Insect Science

Insect Science (2014) 21, 507–514, DOI 10.1111/1744-7917.12045

ORIGINAL ARTICLE

Influence of rice black streaked dwarf virus on the ecological fitness of non-vector planthopper *Nilaparvata lugens* (Hemiptera: Delphacidae)

Hong-Xing Xu[1], Xiao-Chan He[2], Xu-Song Zheng[1], Ya-Jun Yang[1] and Zhong-Xian Lu[1]

[1]*State Key Laboratory Breeding Base for Zhejiang Sustainable Pest and Disease Control, Institute of Plant Protection and Microbiology, Zhejiang Academy of Agricultural Sciences, Hangzhou,* and [2]*Jinhua Academy of Agricultural Sciences, Jinhua, Zhejiang 321017, China*

Abstract Rice black streak dwarf virus (RBSDV) is transmitted by the small brown planthopper (SBPH), *Laodelphax striatellus* (Fallen). Non-vector rice brown planthopper (BPH), *Nilaparvata lugens* (Stål), shares the same host rice plants with SBPH in paddy fields. The changes in nutritional composition of rice plants infected by RBSDV and the ecological fitness of BPH feeding on the infected plants were studied under both artificial climate chamber and field conditions. Contents of 16 detected amino acids and soluble sugar in RBSDV infected rice plants were higher than those in the healthy ones. On the diseased plants BPH had significantly higher nymphal survival rates, nymphal duration of the males, weight of the female adults, as well as egg hatchability compared to BPH being fed on healthy plants. However, there was no obvious difference in female nymph duration, longevity and fecundity. Defense enzymes (superoxidase dismutase, SOD and catalase, CAT) and detoxifying enzymes (carboxylesterase, CAE and glutathione S-transferase, GST) in BPH adults fed on diseased plants had markedly higher activities. The results indicate rice plants infected by RBSDV improved the ecological fitness of the brown planthopper, a serious pest but not a transmitter of the RBSDV virus.

Key words defense enzymes, detoxifying enzymes, ecological fitness, *Nilaparvata lugens*, non-vector, rice black streaked dwarf virus

Introduction

Interactions between plants, insects and the viruses they transmit have co-evolved (Frossart *et al.*, 2010). It has been verified that there are benefits of virus infected plants to the population growth of vector insects directly or indirectly (Belliure *et al.*, 2005; Whitfield *et al.*, 2005; Colvin *et al.*, 2006; Stout *et al.*, 2006; Jiu *et al.*, 2007; Luan & Liu, 2010). Viruliferous insects have been shown to have greater longevity and higher fecundity and the infected host plants become more suitable to the vector insects (Belliure *et al.*, 2005; Stout *et al.*, 2006; Liu *et al.*, 2010). However, a great negative impact on the development, longevity and fecundity of vector insects has also been reported (Rubinstein & Czosnek, 1997; Jimenez-Martenez *et al.*, 2004; Maris *et al.*, 2004; Sinisterra *et al.*, 2005). These studies have focused on the vectors and not explored the effects of virus-infected plants to non-vectors in the ecosystem.

Rice black streak dwarf virus (RBSDV), a member of the genus *Fijivirus* of the family Reoviridae, is transmitted by the small brown planthopper (SBPH), *Laodelphax striatellus*, in a persistent manner. RBSDV was first

Correspondence: Zhong-Xian Lu, Institute of Plant Protection and Microbiology, Zhejiang Academy of Agricultural Sciences, No. 198 Shiqiao Rd, Hangzhou 310021, China. Tel: +86 571 86404077; fax: +86 571 86404225; email: luzxmh@gmail.com

reported as one of the important diseases in rice in eastern China in the 1960s and in maize in Hebei province in the 1970s (Chen & Zhang, 2005). After a brief period of low incidence, outbreaks re-emerged in the late 1990s causing serious yield losses in eastern China and in maize in northern, northwestern and northeastern China (Chen & Zhang, 2005). RBSDV and SBPH have multiple hosts, including maize, barley and wheat, which act as sources to perpetuate transmission in China (Fang *et al.*, 2001; Bai *et al.*, 2002). The virus can be experimentally transmitted to infect rice, maize, wheat and other cereal and grass hosts (Ji *et al.*, 2011). The typical symptoms on rice plants include pronounced stunting, more tillers, darkening leaves and white waxy or black-streaked swellings along the veins on the underside of the leaf blades, sheaths and culms (Zhang *et al.*, 2001). Recently, RBSDV incidence has shown an increasing trend in Zhejiang, Jiangsu and Shandong provinces of eastern China. More than 267 000 hectares of rice fields in Jiangsu province were affected by this disease in 2008, which emerged as a major threat to rice production (Ji *et al.*, 2009, 2011).

In the rice ecosystem, the rice brown planthopper (BPH), *Nilaparvata lugens*, is monophagous but not a vector of RBSDV in east China (Cheng *et al.*, 2003; Cheng, 2009). BPH become serious pests when natural control mechanisms are destroyed (Heong, 2009). In eastern China, rice is often infected by RBSDV and the changes in the infected rice plants can potentially influence BPH development. To investigate this potential we measured the nutritional components, amino acids and soluble sugar in the diseased rice plants and fitness and activities of defense and detoxifying enzymes of BPH when they were bred on RBSDV diseased plant.

Materials and methods

Rice plants

Hybrid rice variety Jiayou 5, a widely adapted *japonica* variety in Jiaxing, Zhejiang Province, China, was used in the experiments. Seeds were sown at the rate of 15 kg per hectare into a flooded paddy field in Jiaxing, where RBSDV outbreaks occurred in the previous rice season. A total of 90 kg N, 90 kg P and 144 kg K per hectare were applied before seed sowing as base fertilizer. Another 90 kg N per hectare was applied in two splits at rice tillering stage (60%) and reproductive stage (40%). Rice plants were naturally infested by SBPH and plants with typical RBSDV-infection symptoms were marked at the 30th day after sowing. Forty-day-old healthy and RBSDV-infected rice plants were collected and planted into clay pots ($\Phi = 15$ cm) and caged individually with 100-mesh nylon gauze nets. Infected plants were molecularly identified following the reverse transcription polymerase chain reaction (RT-PCR) method developed by Ji *et al.* (2009).

Insects

BPH adults were collected from rice fields at the experimental farm of Zhejiang Academy of Agriculture Sciences in Hangzhou, Zhejiang Province and were maintained on the BPH susceptible variety, TN1 rice plants in the insectary at temperatures $26 \pm 1°C$ and lighting of 12 : 12 L : D.

Determination of amino acid contents of rice plants

RBSDV-infected and healthy rice plants were cut above the soil and inactivated at 110°C for 1 h and then dried to a constant weight at 80°C. One gram of outer leaf sheath was weighed and homogenized with 0.1% HCl solution, and then transferred into a 25 mL volumetric flask and 0.1% HCl solution was added to the volume. After filtration, 2 mL of the supernatant was mixed with 4 mL 0.1% trifluoroacetic acid solution and shaken evenly. Contents of free amino acids and total amino acids were determined with Sykam S433D amino acids analyser (SYKAM GmbH, Munich, Germany) after being purified with a SEP-PAK column (Waters, Milford, MA, USA). Each sample of the healthy and RBSDV-infected rice plants was replicated five times.

Determination of soluble sugar content of rice plants

Colorimetric analysis was performed as described by Wang *et al.* (2010). All plant samples were dried to a constant weight and 0.1 g of each sample put in a test tube with 15 mL distilled water. Then the tubes were heated in a boiling water bath for 20 min and cooled with 100 mL distilled water. One mililiter of the sample extraction was mixed with 5.0 mL anthrone reagent and heated in a boiling water bath again for 10 min. After cooling A260 was determined with a spectrophotometer; at the same time, the standard curve of pure anhydrous glucose was made to calculate the content of soluble sugar in the samples. Each treatment of healthy and RBSDV-infected rice plants was replicated five times.

Development and survival rate of BPH nymphs on RBSDV-infected plants

Forty-five-day-old healthy and RBSDV-infected rice plants were cleaned individually and placed into a test tube ($\Phi = 1.5$ cm, h = 18 cm) with 5 mL Kimura B nutrient solution. Ten newly hatched BPH nymphs were introduced into each test tube, plugged with medically purified cotton and kept at 26 ± 1°C and relative humidity (RH) 75%–90%. The survival nymphs were recorded daily and the newly emerged female adults were weighed within 2 h. Rice plants were replaced regularly and the Kimura B nutrient solution was replenished. Each treatment was replicated 10 times.

Longevity and reproductive capacity of BPH adults on RBSDV-infected plants

Forty-five-day-old healthy and RBSDV-infected rice plants were cleaned with tap water and placed in test tubes ($\Phi = 2.5$ cm, h = 25 cm) with 10 mL Kimura B nutrient solution. One pair of BPH adults was introduced into each test tube, sealed with medically purified cotton and kept at 26 ± 1°C and RH 75%–90%. All test tubes were checked daily and adult survival was recorded. Rice plants and Kimura B nutrient solution were regularly replaced. Newly hatched nymphs were counted and removed daily. When no more nymphs were observed for 3 days, the unhatched eggs were counted by dissection. Egg hatchability was computed based on the data of hatched and un-hatched eggs. Meanwhile, some of the rice plants with BPH eggs laid within 12 h were kept in different test tubes separately for the observation of egg duration. Each treatment of healthy and RBSDV-infected rice plants was replicated 10 times, respectively.

Ecological fitness of BPH on RBSDV-infected plants in paddy field

Healthy and RBSDV-infected rice plants in the field were trimmed by removing old outer leaf sheaths and secondary younger tillers. Plants were caged individually with stainless steel framed nylon gauze net with the openings top and bottom of the cages sealed tightly with soil. After cleaning out all arthropods in cages by the Vac-blower sucking machine, two pairs of newly emerged BPH adults were introduced into each cage, and then the top of cages were closed. After 25 days all planthoppers in cages were collected by a Vac-blower sucking machine. The numbers of nymphs, macropterous and brachypterous adults were recorded, and the female adults were frozen at –70°C for defense enzymes and detoxifying enzymes determination. Each treatment of healthy and RBSDV-infected rice plants was replicated 10 times.

Activities of defensive enzymes and detoxified enzymes of BPH infected with RBSDV

Five brachypterous female adults of BPH were collected from healthy and another five from RBSDV-infected rice plants. The collected BPH were homogenized with 600 μL 0.2 mol/L phosphate buffer solution at pH 7.8 using a glass homogenizer under an ice bath. The homogenate was centrifuged at 4°C with 3 322 × g for 10 min. Then the supernatant fluid was separated for measurement. The activities of defensive enzymes, peroxidase (POD), superoxidase dismutase (SOD) and catalase (CAT) and detoxified enzymes, acetylcholinesterase (AchE), carboxylesterase (CAE) and glutathione S-transferase (GST), were detected using the matched test kit provided by Nanjing Jiancheng Bioengineering Institute (Nanjing Jiancheng Technological Co., Ltd., Nanjing, China). The concentration of protein was measured with Bradford's Coomassie brillilliant blue G-250 method and the calibration curve was performed with bovine serum albumin (BSA). Each treatment of healthy and RBSDV-infected rice plants was replicated five times, respectively.

Data analysis

Values in percentages were transformed into arcsine and square-root values before statistical analyses. Analysis of variance (ANOVA) and multiple comparisons using Turkey's honestly significant difference (HSD) test were done using SPSS 13.0 for windows (SPSS Inc., Chicago, IL, USA).

Results

Amino acids and soluble sugar contents in rice plants

The individual and total amino acid content in RBSDV-infected rice plants were higher than those in healthy rice plants. Methionine (Met) and tyrosine (Tyr) in the infected plants were 44.44% and 42.42% higher, respectively, than the healthy plants (Table 1). The total amino acid content in infected plants was 1.31 times higher than that of the healthy plants.

The content of soluble sugar in RBSDV-infected rice plants was 6%, which was about three times higher than that of healthy plants (1.94%) ($P < 0.01$).

Ecological fitness of BPH under laboratory conditions

The survival rate of nymphs reared on virus-infected plants was significantly higher than those reared on

Table 1 Amino contents in rice plants.

Amino acids	Healthy (%)	Infected by RBSDV (%)	Percentage change (%)
Aspartic acid (Asp)	1.38 ± 0.05	1.96 ± 0.01**	29.59
Threonine (Thr)	0.46 ± 0.04	0.62 ± 0.03**	25.81
Serine (Ser)	0.50 ± 0.01	0.67 ± 0.01**	25.37
Glutamate (Glu)	1.48 ± 0.01	1.78 ± 0.11*	16.85
Proline (Pro)	0.50 ± 0.04	0.68 ± 0.04**	26.47
Glycine (Gly)	0.52 ± 0.03	0.71 ± 0.03*	26.76
Alanine (Ala)	0.67 ± 0.01	0.87 ± 0.10	22.99
Valine (Val)	0.50 ± 0.03	0.66 ± 0.01*	24.24
Methionine (Met)	0.05 ± 0.01	0.09 ± 0.03**	44.44
Isoleucine (Ile)	0.39 ± 0.03	0.51 ± 0.04**	23.53
Leucine (Leu)	0.82 ± 0.01	1.06 ± 0.04**	22.64
Tyrosine (Tyr)	0.19 ± 0.01	0.33 ± 0.04*	42.42
Phenylalanine (Phe)	0.55 ± 0.03	0.68 ± 0.04**	19.12
Histidine (His)	0.34 ± 0.01	0.47 ± 0.03*	27.66
Lysine (Lys)	0.55 ± 0.01	0.72 ± 0.04**	23.61
Arginine (Arg)	0.64 ± 0.01	0.70 ± 0.02	8.57
Total	9.54 ± 0.07	12.51 ± 0.16**	23.74

Data are the means of different replicates with SD. The same as in tables followed.
Significant at *5% and **1% probability levels, respectively.
RBSDV, Rice black streak dwarf virus.

healthy plants (95.58% and 85.86%, $P < 0.05$) and the weight of brachypterous female adults were also higher (1.53 mg and 1.28 mg, $P < 0.01$). The nymphal duration of males from the infested rice plants was also markedly higher than that from the healthy plants (15.30 days and 14.29 days, $P < 0.05$). No obvious difference was recorded in female nymphal period and the adult sex ratio (Table 2). The incubation period of BPH eggs on infected plants was markedly shortened ($P < 0.01$) by 1.47 days; however, the hatchability of BPH eggs laid increased from 56.38% to 89.36% ($P < 0.001$) (Table 3).

Ecological fitness of BPH on RBSDV-infected plants in paddy field

Two pairs of newly hatched BPH adults caged on healthy and RBSDV-infected rice plants in the paddy field produced 62.17 and 91.11 individuals, respectively, after 25 days. The sex ratio of the first generation on diseased plants was about 1 : 1, slightly higher than that from healthy plants (0.93 : 1.00) (Table 4).

Activities of defense enzymes and detoxifying enzymes in BPH

Activities of defense enzymes in BPH from the diseased plants increased significantly; SOD and CAT of BPH on infested plants were 8.91 and 169.21 U/mg protein, about 51.84% and 59.29% higher than those from the healthy plants. The same trend was found on POD; activities of BPH on infected plants and healthy plants were 5.54 and 3.12 U/mg protein, respectively (Fig. 1).

Feeding on diseased plants also increased the activities of detoxifying enzymes in BPH. Activities of carboxylesterase (CAE) and glutathione S-transferase (GST) rose by 47.07% and 11.77%, respectively. Activity of acetylcholinesterase (AchE) in BPH on RBSDV-infested

Table 2 Survival and duration of nymph, weight and sex ratio of adult brown planthopper, *Nilaparvata lugens*.

Rice plant	Nymph survival (%)	Nymph duration (days)		Weight of female adult (mg/♀)	Sex ratio (♀ : ♂)
		♀	♂		
Healthy	85.86 ± 3.27	14.73 ± 0.25	14.29 ± 0.27	1.28 ± 0.04	1.69 : 1
Infested by RBSDV	95.58 ± 2.51	15.26 ± 0.32	15.30 ± 0.39	1.53 ± 0.07	1.34 : 1
P	0.026	0.208	0.047	0.003	0.468

RBSDV, Rice black streak dwarf virus.

Table 3 Adult longevity and fecundity, egg duration and hatchability of brown planthopper, *Nilaparvata lugens*.

Rice plant	Longevity (days)	Fecundity (eggs laid/♀)	Egg duration (days)	Hatchability (%)
Healthy	16.29 ± 1.23	112.86 ± 22.25	10.77 ± 0.36	56.38 ± 5.26
Infested by RBSDV	15.71 ± 0.99	92.14 ± 7.07	9.30 ± 0.19	89.36 ± 3.39
P	0.724	0.403	0.002	<0.001

RBSDV, Rice black streak dwarf virus.

Table 4 Population characters of F1 generation of rice brown planthopper under natural conditions.

Rice plant	Total number of F1	No of nymphs	Proration of nymphs (%)	Proration of brachypterous female adult (%)	Sex ratio (♀ : ♂)
Healthy	62.17 ± 15.29	32.84 ± 5.74	59 ± 9	98 ± 2	0.93 : 1
Infested by RBSDV	91.11 ± 13.07	56.50 ± 8.76	63 ± 5	93 ± 2	1.00 : 1
P	0.178	0.066	0.782	0.124	0.674

RBSDV, Rice black streak dwarf virus.

plants was also higher than that from healthy plants (Fig. 2).

Discussion

Plants infected with viruses may directly and indirectly affect insects feeding on them. These effects may be manifested in ecological and physiological characteristics and population growths (Jiu *et al.*, 2007; He *et al.*, 2011). In our experiments, we found that the amino acids and total soluble sugars in BPH reared on the RBSDV-infected rice plants were higher than those reared on healthy plants. The content of Met and Tyr were markedly higher. The high amino acids and soluble sugars from RBSDV-infected plants might contribute to improving the growth and development of the BPH. Nutritional components, such as soluble sugar, amino acid and C/N ratio, can substantially affect the life-history traits and ecological performance of herbivores (Douglas, 2006). Koyama and Mitsuhashi (1977) reported that amino acid arginine (Arg), glutamine (Glu), lysine (Lys), Tyr and valine (Val) can deter oviposition of *Laodephax striatellus* (SBPH). On the other hand, cysteine (Cys) can stimulate oviposition. Similarly in aphids, high contents of histidine (His), Met, threonine (Thr) and Val in host plants had beneficial effects on the survival and development of aphids (Wilkinson & Douglas, 2003). Koyama (1985) found that the essential amino acids (EAA) and total amino acids (TAA) in susceptible rice varieties were always higher than resistant varieties, indicating that these physiological characteristics in plants favor BPH growth as they absorb and utilize amino acids such as alanine (Ala), Met and Tyr (Ding & Dou, 1990; Xu *et al.*, 2008). Fu *et al.* (2001) also reported that free amino acid pools in the body of BPH were significantly influenced by diets with essential amino acids such as Met, Lys, isoleucine (Ile) and tryptophan (Trp).

The nymph survival rate, male nymph duration, weight of female adult, egg development duration and hatchability of BPH fed on RBSDV-infected rice plants were markedly higher than those reared on healthy plants. In the field, BPH adults caged on RBSDV-infected rice plants produced more individuals after 25 days than those caged on the healthy plants, which indicated that BPH feeding on RBSDV-infected plants were fitter. We also found that fecundity of BPH adults on RBSDV-infected rice plants were lower, although the difference was not significant. RBSDV infections also seem to influence rice plant morphology. The plant height, length of leaf sheath and space between vascular bundles in the leaf sheath of RBSDV-infected rice plants were markedly lower than those of the healthy rice plants (Xu H.X., He X.C., Zheng X.S. Yang Y.J., Lu Z.X., unpublished data). The relationship between oviposition of BPH and changes in morphological characteristics of rice plants are now further investigated.

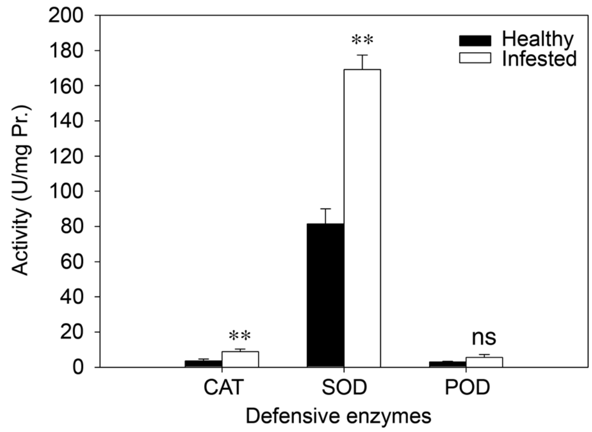

Fig. 1 Activities of defensive enzymes in brown planthopper, *Nilaparvata lugens* on Rice black streak dwarf virus (RBSDV)-infected rice plants. (POD: peroxidase, SOD: superoxidase dismutase and CAT: catalase). Significant at *5% and **1% probability levels, respectively. ns means no significant difference.

Reactive oxygen is produced by organisms to adapt to adverse stresses and injuries. The protective enzyme system composing of SOD, CAT and POD present in insects are mainly to eliminate free radicals (Liu *et al.*, 2006). We found that the activities of SOD and CAT in BPH feeding on RBSDV-infected rice plants were significantly higher, implying that the diseased plants were under stress.

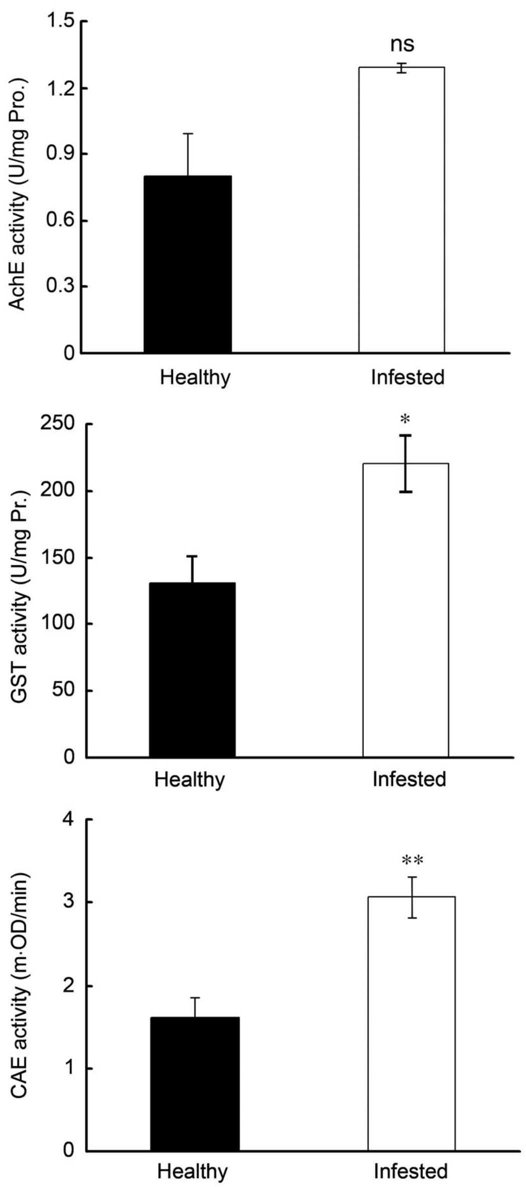

Fig. 2 Activities of detoxifying enzymes in brown planthopper, *Nilaparvata lugens* on Rice black streak dwarf virus (RBSDV)-infected rice plants. (AchE: acetylcholinesterase, CAE: carboxylesterase, and GST: glutathione S-transferase). Significant at *5% and **1% probability levels, respectively. ns means no significant difference.

Although the same trend was found on POD, the difference was not significant. This phenomenon may also be valid for other insects and their closely related environmental stresses. Feeding on RBSDV-infected rice plants may place stress on the insects and the process of ecological fitness. When BPH feed on RBSDV-infected plants, the detoxifying enzyme activities were also increased. This is evident from the marked increase in CAE and GST activities. The AchE activity was also higher, although the difference was not significant. Often insecticides and secondary substances in host plants activate these detoxifying enzymes in insects. Carboxylesterase activity in *Myzus persicae* when fed with tobacco seedlings infected by Cucumber mosaic virus was significantly higher than those fed with healthy tobacco seedlings (Zhang *et al.*, 2007). The activities of defense enzymes (CAT, SOD and POD) and detoxification enzymes (AchE, GST and CAE) were enhanced when white-backed planthopper *Sogatella fucifera* fed on RBSDV-infected rice plants (He *et al.*, 2011). One possible explanation is that the content of secondary metabolites in rice plants infected with RBSDV might have changed and this will need further investigation for confirmation.

The results from a series of experiments on the effects of RBSDV-infected plants on BPH imply that these insects have increased fitness. Since in eastern China field infection of RBSDV is relatively high, the diseased plants may contribute toward BPH increases. Coupled with farmers' routine insecticide uses that destroy essential ecosystem services that keep BPH in check, the increase of BPH fitness can have an effect on the pest's population growth. Thus removing virus-diseased plants from the rice crop should be a normal practice, as it will not only remove the virus source for further transmission but also a source of enhancing BPH population growth.

Acknowledgments

This study was supported by the National Basic Research Program of China (973, Grant No. 2010CB126202), the Agro-Industry R & D Special Fund of China (Grant No. 201003031) and the Zhejiang Provincial Key project on Agricultural Science of China (Grant No. 2011C12022). The authors thank Mr. Qiang Lu for arranging the field experiment and collecting the test rice plants. We are grateful to Dr. K. L. Heong and Professor Heng-Mu Zhang for the revision of the manuscript.

Disclosure

All authors have no any involvement, financial or otherwise, that might potentially bias on his or her work and agree with the submission to *Insect Science*.

References

Bai, F.W., Yan, J., Qu, Z.C., Zhang, H.W., Xu, J., Ye, M.M. and Shen, D.L. (2002) Phylogenetic analysis reveals that a dwarfing disease on different cereal crops in China is due to rice black streaked dwarf virus (RBSDV). *Virus Genes*, 25, 201–206.

Belliure, B., Janssen, A., Maris, P.C., Peters, D. and Sabelis, M.W. (2005) Herbivore arthropods benefit from vectoring plant viruses. *Ecology Letters*, 8, 70–79.

Chen, S.X. and Zhang, Q.Y. (2005) Advance in researches on rice black-streaked dwarf disease and maize rough dwarf disease in China. *Acta Phytophylacica Sinica*, 32, 97–103.

Cheng, J.A. (2009) Rice planthopper problems and relevant causes in China. *Planthoppers:New Threats to the Sustainability of Intensive Rice Production Systems in Asia* (eds. K.L. Heong & B. Hardy), pp. 157–177. International Rice research Institute, Los Banos, Philippines.

Cheng, X.N., Wu, J.C. and Ma, F. (2003) *Brown Planthopper: Occurrence and Control*. China Agriculture Press, Beijing. (in Chinese)

Colvin, J., Omongo, C.A., Govindappa, M.R., Stevenson, P.C., Maruthi, M.N., Gibson, G., Seal, S.E. and Muniyappa, V. (2006) Host-plant via infection effects on arthropod-vector population growth, development and behavior: management and epidemiological implications. *Advances in Virus Research*, 67, 419–452.

Ding, J.H. and Dou, J. (1990) Usage of free amino acid to brown planthopper, *Nilaparvata lugens*. *Chinese Bulletin of Entomology*, 27, 65–67. (in Chinese)

Douglas, A.E. (2006) Phloem-sap feeding by animals: problems and solutions. *Journal of Experimental Botany*, 57, 747–754.

Fang, S., Yu, J., Feng, J., Han, C., Li, D. and Liu, Y. (2001) Identification of rice black-streaked dwarf fijivirus in maize with rough dwarf disease in China. *Archives of Virology*, 146, 167–170.

Froissart, R., Doumayrou, J., Vuillaume, F., Alizon, S. and Michalakis, Y. (2010) The virulence-transmission trade-off in vector-borne plant viruses: a review of (non-)existing studies. *Philosophical Transactions of the Royal Society of London – Series B: Biological Sciences*, 365, 1907–1918.

Fu, Q., Zhang, Z.T., Hu, C., Zhu, Z.W. and Lai, F.X. (2001) Effects of dietary amino acids on free amino acid pools in the body and honeydew of the brown planthopper, *Nilaparvata lugens*. *Chinese Journal of Rice Science*, 15, 298–302. (in Chinese)

He, X.C., Xu, H.X, Zheng, X.S., Yang, Y.J., Gao, G.C., Pan, J.H., Lu, Q. and Lu, Z.X. (2011) Effects of rice black streaked dwarf virus on ecological fitness of non-vector planthopper, *Sogtella fucifera*. *Chinese Journal of Rice Science*, 25, 654–658. (in Chinese)

Heong, K.L. (2009) Are planthopper problems caused by a breakdown in ecosystem services? *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia* (eds. K.L. Heong & B. Hardy), pp. 221–231. International Rice research Institute, Los Banos, the Philippines.

Ji, Y.H., Gao, R.Z., Zhang, Y., Cheng, Z.B., Zhou, T., Fan, Y.J. and Zhou, Y.J. (2011) A simplified method for quick detection of rice black-streaked dwarf virus and southern rice black-streaked dwarf virus. *Chinese Journal of Rice Sciences*, 25, 91–94. (in Chinese)

Ji, Y.H., Ren, C.M., Cheng, Z.B., Zhou, T. and Zhou, Y.J. (2009) Preliminary identification of a newly occurred rice stunt disease in Jiangsu Province. *Jiangsu Journal of Agricultural Sciences*, 25, 1263–1267. (in Chinese)

Jiménez-Martenez, E.S., Bosque-Pérez, N.A., Berger, P.H. and Zemetra, R.S. (2004) Life history of the bird cherry-oat aphid, *Rhopalosiphum padi* (Homoptera: Aphididae), on transgenic and untransformed wheat challenged with barley yellow dwarf virus. *Journal of Economic Entomology*, 97, 203–212.

Jiu, M., Zhou, X.P., Tong, L., Xu, J., Yang, X., Wan, F.H. and Liu, S.S. (2007) Vector-virus mutualism accelerates population increase of an invasive whitefly. *PLoS ONE*, 2, e182.

Koyama, K. (1985) Nutritional physiology of the brown rice planthopper, *Nilaparvata lugens* Stål (Hemiptera: Delphacidae). II: Essential amino acids for nymphal development. *Applied Entomology and Zoology*, 20, 424–430.

Koyama, K. and Mitsuhashi, J. (1977) Effects of amino acids on the oviposition of the smaller brown planthopper, *Laodelphax striatellus* (Hemiptera, Delphacidae). *Entomologica Experimentallis et Applicata*, 22, 156–160.

Liu, J., Li, M., Li, J.M., Huang, C.J., Zhou, X.P., Xu, F.C. and Liu, S.S. (2010) Viral infection of tobacco plants improves performance of *Bemisia tabaci* but more so for an invasive than for an indigenous biotype of the whitefly. *Journal of Zhejiang University- Science B (Biomedicine & Biotechnology)*, 11, 30–40.

Liu, J.L., Yu, J.F. Wu, J.C., Yin, J.L. and Wu, D.H. (2006) Insect reactive oxygen metabolization. *Chinese Bulletion of Entomology*, 43, 752–756.

Luan, J.B. and Liu, S.S. (2010) Roles of vector-virus-plant interactions in biological invasions. *Biodiversity Science*, 18, 598–604. (in Chinese)

Maris, P.C., Joosten, N.N., Goldbach, R.W. and Peters, D. (2004) Tomato spotted wilt virus infection improves host suitability for its vector, *Frankliniella occidentalis*. *Phytopathology*, 94, 706–711.

Rubinstein, G. and Czosnek, H. (1997) Long-term association of tomato yellow leaf curl virus with its whitefly vector *Bemisia tabaci*: effect on the insect transmission capacity, longevity and fecundity. *Journal of General Virology*, 78, 2683–2689.

Sinisterra, X.H., McKenzie, C.L., Hunter, W.B., Powell, C.A. and Shatters, Jr., R.G. (2005) Differential transcriptional activity of plant-pathogenic begomoviruses in their whitefly vector (*Bemibia tabaci*, *Gennadius*: Hemiptera Aleyyrodidae). *Journal of General Virology*, 86, 1525–1532.

Stout, M.J., Thaler, J.S. and Thomma, B.P.H.J. (2006) Plant-mediated interactions between pathogenic microorganisms and herbivorous arthropods. *Annual Review of Entomology*, 51, 663–689.

Wang, B.J., Xu, H.X., Zheng, X.S., Fu, Q. and Lu, Z.X. (2010) Effects of temperature on the resistance of different rice varieties to brown planthopper, *Nilaparvata lugens* (Stål). *Rice Science*, 17, 334–338.

Whitfield, A.E., Ullman, D.E. and German, T.L. (2005) Tospovirus-thrips interaction. *Annual Review of Phytopathology*, 43, 459–489.

Wilkinson, T.L. and Douglas, A.E. (2003) Phloem amino acids and the host plant range of the polyphagous aphid, *Aphis fabae*. *Entomologia Experimentalis et Applicata*, 106, 103–113.

Xu, H.X., Lu, Z.X., Chen, J.M., Zheng, X.S. and Yu, X.P. (2008) Variability of free amino acid content in brown planthopper, *Nilaparvata lugens* (Stål), during adaptation to resistant rice variety IR26. *Chinese Journal of Eco-Agriculture*, 16, 925–928. (in Chinese)

Zhang, H.M., Lei, J.L., Chen, J.P., Lu, Y.P., Chen, S.X. and Xue, Q.Z. (2001) A dwarf disease on rice, wheat and maize from Zhejiang and Hebei is caused by rice black-streaked dwarf virus. *Virologica Sinica*, 16, 246–251.

Zhang, L., Liu, Y.H., and Chen, Y.Z. (2007) Activities of glutathione S-transferases and carboxylesterases in *Myzus periscae* (Suler) fed with CMV-infected tobacco plants. *Tobacco Science and Technology*, 3, 61–64. (in Chinese)

Accepted May 9, 2013