlings infected	Transmission rate (%)
5 min	57	0	0	25	0	0
10 min	46	0	0	54	0	0
30 min	52	6	11.5	60	8	13.3
3 h	50	13	26.0	53	12	22.6
12 h	42	11	26.2	67	15	22.4
24 h	35	19	54.3	42	18	42.9

So far, SRBSDV is the only rice virus species that has been shown to be transmitted by WBPH. There are several other rice viruses that are spread by the vectors BPH and SBPH, e.g., BPH transmits *Rice ragged stunt virus* (RRSV) (Milne, 1982) and *Rice grassy stunt virus* (RGSV) (Hibino, 1986), and SBPH transmits *Rice black-streaked dwarf virus* (RBSDV) (Shikata, 1974) and *Rice stripe virus* (RSV) (Toriyama, 1983). However, SRBSDV may be the most destructive and widely distributed virus infecting rice at present. The distribution and occurrence of a virus largely depends on its vector. For instance, SBPH cannot survive in hot areas and exists mainly in northeastern Asia (Dupo and Barrion, 2009). That limits the distribution of RBSDV and RSV in Japan, South Korea, and China (Shikata, 1974; Toriyama, 1983). Both BPH and WBPH are large-scale migration pests. In Asia, they survive perennially in the tropical Southwest Peninsula, and in every spring their migration expansively spans from northern Vietnam to China, Korea and Japan (Otuka, 2009). However, BPH migration occurs in the late period of rice growth stage (Catingdig et al., 2009), when the plants become resistant to virus infection. Therefore, RGSV and RRSV mainly cause rice damage in southern Asia where BPH is present year-round. In contrast, WBPH migration takes place in the early period of rice growth stage (Catingdig et al., 2009), when the plants are vulnerable to virus infection. Therefore, SRBSDV theoretically might spread and infect rice over most part of Asia. Furthermore, WBPH has active mobility and the nymphs and adults constantly move among rice plants. Consequently, one viruliferous hopper can transmit the virus to infect a large number of plants, i.e., 15.3–17.6 plants in five days (Table 4) or 48.3 plants during its whole lifespan (Cao et al., 2011). Despite the fact that the disease has only been reported in Vietnam, China and Japan so far, great attention should be paid to the potential that this disease could cause threats to rice production throughout Asia.

The transmission characteristics of SRBSDV in rice plants by WBPH were determined in detail in this study. The minimum AAP from diseased rice was 5 min, and the frequency of viruliferous insects increased with longer access time, reaching 50.0% for the nymph population and 25.9% for the adult population after 24 h virus feeding (Table 1). The circulative period averaged 10 days (range 6–14 days) in these conditions. After this time, a few insects retained their ability to transmit the virus for the rest of their life, but in most individuals, the transmission was intermittent over 2–6 days (Table 3). The minimum IAP was 30 min, and the transmission rate increased with feeding time, reaching 54.3% for nymphs and 42.9% for adults after 24 h (Table 2). Within five days, a single hopper was able to transmit the virus to an average of 16.3 rice plants (range 8–25 plants) (Table 4). Our results are consistent with those of Cao et al. (2011), who reported that WBPH transmits SRBSDV with the minimum AAP of 2–8 min, has a circulative period of 3–11 d, and has a minimum IAP of 4–7 min. The slight differences between our results and theirs might due to the different rice varieties and/or test conditions used in experiments.

Our results are consistent with those of Zhou et al. (2008) and Hoang et al. (2011), revealing that WBPH, but not BPH, efficiently transmitted SRBSDV. Zhou et al. (2008) reported that SBPH was a low-efficiency transmission vector, however, we found that it could not transmit the virus under our experimental conditions.

Table 3
Circulative transmission period of Southern rice black-streaked dwarf virus (SRBSDV) in white-backed planthopper(WBPH).



Light grey: unable to transmit SRBSDV; dark grey: able to transmit SRBSDV; D: tested insect died; --: tested rice died

Table 4
Southern rice black-streaked dwarf virus transmission ability of single white-backed planthoppers (WBPH) to infect rice seedlings.

Trial	Viruliferous WBPH male adult		Viruliferous WBPH female adult	
	No. of rice seedlings tested	No. of rice seedlings infected	No. of rice seedlings tested	No. of rice seedlings infected
1	57	11	57	10
2	55	8	55	21
3	56	10	57	8
4	53	20	56	19
5	55	19	54	21
6	57	21	58	9
7	57	8	56	20
8	56	9	57	20
9	55	20	58	23
10	57	25	55	25
11	56	17		
12	57	15		
Mean		27.32%		31.40%

Zhou et al. (2008) tested only 12 SBPH nymphs, and the possibility of contamination from viruliferous WBPH and/or its eggs could not be excluded. In this study, we obtained similar results for the transmission abilities of WBPH, but we concluded that SBPH could not transmit the virus, though it could acquire SRBSDV at a low efficiency from diseased plants. Our results are reliable because of the large number of insects tested and the thorough removal of potential contamination by eliminating all WBPH before the tests.

Some studies have indicated that the gut membrane and accessory salivary gland membrane are two barriers against the entry of plant viruses into the insect body and achieving transmission. This is the main factor accounting for the vector-specificity of circulative-transmission viruses (Gray and Gildow, 2003). Our results suggest that SRBSDV penetrates the gut membrane but not the accessory salivary gland membrane of SBPH. Recently, Wei et al. (Fujian Agriculture and Forestry University, Fuzhou, Fujian Province, China, personal communication) found that SRBSDV can propagate in cultured primary cells of SBPH. Further studies on SRBSDV–SBPH interactions may help to reveal the mechanism of biological barriers in the insects that are related to transmission specificity.

Although WBPH can efficiently acquire SRBSDV from diseased rice plants, some individuals remained non-viruliferous after virus feeding in each of the six experiments (Table 1). This was probably because of the growth conditions used in these experiments, the disease stage and virus titer of the virus-resource plants, and the age and feeding behaviors of the vectors. It is noteworthy that the genetic background of the vector and the microecological system of individual vectors may also have had an impact. Different SBPH lineages with various abilities to acquire RSV can be generated via hybrid breeding (Kisimoto, 1967; Qu et al., 2002), and symbiotic bacteriocins play an important role in virus acquisition and transmission of aphids and *Bemisia tabaci* (van den Heuvel et al., 1994; Morin et al., 1999). However, further studies should be conducted to identify the factors that prevent some WBPH individuals from acquiring SRBSDV.

All the described species in the genus *Fijivirus* have strong vector specificity and are transmitted only by some planthopper species/genera of the family Delphacidae (Milne et al., 2005). However, some viruses can be transmitted by diverse planthoppers. For example, RBSDV can be transmitted by SBPH with high efficiency, meanwhile by *Unkanodes sapporona* and *Ribautodelphax albifascia* with low efficiency via an uncertain transmission mechanism (Chen and Zhang, 2005). Although it was confirmed that BPH and SBPH cannot transmit SRBSDV, it remains unknown if there are other natural vectors for the virus. Many planthoppers of the family Delphacidae can be found in rice fields (including on the weeds) and the genus *Sogatella* has more than 20 species/subspecies; at least five of which have been reported in China (Dupo and Barrion, 2009). Evaluation of SRBSDV transmissibility by these insects will benefit control of the disease caused by this virus.

The host range of vectors and their feeding preferences determine the natural host range of plant viruses and the functional roles of the hosts in the disease cycle. Although WBPH has a wide host range, its optimal host is rice. It survives for shorter periods or sometimes even dies before a generation is completed on other hosts (Shen et al., 2003). WBPH does not prefer to feed on maize, especially on the fully grown plants, and thus hardly acquires SRBSDV from diseased maize, though it transmits the virus to infect maize seedlings at very early growth stage. It has been suggested that maize does not play a crucial role in the infection cycle of SRBSDV, which is similar to the situation of RBSDV transmission by SBPH (Chen and Zhang, 2005).

Similar to other viruses that are transmitted by planthoppers or leafhoppers (Hibino, 1996), SRBSDV needs a 2–6-day circulation period during its intermittent transmission. This property may be used to design a disease control strategy. However, further studies are required to clarify the behaviors of this virus in the vector and the mechanisms of its intermittent transmission.

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