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Variation in planthopper-rice interactions: possible interactions among three species?

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Throughout Asia, extensive programs exist to develop rice varieties with resistance to the brown planthopper, *Nilaparvata lugens*. Although more than 19 genes for *N. lugens* resistance have been identified in rice, *N. lugens* can rapidly adapt to new resistant varieties within several generations in the laboratory and several years in the field. A deeper understanding is needed to determine the factors that underlie variation in planthopper-rice interactions in order to support the widespread efforts to develop and deploy resistant rice varieties. I review host-plant acceptance for *N. lugens* and how it relates to phloem chemistry. I discuss the dependence of *N. lugens* upon yeast-like endosymbionts for the provisioning of essential amino acids. The final section covers *N. lugens* mating systems and evidence for population structure. I conclude by synthesizing the available evidence and developing several hypotheses on factors that could underlie the dramatic variation in planthopper-rice interactions across Asia.

The brown planthopper, *Nilaparvata lugens*, is an enormously successful secondary insect pest that arose from the Green Revolution. *N. lugens* has been able to rapidly adapt to all resistant rice varieties and an array of pesticide chemistries (Liu et al 2005, Yang et al 2005, Yin et al 2008). Rice entomologists and breeders have frequently observed that rice varieties may be resistant to *Nilaparvata lugens* in one geographic region but susceptible in another and rice varieties that were previously resistant may become susceptible over time. Planthopper adaptation to new rice varieties is demonstrated by increases in survival, body weight, honeydew production, and reproduction (Claridge and den Hollander 1980, Pathak and Heinrichs 1982, Denno et al 1989). Planthoppers can also adapt to resistant rice varieties within several generations through continuous rearing in the laboratory. Therefore, it is important to understand the factors underlying variability in planthopper-rice interactions to assist efforts to develop and deploy resistant germplasm.

In this review, I will discuss the factors associated with host selection and acceptance by *N. lugens*. I then review the biochemical basis of rice host-plant resistance and how current genomic tools have contributed to our understanding of rice resistance. The review then focuses on the yeast-like endosymbionts (YLS) within

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planthoppers, and the role they may play in adaptation to plant resistance. Finally, I will cover *N. lugens* mating systems and how they may lead to rapid adaptation and structured populations. The purpose of this review is to synthesize currently available information on planthopper biology, genetics, and host-plant resistance to generate possible hypotheses explaining the variation in planthopper-rice interactions.

Host acceptance of *N. lugens*

The high host specificity of *N. lugens* is characteristic of delphacid planthoppers. Although most planthoppers are highly host-specific (Denno and Roderick 1990), planthopper host location appears to be quite passive (Cook and Denno 1994). In the field, *N. lugens* abundance may be initially similar among rice paddies, unplowed fields, and other crops, suggesting that they do not exhibit landing preferences (Cook and Perfect 1985). Laboratory studies have shown that *N. lugens* is attracted to the odor of host-plant extracts (Saxena and Pathak 1979). However, planthopper specialization does not appear to involve active host-plant location, but rather results from adults remaining on suitable plants (Cook and Denno 1994). The available evidence suggests that the major plant resistance to *N. lugens* is dependent upon phloem chemistry because rejection of a plant occurs only after ingesting phloem sap (Sogawa and Pathak 1970, Sogawa 1982).

Nilaparvata lugens host selection may be due to either plant nutritional content or chemical defense. Host selection by planthoppers is due to phloem chemistry, and likely involves the lack of particular feeding stimulants (Cook and Denno 1994). On resistant rice varieties, silicic and oxalic acid have been found to deter planthopper feeding (Yoshihara et al 1979a,b, 1980a). Phenolic acids in resistant varieties appear to be related to the inability of planthoppers to find and ingest phloem (Fisk 1980). On the other hand, planthoppers are more likely to reject rice varieties with low levels of essential amino acids in the phloem (Sogawa 1982). Shigematsu et al (1982) found that sterols acted as sucking inhibitors for *N. lugens* whereas asparagine stimulated sucking.

Rice resistance to *N. lugens*

Insect herbivore food preferences in grasses appear to be more governed by host nutritional factors than by plant defenses (Tscharntke and Greiler 1995). While grasses generally have fewer allelochemicals (Butler and Bailey 1973, Harbone and Williams 1976), allelochemicals in grasses can still play a role in structuring planthopper host range (Cook and Denno 1994). There is some evidence that the nutritional composition of the rice plant can influence *N. lugens* feeding behavior. The rice phloem sap consists mostly of sucrose (17–25%, w/v) and free amino acids (3–8%, w/v) (Fukumorita and Chino 1982). *N. lugens* feed less and excrete less honeydew when feeding on rice plants deficient in nitrogen (Sogawa 1982). Certain amino acids, sucrose, and organic acids were found to act as feeding stimulants (Sakai and Sogawa 1976). Low concentrations of asparagine may deter extended feeding (Sogawa and Pathak

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1970). On the other hand, lower free amino acid concentrations have been found in resistant rice varieties (Das 1976, Mishra et al 1990). Therefore, amino acid content could vary between rice varieties, and could be related to differences in planthopper performance on different varieties.

Resistant rice varieties appear to have higher levels of phenolic compounds, lower levels of free amino acids, and lower concentrations of reducing sugars (Thayumanavan et al 1990). Resistant varieties contain higher concentrations of three types of flavenoid glycosides, which were shown to inhibit feeding (Grayer et al 1994). As a minor source of resistance, cuticular waxes have been identified as repellents to BPH (Cook et al 1987, Woodhead and Padgham 1988). Silicic acid (Yoshihara et al 1979c), oxalic acid Yoshihara et al (1980b), and β-sitosterol (Kaneda 1982, Shigematsu et al 1982) have been proposed to be feeding inhibitors. Because silicic acid is found outside of the phloem, Yoshihara et al (1979c) suggested that silicic acid may function to localize BPH feeding. However, silicic acid occurs in both resistant and susceptible rice varieties (Saxena 1986). The discovery of both nutritional and defensive compounds strongly suggests that resistant varieties may consist of lower concentrations of nutritional compounds and higher concentrations of defensive compounds.

New molecular techniques have provided insight into rice defensive responses to *N. lugens.* In general, phloem-feeding insects appear to be perceived by plants as pathogens and induce either salicylic acid or jasmonic acid/ethylene-signaling pathways, causing the plants to produce pathogenesis-related proteins (PR) (Walling 2000). Planthopper feeding on rice also induces PR proteins (Kanno et al 2005, Wang et al 2005) and the salicylic acid pathway (Xu et al 2003, Zhang et al 2004). *N. lugens* feeding also induces the expression of protease-inhibitor (PI) genes such as oryzacystatin (Zhang et al 2004, Wang et al 2005), which affects protein digestion in insect midguts (Broadway et al 1986, Jongsma and Bolter 1997). Rice resistance to sap-feeding insects is unlikely to be related to a single compound and is more likely a whole-plant response. The availability of molecular tools such as the rice genomic microarrays will certainly provide insight into the expression profiles and responses of resistant and susceptible plants.

The rice phloem largely consists of water and sugar. It contains some amino acids and phenolic compounds, and the balance between nutritional and defensive compounds appears to influence the feeding preference and nymphal performance of *N. lugens*. Further research should be encouraged that examines the relative importance of nutritional vs. defensive compounds on planthopper performance. For example, studies correlating the biochemical composition of phloem from resistant and susceptible rice varieties, planthopper honeydew biochemical composition, and planthopper feeding behavior could be analyzed using multivariate statistics to help discriminate the key biochemical factors linked with *N. lugens* host acceptance and performance.

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Rapid adaptation to new varieties

The outbreaks of *N. lugens* in the early 1970s spurred intensive efforts to identify and develop germplasm resistant to *N. lugens*. Several genes, such as *bph1*, *bph2*, and *bph3*, were identified and bred into the germplasm by IRRI and other national research institutes in Asia (Khush 1979). While IR26 with the *Bph1* gene initially performed well in the field, planthopper outbreaks resumed within a few years of the release (Gallagher et al 1994). "Virulence," or the ability to exploit resistant varieties, evolves quickly when *N. lugens* are exposed and adapt to new varieties (Claridge and den Hollander 1980, den Hollander and Pathak 1981). The new populations of *N. lugens* that performed well on the resistant germplasm were labeled biotypes 1 and 2 (Pathak and Heinrichs 1982).

An intense debate surrounded these "biotypes" and whether they could be considered reproductively isolated populations (den Hollander and Pathak 1981, Claridge and den Hollander 1983, Saxena and Barrion 1985, Shufran and Whalon 1995). It has now been accepted that *N. lugens* are highly adaptable, and can quickly be selected to improve their performance on resistant varieties within several generations in the laboratory (Claridge and den Hollander 1982). The pattern has been repeated again on many other resistant varieties. Given the extreme variability within each "biotype" and the rapidity with which one biotype can adapt to another resistant variety, the concept of biotypes appears to be more of selected populations rather than host races on their way to speciation (Claridge and den Hollander 1983, Shufran and Whalon 1995). Many genes for resistance exist today, but it is unknown whether each of these genes is linked with a different biochemical product or pathway. The extremely rapid rate by which *N. lugens* can adapt to resistant rice varieties strongly indicates that a mechanistic understanding of planthopper adaptation is needed to guide host-plant resistance breeding activities. Given the variability in a current phenotyping assay such as the Standard Seedbox Screening Test, it will be much more reliable to select plants based upon phloem chemistry than by nymphal feeding preferences.

Endosymbionts support *N. lugens* amino acid metabolism

The nutritional imbalance and limited availability of amino acids in the phloem inhibit the growth and development of phloem-feeding insects. All phloem-feeding hemipteran insects support symbiotic microorganisms (Douglas 1989, 1998), and endosymbionts have recently emerged as a possibly major factor in determining host specialization in sap-feeding insects (Tsuchida et al 2004). Endosymbionts may also facilitate host specialization for *N. lugens* as well. In planthoppers, yeast-like endosymbionts (YLS) within the fungal family Clavicipitaceae (Suh et al 2001) reside intracellularly in the fat body cells of planthoppers (Buchner 1965, Noda 1974, Cheng and Hou 1996).

YLS are thought to provide rare nutrients to planthoppers to compensate for the unbalanced composition of amino acids in plant phloem (Noda and Saito 1977, 1979). Experimental removal of YLS in *N. lugens* nymphs results in weight loss and a reduced growth rate (Wilkinson and Ishikawa 2001). Aposymbiotic *N. lugens*

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contain a lower percentage of total protein, higher concentrations of nonessential free amino acids such as glutamine and arginine, and significantly lower concentrations of the essential amino acid leucine (Wilkinson and Ishikawa 2001). YLS appears to play a role in providing protein through the recycling of uric acid (Sasaki et al 1996). Uric acid is stored in the fat bodies where the symbionts are located and quantities of uric acid within the planthopper decrease when nitrogen is unavailable (Sasaki et al 1996). In addition, YLS also synthesize ergosterol-5,7,24(28)-trienol, which is a precursor of cholesterol and the molting hormone ecdysone (Wetzel et al 1992). This suggests that the absence of YLS could impair successful development to adulthood. Therefore, YLS appear to play an essential role in supporting planthopper nutrition and development.

YLS could cause *N. lugens* reared on particular rice varieties to show higher nymphal survival or performance on that variety (Claridge and den Hollander 1980). Transplants onto “novel” rice varieties are usually coupled with a depression in nymphal performance for one to two generations. A recent study found that planthoppers reared on TN1 and then transplanted onto resistant host plants (ASD7 or Mudgo) showed a decrease in nymphal performance and increased mortality, but this was also accompanied by a decrease in the density of YLS and transaminase activity (Lu et al 2004). The increase in nymphal performance was also correlated with YLS abundance over subsequent planthopper generations. It is difficult to determine whether adaptation to different rice varieties is due to changes in abundance of different endosymbiont species or forms (Chen et al 2006a), environmental factors influencing endosymbiont activity (Chen et al 2006b), or changes in planthopper physiological machinery. Given that endosymbionts are maternally transmitted, variation in endosymbiont activity may give rise to planthopper populations that differ in feeding and metabolic performance. YLS appear to play an essential role in planthopper feeding performance, and may be linked to variation in rice resistance to *N. lugens*. Before any lasting progress can be made in breeding for rice resistance to planthoppers, it is important to understand the biochemical basis of rice resistance and the relationship between rice plants, planthoppers, and their endosymbionts.

Reproductive isolation and population genetic structure of *N. lugens*

Geographic variation in planthopper-rice interactions suggests that mating structures may also spatially structure *N. lugens* populations in the field, despite annual long-distance migration to temperate rice-growing regions. Differentiation in acoustic signaling could maintain reproductive isolation between *Nilaparvata lugens* populations. Prereproductive courtship behavior of *N. lugens* involves acoustic signaling, and the pulse repetition frequency (PRF) appears to play a large part in mate choice and reproduction (Claridge et al 1985a, 1988). Acoustic playback experiments for both sexes confirm the role of acoustic signaling in mate recognition (Claridge et al 1985a). In studies of acoustic signaling of *N. lugens* associated with rice and a grass, *Leersia hexandra*, females selectively mated with males from the same host-associated population (Claridge et al 1984). The particular acoustic signals of the populations are

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retained even when calling occurred on alternate host plants, so the signals were not direct responses to acoustics of the host plant but rather innate population differences (Claridge et al 1985a).

Male planthopper acoustic signaling varies among geographic populations associated with rice (Claridge et al 1985a). *N. lugens* populations from the Solomon Islands, Philippines, and Australia show the greatest differences in PRF and are also the most difficult to hybridize (Claridge et al 1985b). Males that successfully mate with females from another geographic population show PRF values that are more similar to the PRF of the female population (Claridge et al 1984). Also, calls of female planthoppers from the Philippines seem quite different from those of India and Sri Lanka (Claridge et al 1988). Geographic populations of *N. lugens* appear to be more reproductively isolated than a closely related species, *N. bakeri*, because *N. bakeri* shows little variation in PRF between geographic locations, and females appear to be less discriminating (Claridge and Morgan 1993).

Additional biological evidence suggests that rice planthoppers show significant geographic structure. Variation in the ability to migrate may also contribute to population structure. There are geographic differences in the frequency of macroptery, which appears to be under genetic control (Iwanaga et al 1987). Macroptery for *N. lugens* is readily induced in temperate populations, but not in tropical regions (Nagata and Masuda 1980, Iwanaga et al 1987). Therefore, greater gene flow may occur among northern populations than among tropical populations; likewise, tropical planthopper populations may be more differentiated than temperate populations. Planthopper virulence also shows significant variability among geographic populations. *N. lugens* populations in India and Sri Lanka appear to be more virulent against resistant rice varieties than in the rest of Asia (Claridge et al 1982). On the other hand, Australian populations cannot survive on Taichung Native 1, a common rice variety in Asia that is widely considered to be susceptible to planthopper feeding damage (Claridge et al 1988).

Molecular evidence suggests that planthoppers show geographic structure, but the loci used in previous studies did not have the ability to resolve differences between close geographic populations. Frequency differences in several allozyme loci were found among Asian populations, with the largest differences found between Asian and Australian populations (den Hollander 1989). *N. lugens* showed significant genetic variation in mitochondrial DNA among planthopper populations between geographic regions, but populations in Southeast Asia shared the same haplotype (Mun et al 1999). Although these previous studies have suggested that planthoppers show some geographic structure, the use of more variable neutral markers such as microsatellites would enhance the ability to resolve differences between rapidly evolving populations. Microsatellites evolve at a much higher rate, and could be used to resolve recent planthopper history. At IRRI, nine microsatellite loci specific to *N. lugens* have been developed that will be useful for determining *N. lugens* population structure (Ferrater et al, submitted). Also, a newly developed 35K EST library for *N. lugens* should help identify how planthoppers adapt to different rice varieties (Noda et al 2008).

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The application of multilocus genotyping to the study of agricultural insect populations offers new opportunities to examine the origin, migration, and amount of differentiation of planthopper populations. It also offers a common tool that can be shared by rice entomologists to determine the degree of relatedness between regional planthopper populations. These new techniques enable us to (1) identify the ancestral source of immigrants, (2) determine the number of migrants between geographic regions or host plants, (3) determine the amount of genetic diversity, and (4) determine the degree of differentiation between geographic populations. Coupled with the whole-genome microarrays available for *N. lugens* and rice, a wealth of genomic resources are now available for the study of *N. lugens* and rice interactions.

Conclusions

The presence of mutualistic endosymbionts appears to increase the complexity of the interactions between *N. lugens* and rice. Planthoppers appear to respond strongly to variation in amino acid content, suggesting that amino acid content is very important in host-plant selection. The dependence of *N. lugens* on YLS for essential amino acids suggests that variation in YLS activity could help to explain variation in planthopper performance on different rice varieties (Lu et al 2004). If environmental conditions favor YLS populations or species differently, this could also increase variability in planthopper-rice interactions. Therefore, variation in planthopper activity across Asia and on different resistant varieties could be due to variation in endosymbiont activity. Given the host-associated mating system of planthoppers, planthoppers need to accept and feed on a particular variety in order to mate on it. This feeding requirement could result in assortative mating of planthoppers within rice—and lead toward substructure in planthopper populations.

Understanding the factors underlying variability in planthopper-rice interactions will benefit both breeding and deployment strategies. One of the key pieces currently lacking is a solid understanding of how phloem chemistry influences planthopper host acceptance and performance. Research activities could study whether resistance is due to nutritional or defensive chemicals in the phloem. Given the increasingly important role of endosymbionts in structuring herbivore diet breadth and activity, research on the role of endosymbionts in planthopper performance should also be prioritized. Further research could use multivariate statistical tools to correlate how the relative abundance of nutritional and defensive compounds in the phloem influences planthopper and YLS activity. Finally, a wide array of new genetic, biochemical, and genomics tools is now available to study YLS, planthoppers, and rice. These insights will certainly support the widespread efforts to develop and deploy resistant rice varieties throughout Asia.

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References

Broadway RM, Duffey SS, Pearce G, Ryan CA. 1986. Plant proteinase-inhibitors: a defense against herbivorous insects. Entomol. Exp. Appl. 41:33-38.

Buchner P. 1965. Endosymbiosis of animal with plant microorganisms. New York, N.Y. (USA): Interscience.

Butler GW, Bailey RW. 1973. Chemistry and biochemistry of herbage. London (UK): Academic Press.

Chen FJ, Zhang JF, Xia ZE, Lu ZX, Yu XP. 2006a. Morphological observation on the yeast-like endosymbiotes in brown planthopper, *Nilaparvata lugens*. Acta Zootaxon. Sin. 31:55-62.

Chen FJ, Zhang JF, Zhou YQ, Ye GY, Lu ZX, Yu XP. 2006b. Individual size and abundance of the yeast-like endosymbiote in different geographic populations of brown planthopper, *Nilaparvata lugens*. Chinese Bull. Entomol. 43:460-465.

Cheng DJ, Hou RF. 1996. Ultrastructure of the yeast-like endocytobiont in the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). Endocyt. Cell Res. 11:107-117.

Claridge MF, den Hollander J. 1980. The biotypes of the rice brown planthopper, *Nilaparvata lugens*. Entomol. Exp. Appl. 27:23-30.

Claridge MF, den Hollander J. 1982. Virulence to rice cultivars and selection for virulence in populations of the brown planthopper *Nilaparvata lugens*. Entomol. Exp. Appl. 32:213-221.

Claridge MF, den Hollander J. 1983. The biotype concept and its application to insect pests of agriculture. Crop Prot. 2:85-95.

Claridge MF, den Hollander J, Furet I. 1982. Adaptations of brown planthopper (*Nilaparvata lugens*) populations to rice varieties in Sri Lanka. Entomol. Exp. Appl. 32:222-226.

Claridge MF, den Hollander J, Morgan JC. 1984. Specificity of acoustic-signals and mate choice in the brown planthopper *Nilaparvata lugens*. Entomol. Exp. Appl. 35:221-226.

Claridge MF, den Hollander J, Morgan JC. 1985a. The status of weed-associated populations of the brown planthopper, *Nilaparvata lugens* (Stål): host race or biological species? Zool. J. Linnean Soc. 84:77-90.

Claridge MF, den Hollander J, Morgan JC. 1988. Variation in hostplant relations and courtship signals of weed-associated populations of the brown planthopper, *Nilaparvata lugens* (Stål), from Australia and Asia: a test of the recognition species concept. Biol. J. Linnean Soc. 35:79-93.

Claridge MF, den Hollander J, Morgan JC. 1985b. Variation in courtship signals and hybridization between geographically definable populations of the rice brown planthopper, *Nilaparvata lugens* (Stål). Biol. J. Linnean Soc. 24:35-49.

Claridge MF, Morgan JC. 1993. Geographical variation in acoustic-signals of the planthopper, *Nilaparvata bakeri* (Muir), in Asia: species recognition and sexual selection. Biol. J. Linnean Soc. 48:267-281.

Cook AG, Denno RF. 1994. Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense, and host plant specialization. In: Denno RF, Perfect TJ, editors. Planthoppers: their ecology and management. New York, N.Y. (USA): Chapman & Hall. p 114-139.

Cook AG, Perfect TJ. 1985. The influence of immigration on population development of *Nilaparvata lugens* Stål and *Sogatella furcifera* Horvath (Homoptera: Delphacidae) and its interaction with immigration by predators. Crop Prot. 4:423-433.

Pp 315-326 IN Heong KL, Hardy B, editors. 2009. Planthoppers: new threats to the sustainability of intensive rice production systems in Asia. Los Baños (Philippines): International Rice Research Institute.

Cook AG, Woodhead S, Magalit V, Heinrichs EA. 1987. Variation in feeding behavior of *Nilaparvata lugens* on resistant and susceptible rice varieties. Entomol. Exp. Appl. 43:227-235.

Das YT. 1976. Some factors of resistance to *Chilo suppressalis* in rice varieties. Entomol. Exp. Appl. 20:131-134.

den Hollander J. 1989. Electrophoretic studies on planthoppers and leafhoppers of agricultural importance. In: Loxdale HD, den Hollander J, editors. Electrophoretic studies on agricultural pests. Oxford (UK): Clarendon Press. p 297-315.

den Hollander J, Pathak PK. 1981. The genetics of the "biotypes" of the rice brown planthopper, *Nilaparvata lugens*. Entomol. Exp. Appl. 29:76-86.

Denno RF, Olmstead KL, McCloud ES. 1989. Reproductive cost of flight capability: a comparison of life-history traits in wing dimorphic planthoppers. Ecol. Entomol. 14:31-44.

Denno RF, Roderick GK. 1990. Population biology of planthoppers. Annu. Rev. Entomol. 35:489-520.

Douglas AE. 1989. Mycetocyte symbiosis in insects. Biol. Rev. 69:409-434.

Douglas AE. 1998. Nutritional interactions in insect-microbial symbioses: aphids and their symbiotic bacteria *Buchnera*. Annu. Rev. Entomol. 43:17-37.

Ferrater JB, Glenn TC, Chen YH. In revision. Isolation of microsatellites for the brown planthopper, *Nilaparvata lugens*. Molecular Ecology Resources.

Fisk J. 1980. Effects of hydrogen. Entomol. Exp. Appl. 27:211-222.

Fukumorita T, Chino M. 1982. Sugar, amino acid and inorganic contents in the rice phloem sap. Plant Cell Physiol. 23:273-283.

Gallagher KD, Kenmore PE, Sogawa K. 1994. Judicial use of insecticides deters planthopper outbreaks and extend the life of resistant varieties in Southeast Asian rice. In: Denno RF, Perfect TJ, editors. Planthoppers: their ecology and management. New York: Chapman & Hall. p 599-614.

Grayer RJ, Harborne JB, Kimmins FM, Stevenson PC, Wijayagunasekera HNP. 1994. Phenolics in rice phloem sap as sucking deterrents to the brown planthopper, *Nilaparvata lugens*. Acta Hortic. 381:691-694.

Harbone JB, Williams CA. 1976. Flavonoid patterns in leaves of the Graminae. Biochem. Syst. Ecol. 4:267-280.

Iwanaga K, Nakasuji F, Tojo S. 1987. Wing polymorphism in Japanese and foreign strains of the brown planthopper, *Nilaparvata lugens*. Entomol. Exp. Appl. 43:3-10.

Jongsma MA, Bolter C. 1997. The adaptation of insects to plant protease inhibitors. J. Insect Physiol. 43:885-895.

Kaneda C. 1982. Breeding approaches for resistance to BPH in Japan. In: International Rice Research Conference, International Rice Research Institute, Los Baños, Philippines.

Kanno H, Satoh M, Kimura T, Fujita Y. 2005. Some aspects of induced resistance to rice blast fungus, *Magnaporthe grisea*, in rice plant infested by white-backed planthopper, *Sogatella furcifera*. Appl. Entomol. Zool. 40:91-97.

Khush GS. 1979. Genetics of and breeding for resistance to the brown planthopper. In: International Rice Research Institute, editor. The brown planthopper: threat to rice production. Los Baños (Philippines): IRRI.

Liu ZW, Williamson MS, Lansdell SJ, Denholm I, Han ZJ, Millar NS. 2005. A nicotinic acetylcholine receptor mutation conferring target-site resistance to imidacloprid in *Nilaparvata lugens* (brown planthopper). Proc. Natl. Acad. Sci. USA 102:8420-8425.

Pp 315-326 IN Heong KL, Hardy B, editors. 2009. Planthoppers: new threats to the sustainability of intensive rice production systems in Asia. Los Baños (Philippines): International Rice Research Institute.

Lu ZX, Yu XP, Chen JM, Zheng XS, Xu HX, Zhang JF, Chen LZ. 2004. Dynamics of yeast-like symbiote and its relationship with the virulence of brown planthopper, *Nilaparvata lugens* Stål, to resistant rice varieties. J. Asia-Pacific Entomol. 7:1-7.

Mishra BK, Sontakke BK, Mohapatra H. 1990. Antibiosis mechanisms of resistance in rice varieties to yellow stem borer *Scirpophaga incertulas* Walker. Indian J. Plant Prot. 18:81-83.

Mun JH, Song YH, Heong KL, Roderick GK. 1999. Genetic variation among Asian populations of rice planthoppers, *Nilaparvata lugens* and *Sogatella furcifera* (Hemiptera: Delphacidae): mitochondrial DNA sequences. Bull. Entomol. Res. 89:245-253.

Nagata T, Masuda T. 1980. Insecticide susceptibility and wing-form ratio of the brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) and the white backed planthopper, *Sogatella furcifera* (Horvath) (Hemiptera: Delphacidae) of southeast Asia. Appl. Entomol. Zool. 15:10-19.

Noda H. 1974. Preliminary histological observation and population dynamics of intracellular yeast-like symbiotes in the smaller brown planthopper, *Laodelphax striatellus* (Homoptera: Delphacidae). Appl. Entomol. Zool. 9:275-277.

Noda H, Kawai S, Koizumi Y, Matsui K, Zhang Q, Furukawa S, Shimomura M, Mita K. 2008. Annotated ESTs from various tissues of the brown planthopper *Nilaparvata lugens*: a genomic resource for studying agricultural pests. *Bmc* Genomics 9:117-135.

Noda H, Saito T. 1977. Histological and histochemical observation of intracellular yeastlike symbiotes in the fat body of the smaller brown planthopper, *Laodelphax striatellus* (Homoptera: Delphacidae). Appl. Entomol. Zool. 12:134-141.

Noda H, Saito T. 1979. The role of intracellular yeastlike symbiotes in the development of *Laodelphax striatellus* (Homoptera: Delphacidae). Appl. Entomol. Zool. 14:453-458.

Pathak PK, Heinrichs EA. 1982. Selection of biotype population-2 and population-3 of *Nilaparvata lugens* (Homoptera, Delphacidae) by exposure to resistant rice varieties. Environ. Entomol. 11:85-90.

Sakai T, Sogawa K. 1976. Effects of nutrient compounds on sucking response of the brown planthopper *Nilaparvata lugens*. Appl. Entomol. Zool. 11:82-88.

Sasaki T, Kawamura M, Ishikawa H. 1996. Nitrogen recycling in the brown planthopper, *Nilaparvata lugens*: involvement of yeast-like endosymbionts in uric acid metabolism. J. Insect Physiol. 42:125-129.

Saxena RC. 1986. Biochemical-bases of insect resistance in rice varieties. ACS Symposium Series 296:142-159.

Saxena RC, Barrion AA. 1985. Biotypes of the brown planthopper, *Nilaparvata lugens* (Stål) and strategies in deployment of host plant resistance. Insect Sci. Appl. 6:271-289.

Saxena RC, Pathak MD. 1979. Factors governing susceptibility and resistance of certain rice varieties to the brown planthopper. In: Brown planthopper threat to rice production in Asia. Los Baños (Philippines): International Rice Research Institute. p 303-317.

Shigematsu Y, Murofushi N, Ito K, Kaneda C, Kawabe S, Takahashi N. 1982. Sterols and asparagine in the rice plant, endogenous factors related to resistance against the brown planthopper (*Nilaparvata lugens*). Agric. Biol. Chem. 46:2877-2879.

Shufran KA, Whalon ME. 1995. Genetic analysis of brown planthopper biotypes using random amplified polymorphic dna-polymerase chain reaction (RAPD-PCR). Insect Sci. Appl. 16:27-33.

Sogawa K. 1982. The rice brown planthopper: feeding physiology and host plant interactions. Annu. Rev. Entomol. 27:49-73.

Pp 315-326 IN Heong KL, Hardy B, editors. 2009. Planthoppers: new threats to the sustainability of intensive rice production systems in Asia. Los Baños (Philippines): International Rice Research Institute.

Sogawa K, Pathak MD. 1970. Mechanisms of brown planthopper resistance in Mudgo variety of rice (Hemiptera: Delphacidae). Appl. Entomol. Zool. 5:145-158.

Suh SO, Noda H, Blackwell M. 2001. Insect symbiosis: derivation of yeast-like endosymbionts within an entomopathogenic filamentous lineage. Mol. Biol. Evol. 18:995-1000.

Thayumanavan B, Velusamy R, Sadasivam S, Saxena RC. 1990. Phenolic compounds reducing sugars and free amino acids in rice leaves of varieties resistant to rice thrips. Int. Rice Res. Newsl. 15:14-15.

Tscharntke T, Greiler HJ. 1995. Insect communities, grasses, and grasslands. Annu. Rev. Entomol. 40:535-558.

Tsuchida T, Koga R, Fukatsu T. 2004. Host plant specialization governed by facultative symbiont. Science 303:1989.

Walling LL. 2000. The myriad plant responses to herbivores. J. Plant Growth Reg. 19:195-216.

Wang XL, He RF, He GC. 2005. Construction of suppression subtractive hybridization libraries and identification of brown planthopper-induced genes. J. Plant Physiol. 162:1254-1262.

Wetzel JM, Ohnishi M, Fujita T, Nakanishi K, Naya Y, Noda H, Sugiura M. 1992. Diversity in steroidogenesis of symbiotic microorganisms from planthoppers. J. Chem. Ecol. 18:2083-2094.

Wilkinson TL, Ishikawa H. 2001. On the functional significance of symbiotic microorganisms in the Homoptera: a comparative study of *Acyrthosiphon pisum* and *Nilaparvata lugens*. Physiol. Entomol. 26:86-93.

Woodhead S, Padgham DE. 1988. The effect of plant surface characteristics on resistance of rice to the brown planthopper, *Nilaparvata lugens*. Entomol. Exp. Appl. 47:15-22.

Xu T, Zhou Q, Chen W, Zhang GR, He GF, Gu DX, Zhang WQ. 2003. Involvement of jasmonate-signaling pathway in the herbivore-induced rice plant defense. Chinese Sci. Bull. 48:1982-1987.

Yang ZF, Zhang F, He Q, He GC. 2005. Molecular dynamics of detoxification and toxin-tolerance genes in brown planthopper (*Nilaparvata lugens* Stål, Homoptera: Delphacidae) feeding on resistant rice plants. Arch. Insect Biochem. Physiol. 59:59-66.

Yin JL, Xu HW, Wu JC, Hu JH, Yang GQ. 2008. Cultivar and insecticide applications affect the physiological development of the brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae). Environ. Entomol. 37:206-212.

Yoshihara T, Sogawa K, Pathak MD, Juliano B, Sakamura S. 1979a. Soluble silicic acid as a sucking inhibitory substance on rice against the brown planthopper (Delphacidae, Homoptera). Entomol. Exp. Appl. 26:314-322.

Yoshihara T, Sogawa K, Pathak MD, Juliano B, Sakamura S. 1980. Oxalic acid as a sucking inhibitor of the brown planthopper in rice (Delphacidae, Homoptera). Entomol. Exp. Appl. 27:149-155.

Yoshihara T, Sogawa K, Pathak MD, Villareal R. 1979b. Comparison of oxalic acid concentration in rice varieties susceptible to the brown planthopper. Int. Rice Res. Newsl. 4:10-11.

Yoshihara T, Sogawa MD, Pathak MD, Juliano BO, Sakamura S. 1979c. Soluble silicic acid as a sucking inhibitory substance in rice against the brown planthoppper (Delphacidae: Homoptera). Entomol. Exp. Appl. 26:314-322.

Zhang F, Zhu L, He GC. 2004. Differential gene expression in response to brown planthopper feeding in rice. J. Plant Physiol. 161:53-62.

Pp 315-326 IN Heong KL, Hardy B, editors. 2009. Planthoppers: new threats to the sustainability of intensive rice production systems in Asia. Los Baños (Philippines): International Rice Research Institute.

Notes

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