Dynamics of *Southern rice black-streaked dwarf virus* in Rice and Implication for Virus Acquisition

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Accepted for publication 28 December 2012.

ABSTRACT

Matsukura, K., Towata, T., Sakai, J., Onuki, M., Okuda, M., and Matsumura, M. 2013. Dynamics of *Southern rice black-streaked dwarf virus* in rice and implication for virus acquisition. *Phytopathology* 103:509-512.

A novel viral disease of rice caused by *Southern rice black-streaked dwarf virus* (SRBSDV) has spread throughout East and Southeast Asia since the mid-2000s. Outbreaks of this viral disease occur yearly in southern parts of Japan concurrently with overseas migration of the planthopper vector *Sogatella furcifera* from southern China during the rainy season (from late June to early July). We examined the dynamics

(changes in titer and localization) of SRBSDV on rice using reverse-transcription real-time polymerase chain reaction and determined the relationship between virus titer in plants and virus acquisition by *S. furcifera*. Under a constant temperature of 27°C, a substantial increase of SRBSDV titer in the leaf sheath together with typical symptoms (stunted growth and twisting of leaf tips) was observed at 20 days after the end of a 7-day exposure of viruliferous *S. furcifera*. Approximately 40% of *S. furcifera* acquired SRBSDV through feeding for 5 days on rice plants that were infected following exposure to viruliferous vectors for 10 to 15 days. These results suggest that rice infected by *S. furcifera* can be a source of SRBSDV before the next generation of *S. furcifera* emerges.

Southern rice black-streaked dwarf virus (SRBSDV) is from a recent outbreak of a fijivirus (family *Reoviridae*) that causes serious stunted growth and twisted leaf tips on rice (*Oryza sativa*) (2,4,22). It was initially discovered in the province of Guangdong, China in 2001, and remained within limited areas of southern China for the first few years. After the mid-2000s, this disease spread throughout an extensive area of southern China (22) and large areas of North and Central Vietnam (2,4). In August 2010, SRBSDV was detected in forage rice in Kyushu, Japan (9). The spread of SRBSDV overseas seemed to be caused by emigration of the white-backed planthopper, *Sogatella furcifera* (9), which is a main vector of the virus (22).

The symptoms of SRBSDV are similar to those of *Rice black-streaked dwarf virus* (RBSDV), a closely related virus species that infects rice, maize (*Zea mays*), wheat (*Triticum aestivum*), and other gramineous plants (3). According to Zhou et al. (22) and Hoang et al. (4), leaves of rice infected with SRBSDV show stunted elongation with twisting of leaf tips, and the leaf becomes dark green. Large numbers of tillers develop on diseased plants at the tillering stage. Unlike RBSDV, no up-growing rootlets are observed on the stem nodes of rice infected with SRBSDV (22), although some researchers have observed this symptom on SRBSDV-infected rice together with black streaks of leaf vein on the leaf sheath (D. V. Thanh, *personal communication*). Maize, sorghum (*Sorghum bicolor*), wild oat (*Avena fatua*), and goosegrass (*Eleusine indica*) are also known host plants of SRBSDV and, like RBSDV, infection by SRBSDV causes serious stunted growth of maize (21,23).

It is likely that the yearly migration of viruliferous *S. furcifera* from China or Vietnam is a main source of SRBSDV in Japan. This virus does not appear to overwinter in Japan, likely because low seasonal temperatures restrict overwinter survival of the main

vector, *S. furcifera* (17), and rice, the main host plant of SRBSDV, is not harvested throughout the winter in most parts of Japan. The overseas migration of *S. furcifera* is usually observed from mid-June to mid-July, when the rice plant is at the planting or early tillering stage in southern parts of Japan. Therefore, viruliferous, immigrant *S. furcifera* can transmit SRBSDV to young rice plants. Transovarial transmission has not been observed for SRBSDV as for RBSDV (3).

SRBSDV infection routes between *S. furcifera* and rice are well reported. Approximately 25% of adults and 50% of nymphs of *S. furcifera* acquire SRBSDV by feeding on diseased rice for 1 day (14), and SRBSDV can be acquired after 5 min of feeding (14). Their inoculation access period is usually 3 days (4,22) but 30 min may be sufficient (14). The circulative transmission period by *S. furcifera* is 6 to 14 days (14). SRBSDV was also shown to be transmitted by the small brown planthopper, *Laodelphax striatellus*, although at a much lower rate than *S. furcifera*; however, this findings were not confirmed (5,14). Limited information is available on SRBSDV dynamics in infected plants and the relationship with virus acquisition.

In this study, we examined SRBSDV localization in rice seedlings infected following *S. furcifera*-mediated transmission and determined the effect of virus titer on virus acquisition by *S. furcifera*.

MATERIALS AND METHODS

Insect and virus. *S. furcifera* planthoppers, originally collected from Koshi, Kumamoto (32.87°N, 130.74°E) on 23 June 2010, were used in this study. The insects were mass-reared on rice seedlings ('Reiho') at 25°C with a photoperiod of 16 h of light and 8 h of darkness, as described in a previous report (10). Early experiments showed that 35 of 40 adult viruliferous males transmitted SRBSDV after 5 days of feeding on rice seedlings whereas only 3 of 20 viruliferous nymphs (third to fifth stage) transmitted SRBSDV under the same condition. Therefore, adult *S. furcifera* were used as vectors in this study.

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<http://dx.doi.org/10.1094/PHYTO-10-12-0261-R>
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The SRBSDV strain used in the present study was originally collected from Amakusa, Kumamoto (32.33°N, 130.12°E) on 6 September 2010. The strain was maintained in the greenhouse according to the following protocol. Young *S. furcifer* nymphs (first or second stage) were released on mature rice plants (late tillering stage) infected with SRBSDV. After ≈2 weeks, the adults emerged and three adult males were transferred to a new young rice plant (at the second- or third-leaf stage). This SRBSDV transmission procedure from mature plants to young rice plants achieved a high infection rate (K. Matsukura, unpublished).

SRBSDV quantification by reverse-transcription real-time quantitative polymerase chain reaction. SRBSDV titer in plants was determined using reverse-transcription real-time quantitative polymerase chain reaction (RT-qPCR). Plant tissue (≈50 mg) was soaked in a mixture of 250 µl of TriPure Isolation Reagent (Roche Diagnostics Co., Ltd., Tokyo) and 50 µl of chloroform and crushed with a Multibeads Shocker (Yasui Kikai Co., Ltd., Osaka, Japan) at 2,000 rpm for 30 s. After centrifuging at $6,500 \times g$ for 10 min, the supernatant was transferred to a new tube and an equal amount of isopropanol was added. After centrifuging at $20,000 \times g$ for 15 min, the precipitate was rinsed with 300 µl of 80% ethanol. After vacuum drying, the precipitate was resuspended in 25 µl of distilled water.

RT-qPCR was conducted with a Lightcycler 480FLM (Roche Diagnostics Co., Ltd.) using TaKaRa Onestep SYBR PrimeScript RT-PCR kit (Takara Bio Co. Ltd., Shiga, Japan). A primer set (forward: 5'-gag cgg agt ctc ctc att ta-3', reverse: 5'-gca acg atg aac ctt tct ct-3') designed in the capsid protein gene of SRBSDV (GenBank accession number HQ916872) was used for specific amplification of SRBSDV. A primer set (forward: 5'-agg aaa tgg aga ctg cca aga c-3', reverse: 5'-tat gaa gga agg ctg gaa gag g-3') designed in the rice actin gene (11) was used as a control for relative quantification. Calibration curves of the two primer sets were constructed with efficiencies of 1.976 and 2.361 for SRBSDV and rice actin, respectively. Using these calibration curves, the titer of SRBSDV relative to the actin gene expression level was determined for each sample.

Thermal conditions were 1 cycle of reverse transcription (42°C for 5 min and 95°C for 10 s), 40 cycles of amplification (95°C for 10 s, 60°C for 10 s, and 74°C for 15 s), 1 cycle of melting curve analysis (95°C for 5 s, 65°C for 1 min, and 97°C, with increment rates of 0.11°C/s), and cooling (40°C for 30 s).

Infection of SRBSDV in rice seedlings. We used rice seedlings at the second-leaf stage to examine SRBSDV transmission by immigrant generation. Rice sprouts ('TN1') were individually transplanted into 200-ml plastic cups filled with soil (Hinokuni-Syodo; Ryoto Hiryo Co., Ltd., Oita, Japan) and cultivated for 7 days at 25°C with a photoperiod of 16 h of light and 8 h of darkness. One male adult viruliferous *S. furcifer* that was kept on SRBSDV-infected rice at the tillering stage for 7 days was released on the rice seedlings. One male adult SRBSDV-free *S. furcifer* was released on the control rice. After a 5-day exposure, all *S. furcifer* planthoppers were removed from rice plants using a sucking tube, and the rice plants were cultivated in the greenhouse at 27°C and natural daylight length (≈14 h of light and 10 h of darkness).

Growth of rice seedlings infected with SRBSDV. Plant height, number of leaves, and development of symptoms of infected ($n = 5$) and mock-treated (control, $n = 4$) rice plants were examined at 0, 5, 10, 15, 20, and 25 days after the 5-day exposure to *S. furcifer*. Twisting of leaf tips was regarded as a symptom characteristic of infection.

SRBSDV localization and changes of titer in rice. SRBSDV titer was quantified in discrete plant parts at 25 days after the end of exposure to viruliferous planthoppers when SRBSDV titer was expected to be the highest. Roots, meristem, leaf sheath of the first and second leaves, dead (yellow-colored) leaf (the second leaf on which viruliferous *S. furcifer* fed), the oldest green leaf

(the third or fourth leaf), the latest leaf (the seventh leaf), leaves with twisting on the tips (the sixth leaf), and first tillers were collected from diseased plants for SRBSDV titer determination by RT-qPCR ($n = 5$ for each plant tissue).

Viral titer in leaf sheaths and old green leaves of rice plants at 5, 10, 15, 20, and 25 days after the 5-day exposure to *S. furcifer* were examined. Leaf sheaths and old green leaves were collected from plants at each sampling time to determine SRBSDV titer by RT-qPCR ($n = 10$ for each treatment).

Virus acquisition from infected rice by *S. furcifer*. To clarify the relationship between virus titer and acquisition by *S. furcifer*, 10 adults of SRBSDV-free *S. furcifer* were released on diseased rice plants at 0, 5, 10, 15, and 20 days after the 5-day exposure to viruliferous *S. furcifer*. After 5 days of feeding on infected plants, SRBSDV acquisition by adults was examined with RT-qPCR. The RT-qPCR method can detect SRBSDV from *S. furcifer* after 12 h of feeding on infected rice (K. Matsukura, unpublished). Adults with <30 threshold cycle in the RT-qPCR were regarded as viruliferous. We used four or five rice plants (≈40 or 50 adults of SRBSDV-free *S. furcifer*) in each treatment.

Statistical analyses. The effect of SRBSDV infection on plant height was examined by repeated-measures analysis of variance (ANOVA), and plant height between SRBSDV-infected and healthy (control) plants at the same stage was compared by *t* test with Bonferroni correction. Effects of SRBSDV infection and days after infection on leaf stage of rice were examined by analysis of ranked data (15), and leaf stage at the same time period was compared by Mann-Whitney U test with Bonferroni correction. SRBSDV titers were log transformed and compared among plant tissue by ANOVA followed by Tukey's honestly significant difference (HSD) test. Pearson's product-moment correlation analysis after log transformation of data was used to examine the relationship between SRBSDV titer on rice and virus acquisition efficiency by *S. furcifer*.

RESULTS

Effect of SRBSDV on rice plants following planthopper-mediated transmission. Infection with SRBSDV on rice resulted in lower plant height (repeated-measures ANOVA, $F = 89.48$, $df = 1$, $P < 0.001$) and slower plant growth (analysis of ranked data, $\chi^2 = 28.52$, $df = 1$, $P < 0.001$). These differences became significant 20 days after exposure to viruliferous *S. furcifer* (Fig. 1). Twisted leaf tips were also observed 20 days after exposure on the sixth leaf and leaves of the first tiller (Table 1).

Distribution of SRBSDV in rice plant. SRBSDV was detected in all tested plant parts, except the growth point (Fig. 2). The virus titer was significantly different among plant parts (ANOVA, $F = 4.257$, $df = 7$, $P = 0.002$). The leaf sheath contained the highest SRBSDV titer followed by the oldest green leaf (Tukey's HSD test, $\alpha = 0.05$).

SRBSDV titer on the leaf sheath varied significantly with plant age (ANOVA, $F = 17.43$, $df = 4$, $P < 0.001$) but there was a substantial increase at 20 days after exposure to viruliferous planthoppers (Fig. 3) (note that virus titer in rice was determined 5 days after release of SRBSDV-free *S. furcifer*). Although not significant ($F = 0.917$, $df = 4$, $P = 0.463$), a similar trend in changes of SRBSDV titer was observed on old green leaves.

Effect of virus titer on virus acquisition by *S. furcifer*. Virus acquisition efficiency by *S. furcifer* varied with the stages after plant exposure to viruliferous planthoppers (Fig. 3). No viruliferous *S. furcifer* insects were obtained from rice plants at 0 and 5 days after exposure. In all, ≈40% (18 of 50) and more than 80% (32 of 40 at 15 days and 37 of 40 at 20 days) of *S. furcifer* planthoppers acquired SRBSDV at 10 and 15 to 20 days after exposure. Virus titer in leaf sheath (Pearson's product moment correlation, $r = 0.918$, $df = 3$, $P = 0.028$) and old green leaf ($r =$

0.889, df = 3, $P = 0.044$) was positively correlated with virus acquisition efficiency by *S. furcifera*.

DISCUSSION

SRBSDV-infected rice seedlings showed leaf tip twisting and stunted growth at 3 weeks postinfection under constant temperature (27°C) (Table 1; Fig. 1). The twisted leaf tip was observed not only on the main stem but also on the first tiller, which was not fed upon by viruliferous *S. furcifera* (Fig. 2), suggesting that this virus can translocate to other stems (tillers) of the infected plants, as reported for RBSDV-infected rice plants (16). There was a substantial increase in virus titer on the leaf sheath at 20 days after exposure to viruliferous planthoppers (Fig. 3), when symptoms of the disease became apparent (Table 1; Fig. 1). This suggests that accumulation of SRBSDV in the plant correlates with the appearance of symptoms. Further physiological analysis and more detailed quantification of the virus titer are needed to

ascertain the correlation between virus infection and symptom expression.

From the perspective of the unique situation in Japan, where SRBSDV is brought overseas by yearly migrations of *S. furcifera* during the rainy season (6,13), we propose the following model of disease outbreak in rice fields. Viruliferous adults of the immigrant generation feed on young rice plants (2 to 3 weeks after transplanting) and transmit SRBSDV. Based on our experiments at 27°C, which is close to the daily average temperature in July in the plains of southern Japan, infected rice plants show disease symptoms 3 to 4 weeks after infection. Symptomatic rice plants, therefore, would begin to appear in the field in late July.

Our results indicate that rice seedlings infected with SRBSDV can be a virus source at ≈2 weeks after infection at 27°C (Fig. 3). *S. furcifera* takes ≈16 days from egg to adult stage at 28°C (12), and transovarial transmission has not been observed in *S. furcifera*. However, even without a vertical infection, viruliferous offspring can be produced through feeding on diseased rice inoculated by their parents. In Japan, *S. furcifera* density in paddy fields usually becomes higher in the first generation than the immigrant population (19) due to the appearance of brachypterous adults (8). If most nymphs of the first generation become viruliferous, damage of SRBSDV would be severe. Further experiment are needed to clarify the effect of secondary infection on SRBSDV epidemics in fields.

Rouging infected plants is effective to prevent spread of viral diseases (1,7,20). However, as indicated in the present study, rice seedlings may become a source of virus acquisition for *S. furcifera* before symptoms become apparent. Because farmers dis-

Fig. 1. Changes in plant height and leaf position of rice seedlings infected with Southern rice black-streaked dwarf virus (SRBSDV). One adult male viruliferous *Sogatella furcifera* was released on a rice plant at the second-leaf stage for 7 days. After removal of *S. furcifera*, plant height and leaf stage were checked every 5 days. Asterisks indicate a significant difference between diseased and healthy rice at the same time period (t test with Bonferroni correction, $P < 0.05$ for plant height; Mann-Whitney U test with Bonferroni correction, $P < 0.05$ for leaf stage).

Fig. 2. Southern rice black-streaked dwarf virus (SRBSDV) titer in plant tissue of diseased rice. Rice plants at the sixth- or seventh-leaf stage with disease symptoms were used for the analysis. The virus titer was determined as the relative ratio of the SRBSDV capsid protein gene expression to rice actin gene expression. The same letters above each vertical bar, which indicate standard deviation, indicate no significant difference in virus titer between plant tissues (Tukey's honestly significant difference test, $\alpha = 0.05$).

TABLE 1. Appearance of Southern rice black-streaked dwarf virus symptoms (twisted leaf tip) on rice plants exposed to viruliferous *Sogatella furcifera* for 7 days at the second-leaf stage^a

Days ^b	Leaf position						First tiller
	1	2	3	4	5	6	
0	0 (5)	0 (5)	0 (5)	...	...	...	...
5	0 (5)	0 (5)	0 (5)	0 (4)	...	...	...
10	...	0 (5)	0 (5)	0 (5)	0 (5)	...	...
15	...	0 (5)	0 (5)	0 (5)	0 (5)	0 (4)	0 (2)
20	...	...	0 (5)	0 (5)	0 (5)	1 (2)	1 (1)
25	...	...	0 (5)	0 (5)	0 (5)	4 (5)	1 (5)

^a Numbers in each column indicate number of leaves with a twisted leaf tip. Numbers in parenthesis indicate number of observed plants.

^b Days after the end of exposure.

Fig. 3. Effect of Southern rice black-streaked dwarf virus (SRBSDV) titer in rice on virus acquisition efficiency by *Sogatella furcifera*. Ten adult male SRBSDV-free *S. furcifera* were released on each diseased rice plant. At 5 days after release, the rate of virus acquisition by *S. furcifera* and SRBSDV titer in rice plants were examined by reverse-transcription real-time quantitative polymerase chain reaction. Numbers in each circle indicate the number of days between the release of SRBSDV-free *S. furcifera* and the 7 days of feeding by viruliferous *S. furcifera* on the rice plants. The same letters on the upper right of each circle indicate no significant difference in SRBSDV titer on the leaf sheath between treatments. Vertical and horizontal bars on each circle indicate standard deviations of virus acquisition efficiency and SRBSDV titer.

criminate infected rice seedlings only based on the appearance of symptoms, removing infected rice plants from paddy fields may not be effective because the virus may have been spread by the viruliferous first generation of *S. furcifera*. A combination of rouging of infected seedlings and proper chemical control (10) to reduce the first generation of *S. furcifera* population are thought to be management strategies to reduce the impact of SRBSDV. These approaches could be combined with a diagnostic method such as dot-enzyme-linked immunosorbent assay (18) that can detect asymptomatic SRBSDV-infected rice plants to help farmers rapidly determine whether their field is infected.

ACKNOWLEDGMENTS

This study was supported by research and development projects for application in promoting new policy of agriculture, forestry, and fisheries (23034) from the Ministry of Agriculture, Forestry, and Fisheries of Japan. We thank K. Abe and R. Yamada for preparation of insects for our experiments, S. Sanada-Morimura and K. Yoshida for their valuable suggestions, and the reviewers for editorial suggestions.

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