Virulence of brown planthopper (*Nilaparvata lugens*) populations from South and South East Asia against resistant rice varieties

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28 Running header: Rice resistance to *Nilaparvata lugens*

29 **Abstract:** This study examines the utility of resistant varieties and their associated resistance
30 genes against brown planthopper, *Nilaparvata lugens* (Stål), populations from South and South
31 East Asia. A collection of 39 rice accessions that included resistant, tolerant and susceptible
32 varieties and breeding lines were examined for performance against populations of *N. lugens*
33 from India (4), Bangladesh (1), Myanmar (1), Vietnam (1), Indonesia (1), China (1), Taiwan (1),
34 and the Philippines (2). Planthopper virulence varied between regions; however **only** 6 varieties
35 were generally less damaged than the susceptible check Taichung Native 1 (TN1) among $\geq 50\%$
36 of the test populations. **Each of these 6 varieties contained** multiple resistance genes. **One further**
37 **variety, also with multiple resistance genes, and a modern cultivar** (possibly with the *Bph3* gene)
38 were moderately effective against the South Asian populations, **whereas a traditional variety** with
39 the *Bph6* gene was effective against South East Asian populations. *Bph1*, *bph2*, *bph5*, *bph7*,
40 *bph8*, *Bph9*, *Bph10* and *Bph18* were ineffective against most planthopper populations. *Bph20*,
41 *Bph21*, and *Bph17* have potential to be used in resistance breeding in both South and South East
42 Asia, whereas *BPH25* and *BPH26* have potential for use in South Asia. The results indicate that
43 only a few of the currently available resistance genes will be effective in monogenic rice lines;
44 but that pyramiding of two or more genes with strong to weak resistance could improve
45 resistance strength and durability as apparent with the most resistant, traditional varieties.
46 Strategies to avoid planthopper adaptation to resistant rice varieties are discussed.

47 **Keywords:** adaptation, *Bph3* gene, host-plant resistance, resistance genes, standard seedbox
48 screening test, tolerance

1 Introduction

The brown planthopper (*Nilaparvata lugens* [Stål]) is regarded as one of the most damaging pests of rice (*Oryza sativa* L.) in Asia (Bottrell and Schoenly, 2012). The planthopper, a phloem feeder, is largely monophagous on rice (Sogawa, 1982). For several decades, host plant resistance has been the main focus of public research to combat the planthopper (Brar et al., 2009; Fujita et al., 2013). A recent review by Fujita et al. (2013) listed 29 major resistance genes from *O. sativa* and related wild rice species (*Oryza australiensis* and *Oryza minuta*) that have been identified against the brown planthopper. Since the review was published, at least a further 5 tentative genes have been identified (He et al., 2013; Huang et al., 2013; Wu et al., 2014; Hi et al., 2015). The pace of gene identification has increased in recent years in response to an increasing frequency of planthopper outbreaks since the early 2000s. For example, it is estimated that since 2000 China has lost about 1 million tons of rice production annually because of planthopper damage; over 3 million hectares of rice was damaged in Thailand between 2009 and 2011 (IRRI, 2011); and an estimated 200,000 hectares of rice was destroyed in Central Java (Indonesia) in 2011 (Horgan and Stuart, unpublished data). Therefore, despite the constant attention to host plant resistance against the brown planthopper since the 1970s, the success of the method has been limited.

Early results in the development of host plant resistance in rice were promising: IR24 and related varieties that possessed the *Bph1* gene derived from the Indian cultivar Mudgo were widely distributed in Asia in the 1970s and 1980s after severe planthopper outbreaks had been recorded at that time; however, the planthoppers quickly adapted to the varieties and by the 1980s the *Bph1* gene was ineffective throughout Asia (Alam and Cohen, 1998; Horgan, 2012). Varieties with the *bph2* gene were subsequently released (1980s), but again planthoppers adapted

quickly to this gene (Horgan, 2012). Currently, it appears from several reports that planthopper populations throughout much of South and South East Asia are now adapted to both the *Bph1* and *bph2* genes (Tanaka and Matsumura, 2000; Ali et al., 2012; Myint et al., 2009). Since the 1980s, no other genes have been widely deployed in modern rice varieties. Nevertheless, it is apparent that planthopper populations have increased in virulence even against genes that have never been widely deployed (i.e., *bph8*, *Bph9*, *BPH25*, *BPH26*; Myint et al., 2009; Srinivasan et al., 2015). Furthermore, it is clear that planthopper populations from different regions (including different countries and different districts within countries (Verma et al., 1979; Jairin et al., 2007a) differ in their responses to rice varieties with the same resistance genes.

Rice breeders continue to search for ways to improve rice resistance against the brown planthopper. In response to the apparent increased virulence of planthopper populations in Asia, breeders have looked for ways to increase the durability of resistance by opting for stronger genes (genes with marked effects on planthopper fitness) and by pyramiding two or more resistance genes within a single variety (Fujita et al., 2013; Hu et al., 2013). However, to select the optimal resistance genes for deployment in a given region, information on virulence patterns across regions are needed. There has been no large-scale evaluation of the effectiveness of major resistance genes in South and South East Asia. Comparative studies of selected varieties or genes have been conducted by Myint et al. (2009) in Japan, Peñalver Cruz et al. (2011) in the Philippines, and Qiu et al. (2011) in China; studies that use similar evaluation methods and share common host varieties have been conducted in South Asia (Bangladesh: Ali et al., 2012; India: Bhanu et al., 2014). However, these studies vary greatly in the details of the screening methods, i.e., using different groups of varieties in their tests, or using different accessions of the same varieties.

In the present study, we **examined** the virulence of 12 planthopper populations from across South (6 populations) and South East (6 populations) Asia. **We evaluated** the effectiveness of a large collection of resistant, tolerant and susceptible varieties (39 lines) using a standardized screening test at 11 different rice research institutes. All the varieties were sourced through the International Rice Research Institute (IRRI) and were therefore standardized for accession and breeding generation (batch). To our knowledge, this study represents the largest single evaluation, in terms of the number of varieties screened and the number of planthopper populations tested, and is the most geographically widespread evaluation of rice resistance genes. The study **aimed** to assess virulence of planthoppers across the two major regions and thereby assist rice breeders in better selecting regionally appropriate genes for deployment against the brown planthopper. We discuss our results in light of improving information on the effectiveness of resistance and in conserving resistance genes through proper management.

2 Materials and methods

2.1 Planthopper colonies

The brown planthopper occurs throughout South and South East Asia, on some South Pacific Islands and in Australia (Bottrell and Schoenly, 2012). The species feeds and reproduces throughout the year in tropical and sub-tropical regions; however, each year populations from regions close to the equator undertake a Spring migration northward that largely allows them to colonize newly planted rice fields in northern China, Japan and Korea (Kisimoto and Sogawa, 1992), and in north India and Pakistan (Riley et al., 1995). A smaller Autumn migration carries **planthoppers** back southwards from North East Asia (Wada et al., 1987). Planthoppers cannot overwinter above ca. 25° north of the equator (Chen et al., 1982).

We used 12 colonies of planthopper located at 11 institutes in South and South East Asia (Table 1, Figure 2). Details of colony maintenance were decided with all collaborators during a workshop held at IRRI in 2010. The colonies were initiated with recently wild caught individuals collected from rice fields near each participating research institute. Colonies were initiated with >500 individuals and reared on locally available susceptible varieties (predominantly Taichung Native 1 [TN1]) (Table 1). The colonies were usually maintained **not** longer than 60 months prior to evaluation of resistance. Depending on the population, this consisted of between 2 and 60 generations on the susceptible variety before evaluation.

2.2 Plant materials

We used 39 rice varieties in the evaluation. Varieties were selected to represent all the available planthopper (brown planthopper and **whitebacked** planthopper, *Sogatella furcifera* [Horváth]) resistance genes from the IRRI Genebank at the time the project was initiated in 2010. Lines with resistance to **whitebacked** planthoppers were included because of possible cross-resistance between brown planthopper and **whitebacked** planthopper resistance genes (Srinivasan et al., 2015).

The materials consisted of several types of plant including donor lines from which resistance genes have been identified - these often had associated genetic markers, breeding lines - that included lines introgressed with wild rice species, and modern IR varieties (varieties bred at IRRI) for which breeding pedigrees and breeding selection suggest the presence of one or more resistance genes (Table 2). Donor lines included traditional cultivars and land races. The varieties mainly represented the *O. sativa indica* subspecies; however, *O. sativa japonica* varieties (Asiminori and T65) were also included among the materials. We also included

varieties with known tolerance and susceptibility to planthoppers. These latter were used as susceptibility checks. Twenty nine genes have been identified from the materials we used, these were *Bph1*, *bph2*, *Bph3*, *bph4*, *bph5*, *Bph6*, *bph7*, *bph8*, *Bph9*, *Bph10*, *Bph18*, *Bph20*, *Bph21*, *BPH25*, and *BPH26* against the brown planthopper; *Wbph1*, *Wbph2*, *Wbph3*, *wbph4*, *Wbph5*, *Wbph6*, *WbphAR*, *WbphN*, *WbphO*, *WbphM1*, and *WbphM2* against whitebacked planthopper; *Glh2* against green leafhopper (*Nephotettix virescens* [Distant]; and *Zlh1* and *Zlh2* against zigzag leafhopper (*Recilia dorsalis* [Motschulsky]); Furthermore, lines with notable resistance, such as Asiminori that has genes for induced egg mortality (possibly *ovc* gene: Horgan, unpublished) were included (Table 2). The materials, particularly the traditional varieties, also likely possessed several other unidentified resistance genes.

Seed was acquired from the IRRI Genebank and from the Plant Breeding, Genetics and Biotechnology Division of IRRI. Only about 20 g of seed was available for most lines/varieties. Therefore, the seed was bulked-up in a screenhouse at IRRI during 2010-2011 to attain enough seed for all collaborators. Seed was then shipped to collaborators as 20 g packets following correct export-importation protocols for each country. The seed was often bulked up a second time at each participating research institute before initiating screening experiments.

2.3 Evaluation of resistance

We used the standard seedbox screening test (SSST) to evaluate the varieties/colonies. The SSST is widely used in rice breeding programs throughout Asia and has been described in detail in several publications (Velusamy et al., 1986; Horgan, 2009). We used this test because it is easy to standardize among different institutes and each institute had prior experience with the test.

The seedbox test is a choice test by which rice varieties can be ranked according to damage caused by planthopper nymphs. Details of the test were outlined at a workshop in 2010 and the protocol was distributed to all participants in the study. Seedboxes of 130×100×10cm (L×W×H) were recommended for the study. The boxes were filled with paddy soil to below the rim of the box. Twenty five to 30 seedlings of each rice variety were sown in lines from the edge of the box to before the middle of the box. The 39 varieties were randomly assigned to rows in each seedbox with randomization conducted separately for each replicate. The susceptible check TN1 was interspersed among the test varieties as a central strip through the middle of the seedbox perpendicular to the rows, as extra rows at each end of the box, and at 5 row intervals interspersed with the test lines. A space of about 5cm was left between adjacent seed rows. The seedlings were allowed to develop for 7 days after which time the rows were thinned to 20 plants per row. After 7 days, the seedlings were infested with newly emerged and first instar planthopper nymphs (second to third instars at the Indonesian Center for Rice Research) at a density of 8 nymphs per seedling.

When the susceptible checks were completely wilted due to planthopper feeding, the experiments were stopped and the condition of the seedlings scored using the standard evaluation system (SES) where 0 = no damage, 1 = slight damage to a few plants within a row, 3 = first and second leaves of each plant partially yellowing, 5 = pronounced yellowing or stunting of the plants or between 10 and 25% of plants wilted within a row, 7 = more than 50% of the plants wilted or dead and the remaining plants severely stunted or dying, and 9 = all plants wilted or dead. The SSST was replicated three times for each population except for the population at Hangzhou, China where there were no replicates because of poor germination of seed, and at IRRI (Laguna population) where the test was replicated 5 times. Because of poor seed

germination, some varieties were not evaluated at all the institutes; furthermore, only 11 varieties were evaluated at Yezin Agricultural University (Myanmar).

2.4 Data analyses

Data were ranked within replicates. The number of test varieties often varied between tests and replicates at each site because of poor germination of some varieties and lines (Tables 1 and 2). Therefore, the ranks were weighted according to the number of varieties used within each replicate and standardized to the full complement of 39 varieties. Resistance ranks were compared for each planthopper population using general linear models (GLM). Pair-wise comparisons of damage scores were conducted using Dunnett's 'many-to-one comparison' tests with relevant Bonfaroni adjustments. Rank scores of the common varieties for pair-wise combinations of each of 12 planthopper populations were examined using Spearman's rank correlations. A cluster diagram was prepared based on similarities in planthopper responses according to the correlation coefficients.

3 Results

3.1 Responses by planthoppers to test varieties

Three of 34 varieties were less damaged than TN1 by planthoppers at DRR (India – Hyderabad 2010); 8 of 33 at PHPL (India – Hyderabad 2007), 8 of 34 at PAU (India – Ludhiana), 15 of 29 at APRRI (India – Maruteru) and 18 of 39 at BRRI (Bangladesh). A small number of varieties were apparently resistant/tolerant to planthoppers from 4 or more South Asian locations; these varieties were IR71033-121-15, MOI , Rathu Heenati, ADR52, and PTB33 (Table 3). Despite indications of generally high resistance/tolerance, Rathu Heenati performed poorly at DRR (India – Hyderabad 2010), and ADR52 and PTB33 were ranked

among the most susceptible varieties at BRRI (Bangladesh). Only 11 varieties were tested at YAU (Myanmar). Four of these (Rathu Heenati, Balamawee, Jia Nong 66, and ARC10550) were less damaged than TN1 in the tests. IR71033-121-15 and MOI were apparently resistant to all South Asian populations tested; Rathu Heenati, ADR52, and PTB33 were resistant to over 80% of the South Asian populations tested, and IR74 was resistant to 75% of the South Asian populations tested. Other varieties that were often significantly less damaged than TN1 by some of the planthopper populations included Mudgo and Babawee (Table 3).

Only one, unreplicated SSST was conducted at ZAAS (China); nevertheless, the results were generally consistent from this planthopper population with results from the other South East Asian populations. At Hangzhou, Rathu Heenati, Balamawee, PTB33, IR71033-121-15, MOI and IR74 were among the least damaged varieties (Table 4). Thirteen of 35 varieties were significantly less damaged than TN1 at CAES (Taiwan), 3 of 35 at SRPPC (Vietnam), 13 of 33 at ICRR (Indonesia), and 6 of 38 for the IRRI Laguna population (Philippines). No varieties were less damaged than TN1 during screening of the IRRI Mindanao (Philippines) population (Table 4); however, the relative rankings from the Mindanao population were generally well correlated with other populations from the region (Table 5). Among the most resistant varieties were Rathu Heenati, Balamawee, Swarnalata and PTB33 (each resistant/tolerant to over 60% of the populations tested) (Table 4).

3.2 Comparison of responses across sites

The least damaged varieties across all sites were Rathu Heenati (less damage than control for 82% of populations tested), PTB33 (70%), MOI (70%), IR71033-121-15 (67%), Balamawee (55%) and ADR52 (50%). ADR52 appeared more effective in reducing damage

from South Asian planthopper populations (80%) than South East Asian populations (20%). In contrast Swarnalata was more effective in reducing damage from South East Asian populations (60%) than from South Asian populations (0%). The noted exception among South East Asian populations was at Hangzhou, where Swarnalata was among the most damaged varieties. Mudgo was also apparently more resistant to South Asian populations (50%) than South East Asian populations (0%). IR74 and ARC 6650 were less damaged than TN1 in $\geq 40\%$ of the tests. The rank orders of damage ratings for South East Asian populations were generally more similar to each other than to those of South Asian populations (Table 5). Among the populations that were screened using ≥ 28 varieties, there were two apparent groups (Figure 2). The first group included all South East Asia populations as well as the Hyderabad 2007 and Maruteru populations from India. The second group included the remaining Indian populations and the Bangladesh population. The Myanmar population was an outlier within the study (Figure 2); however this was likely influenced by the small number of varieties that were screened against this population. Adding the Myanmar data did not alter groupings among the remaining populations in figure 2.

4 Discussion

Two worrisome trends are apparent from current literature on rice resistance to the brown planthopper: The first is that newly identified resistant varieties and genes appear less effective than the varieties and genes that were identified in the 1970s and 1980s. For example, *Bph1* had noted high resistance to planthoppers including causing high nymph mortality in the years prior to widespread planthopper adaptation (Athwal et al., 1971). In contrast, many of the more recently identified genes such as *Bph10*, *BPH25* and *BPH26*, appear unstable, do not generally cause nymph mortality, and are rapidly overcome by adapting planthopper populations (Ferrater

et al., 2015; Srinivasan et al., 2015). Many of the genes evaluated in the present study had narrow resistance spectrums (effective against only one or two populations), or did not reduce damage in the SSSTs to below the levels observed for TN1 (i.e., *bph5*, *bph7* and *bph8*). The second trend is that planthopper populations have become increasingly virulent against resistance genes, even where the genes in question have never been widely deployed. Myint et al. (2009) gave the best example of this by evaluating the virulence of relict planthopper populations in Japan against a series of resistant varieties and noting that resistance decreased from 100% in 1966, to 50% in 2005 from a total of 8 varieties. Srinivasan et al. (2015) indicated that planthopper populations in the Philippines have progressively overcome *BPH25* and *BPH26* resistance apparently without either gene ever being widely deployed. The results of the present study further indicate that the availability of resistance genes against the brown planthopper may not be as extensive as suggested in related literature: Only 6 varieties were consistently less damaged than the susceptible standard variety TN1 from a total of 39 varieties representing 15 known brown planthopper resistance genes as well as genes for resistance against other hopper species. Furthermore, genes and varieties that were previously identified as bestowing resistance against planthopper populations in Bangladesh (Kabir and Khush, 1988) and South India (Chelliah, 1986) often failed to reduce damage in the corresponding tests that we conducted (i.e., Jia Nong 66 [*bph7*] and ARC 11367 not resistant in Bangladesh, and ARC 6650 not resistant in South India); however, this may be due to different seed sources or accessions used in these evaluations.

The SSST is a rapid and simple technique to evaluate the relative susceptibility of seedlings against target insects such as planthoppers. The method is a choice test that is sensitive to environmental factors including ambient temperatures and humidity, as well as the proportions

of resistant to susceptible materials and the layout of the test materials within the seedbox (Horgan, 2009). However, if replicated properly, consistent patterns will emerge to indicate plant materials that survive longer or are least damaged by the test herbivores. One of the principal shortcomings of the SSST is that it only assesses responses by nymphs and is therefore limited to detection of antibiotic resistance; furthermore, the results cannot be used to distinguish between resistance and tolerance (Horgan, 2009). For example, the tolerant variety Triveni occasionally gave results similar to several of the true resistant varieties in the present study. However, Triveni does not deter planthopper attack in terms of insects settling on the plant or reduce attack efficiency in terms of the amount of honeydew secreted, but instead compensates for nymph damage (Ho et al., 1982). The results of this study should be considered in light of these limitations.

In the present study, several varieties were noted as resistant or tolerant to the different planthopper populations; however, in some of the tests, these apparently resistant varieties included IR22 (Bangladesh and Indonesia) and IR24 (Bangladesh and India - Maruteru), varieties with recognized susceptibility to planthoppers. Those varieties that appeared resistant or tolerant in only a few tests may have included false readings that occurred because of proximities to strongly resistant varieties or because these were at a distance from lighted areas of the greenhouse or cage (despite randomization) where planthoppers congregate. Some varieties that were less damaged than TN1 in one or two tests may be true resistant or tolerant varieties, but will require further evaluation for clarification of mechanisms and planthopper responses at the particular test locations (i.e., Jia Nong 66, Yagyaw, and IR60). However, because of the high proportion of potentially resistant materials in our tests, it should be noted that the TN1 control seedlings, through which the duration of the tests was determined, would have succumbed to

damage quite quickly as planthoppers were ‘pushed’ toward the most susceptible lines. This suggests that the relative strength of resistance/tolerance among the remaining lines was likely overestimated.

The varieties that appeared resistant in many of the tests (against several populations) in the present study are of particular interest as these have the greatest strength and spectrum of resistance, and are among the most durably resistant varieties (see publication dates in Table 2). These varieties include Rathu Heenati, PTB33, MOI, IR71033-121-15 and Balamawee, as well as ADR52 in South Asia and Swarnalata in South East Asia. From among the 39 varieties included in the study, these varieties have some common features that may explain factors underlying resistance strength and durability. All of the traditional varieties or landraces in this group are of South Asian origin (Sri Lanka, India or Bangladesh: Table 2); Multiple genes have been identified from many of the varieties (i.e., Rathu Heenati = *Bph3*, *Bph17*, *Zlh1*; IR71033-121-15 = *Bph20*, *Bph21*; MOI = *WbphN*, *WbphO*, etc.: Table 2) and these include suggested genes for resistance to multiple herbivores such as the whitebacked planthopper and zigzag leafhopper as well as the brown planthopper (i.e., Rathu Heenati, PTB33, ADR52: Table 2). These varieties therefore have broad resistance not only to different populations of brown planthoppers, but to planthoppers and leafhoppers in general. Furthermore, many of the varieties are photosensitive, slow-growing and low yielding (Srinivasan et al., 2015; personal observations). It is therefore unsurprising that these varieties are among the most resistant since they are the sources for several resistance genes and have invested heavily in defenses, possibly with high ecological costs to growth and yield.

Among the varieties that scored high for resistance/tolerance were IR74 and IR62, two modern varieties that possess the *Bph3* gene, and Babawee that possesses the closely related

320 *bph4* gene. Swarnalata with the *Bph6* gene was resistant against most South East Asian
321 populations. These varieties and genes will be particularly useful in future breeding programs
322 since they bestow moderate to strong resistance in apparently monogenic resistant varieties often
323 without appreciable yield or growth penalties. For example, IR74 (*Bph3*), IR62 (*Bph3*) and IR66
324 (*bph4*) can attain rice grain yields of 5.4, 5.8 and 5.8 tons ha⁻¹, respectively (dry season grain
325 yield in the Philippines: Khush and Virk, 2005). The results of this study also generally confirm
326 that the *Bph1* and *bph2* genes are no longer effective throughout South and South East Asia
327 (Mudgo, like the traditional varieties listed above has broad resistance with several noted
328 resistance genes other than *Bph1*: Table 2); furthermore, *bph5* (ARC 10550), *bph7* (Jia Nong
329 66), *bph8* (Chinsaba), *Bph9* (Pokkali), *Bph10* (IR65482-4-136-2-2) and *Bph 18* (IR65482-7-216-
330 1-2) were generally not effective against the planthoppers according to the present study. Several
331 varieties with noted resistance to the whitebacked planthopper were also ineffective against the
332 brown planthopper (i.e., Da Hua Gu, N22, ARC 10239, ARC 11367). It is surprising that many
333 of these ineffective genes have never been widely deployed in modern rice varieties (Table 2).
334 This suggests that long-term and wide-area exposure to resistant varieties has not been the
335 mechanism underlying planthopper adaptation to these genes. Other possibilities will need to be
336 addressed in future studies including possible cross-virulence against resistance genes that share
337 similar resistance mechanisms or are closely positioned on the rice genome. For example,
338 adaptation by planthoppers to varieties with the *Bph3* gene has been shown to reduce the
339 effectiveness of the *bph4* gene (Peñalver Cruz et al., 2011) and adaptation to *Bph9* may reduce
340 the effectiveness of *bph8* (Ketipearachchi et al., 1998). However, with only *Bph1* and *bph2*
341 widely deployed, this mechanism is also unlikely to underlie failing resistance genes.

Several studies have attempted to understand planthopper migration (Iwanaga et al., 1987) and genetic differences between planthoppers on the basis of reactions to intraspecific crowding, insecticides (Matsumura et al., 2008), or resistant rice varieties (Jairin et al., 2007a; Myint et al., 2009). Many of these studies have focused on South East Asia where a single continuous population migrates from south to north in the Spring time and returns south in the Autumn (Kisimoto and Sogawa, 1992). These studies suggest that Vietnam in particular is a source of virulent planthopper populations, indeed Vietnamese planthoppers are often relatively more resistant to insecticides (Matsumura et al., 2008) and more virulent on resistant varieties (Wada et al., 1994; Srinivasan et al., 2015) than for example Japanese or Philippine populations. Furthermore, there is evidence of similar migration patterns in South Asia, with planthoppers migrating from southern India toward the north in the Spring (Riley et al., 1995). Our results with some varieties (i.e., ADR52, Mudgo and Swarnalata) corroborate suggestions that South and South East Asian planthopper populations are somewhat isolated. This offers an opportunity for resistance breeding since genes that are ineffective in South East Asia (i.e., *BPH25* and *BPH26*; Srinivasan et al., 2015), could potentially be recycled in South Asia. Furthermore, the most resistant varieties in this study were generally of South Asian origin, and these were notably effective against planthoppers from the same region, suggesting that durable resistance is possible, albeit with likely agronomic penalties.

The present research includes one of the largest systematic studies to evaluate planthopper virulence and rice resistance in Asia. The logistics of completing such a study were understandably complex and inherent shortcomings were expected. Among the limitations encountered in this research were the varied environments and differences in protocols at the different research centers that may have reduced clarity in the overall results. Future studies

would do well to conduct screening under more controlled temperatures and humidity and with more objectively quantifiable parameters using validated seeds and careful attention to seed germination success. Nevertheless, the results from this study, although preliminary in nature, do have implications for resistance breeding and planthopper management in general. Firstly, evidence suggests that strong resistance, broad resistance and durable resistance are possible, and that these are determined by the number of resistance genes in the variety (naturally pyramided in landraces and traditional varieties). Secondly, a few genes continue to effectively reduce damage in modern monogenic rice varieties. These will be useful in breeding programs, but need to be managed carefully. For example, widespread deployment of *Bph3* at a scale equivalent to the deployment of *Bph1* or *bph2* in the 1970s and 1980s, is likely to promote planthopper adaptation. Regional strategies to conserve these rare resistance genes would be helpful. Thirdly, despite the continued attention to rice resistance against the brown planthopper, often at the expense of research in other management approaches, the effective development of modern resistant varieties has been limited. The brown planthopper continues to be a major pest of rice in Asia. Outbreaks have been linked to poor crop management, particularly the overuse of nitrogenous fertilizers and prophylactic applications of insecticides that eliminate natural enemies (Bottrell and Schoenly, 2012; Horgan and Crisol, 2013). More attention to sustainable solutions against planthopper damage that include resistance as a component of integrated pest management and not as a safeguard against poor crop management is required.

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Table 1 Details of institutes, *Nilaparvata lugens* populations and screening conducted

Location	Institute	<i>N. lugens</i> population source	Year of collection	Year of evaluation	Rice lines evaluated
India (Hyderabad)	Directorate of Rice Research (DRR)	Miryalguda, Nalgonda District, Andhra Pradesh, India	2010	2011	35
India (Hyderabad)	Hi-Bred Private Limited (PHPL)	Toopran farm, Medak District, Andhra Pradesh, India	2007	2011	33
India (Maruteru)	Andhra Pradesh Rice Research Institute (APRRI)	Regional Agricultural Research Station, Maruteru, Andhra Pradesh, India	2004	2011	29
India (Ludhiana)	Punjab Agricultural University (PAU)	Jand Village, Ludhiana District, Punjab, India	2007	2011	33
Bangladesh (Gazipur)	Bangladesh Rice Research Institute (BRRI)	BRRI farm, Gazipur, Bangladesh	2011	2011	39
Myanmar (Yezin)	Yezin Agricultural University (YAU)	YAU farm, Yezin, Myanmar	2013	2013	11
China (Hangzhou)	Zhejiang Academy of Agricultural Sciences (ZAAS)	Hangzhou rice fields, China	2010	2011	37
Taiwan (Chiayi)	Taiwan Agricultural Research Institute and Chiayi Agricultural Experiment Station (CAES)	Chiayi Agricultural Experiment Station, Chiayi, Taiwan	2012	2012	35
Vietnam (Ling Dinh)	Southern Regional Plant Protection Centre (SRPPC)	Ling Dinh rice fields, Vietnam	2012	2014	35
Indonesia (Subang)	Indonesian Centre for Rice Research (ICRR)	Subang rice fields, West Java, Indonesia	2011	2012	33
Philippines (Luzon)	International Rice Research Institute (IRRI)	Victoria and Pila rice fields, Laguna, Philippines	2009	2013	38
Philippines (Mindanao)	International Rice Research Institute (IRRI)	Rice fields near Surallah, South Cotabato, Mindanao, Philippines	2012	2013	38

Table 2 Rice varieties screened for resistance against 12 *Nilaparvata lugens* populations with proposed resistance genes

Variety (accession)	Origin	Suggested genes and noted resistance	Variety deployment	<i>N. lugens</i> populations tested
Mudgo (Ac. 6663)	India	<i>Bph1</i> ¹ , <i>WbphM1</i> ² , <i>WbphM2</i> ²	Traditional ¹	12
ASD7 (Ac. 6303)	India	<i>bph2</i> ¹ , <i>Glh2</i> ³	Extensive	12
PTB33 (Ac. 19325)	India	<i>bph2</i> ⁴ , <i>Bph3</i> ^{4,5} , <i>Zlh3</i> ⁴	Traditional ⁴	11
Rathu Heenati (Ac. 11730)	Sri Lanka	<i>Bph3</i> ^{6,7} , <i>Bph17</i> ⁸ , <i>Zlh1</i> ⁴	Traditional ⁷ and localized ³⁸	12
Babawee (Ac. 6730)	Sri Lanka	<i>bph4</i> ^{6,7,9}	Traditional ⁷	12
ARC 10550 (Ac. 12507)	India	<i>bph5</i> ¹⁰	Localized ¹⁰	12
Swarnalata (Ac. 33964)	Bangladesh	<i>Bph6</i> ^{11,12}	Localized ¹²	12
Jia Nong 66 (Ac. 59689)	China	<i>bph7</i> (<i>T12</i> resistant to <i>BPH</i> in <i>Bangladesh</i>) ^{11,13}	No available record	6
Chinsaba (Ac. 33016)	Myanmar	<i>bph8</i> ¹⁴	Traditional ¹⁴	12
Balamawee (Ac. 8919)	Sri Lanka	<i>Bph9</i> ¹⁴ , <i>Bph27(t)</i> ¹⁵	Traditional ¹⁴	12
Pokkali (Ac. 15602)	Sri Lanka	<i>Bph9</i> ^{14,16}	Traditional ¹⁴	10
IR65482-4-136-2-2 (IRTP 19029)	Introgressed with <i>Oryza australiensis</i> – from Australia	<i>Bph10</i> ¹⁷	None	11
IR65482-7-216-1-2 (IRTP 26968)	Introgressed with <i>O. australiensis</i> – from Australia	<i>Bph18</i> ¹⁸	None	9
IR71033-121-15 (IRTP 23991)	Introgressed with <i>Oryza minuta</i> – from Philippines	<i>Bph20</i> ¹⁹ , <i>Bph21</i> ¹⁹	None	10
ADR52 (Ac. 40638)	India	<i>BPH25</i> ²⁰ , <i>BPH26</i> ²⁰ , <i>Wbph3</i> ²¹	Traditional ²⁰	11
Yagyaw (Ac. 33849)	Vietnam	4 <i>QTLs</i> - <i>Qbph3</i> , <i>Qbph9</i> ²²	Landrace ²²	11
Asiminori (Ac. 39942)	Korea	Egg mortality of <i>N. lugens</i> and <i>S. furcifera</i> in Philippines ²³ (possibly <i>Ovc</i> gene ²⁴)	No available record	5
Nagina 22 (N22: Ac. 4819)	India	<i>Wbph1</i> ²⁵	Localized ²⁵	11
ARC 10239 (IRTP 9677)	India	<i>Wbph2</i> ²⁶	Localized ²⁶	10
ARC 6650 (Ac. 12308)	India	<i>wbph4</i> ²⁷ (resistant to <i>N. lugens</i> in South India ²⁸)	Localized ²⁸	11
N'Diang Marie (Ac. 15859)	Senegal	<i>Wbph5</i> ²⁹	Traditional ²⁹	11
Da Hua Gu (Ac. 79597)	China	<i>Wbph6</i> ³⁰	Traditional ³⁰	10
ARC 11367 (Ac. 21355)	India	<i>wbphAR</i> ² (resistant to <i>N. lugens</i> in Bangladesh ¹¹)	Localized ^{2,11}	10

MOI (Ac. 6353)	India	<i>WbphN</i> ² , <i>WbphO</i> ²	No available record	11
Triveni (Ac. 14785)	India	Tolerance ³¹	Traditional ³¹	11
Utri Rajapan (Ac. 16684)	Indonesia	Tolerance to <i>N. lugens</i> ^{32,33} and some resistance to <i>S. furcifera</i> ³⁴	Traditional ³³	11
TN1	Taiwan	None ³⁵	Low ³⁵	12
IR22 (Ac. 11356)	Philippines	None ^{36,37}	Extensive ³⁶	11
T65 (Ac. 79/IRTP 07579)	Taiwan	None ³⁵	Low ³⁵	7
IR24	Philippines	<i>Bph1</i> ^{36,37}	Extensive during 1970s-1980s ³⁶	11
IR64	Philippines	<i>Bph1</i> ^{36,37} and unidentified QTLs ³⁸	Extensive ³⁶	7
IR40	Philippines	<i>bph2</i> ^{36,37}	Localized ³⁶	11
IR56	Philippines	<i>Bph3</i> ^{36,37}	Localized ³⁶	5
IR60	Philippines	<i>Bph3</i> ^{36,37}	Widespread in some regions ³⁶	7
IR62	Philippines	<i>Bph3</i> ^{36,37}	Localized ³⁶	11
IR70	Philippines	<i>Bph3</i> ^{36,37}	Localized ³⁶	10
IR72	Philippines	<i>Bph3</i> ^{36,37}	Widespread in some regions ³⁶	11
IR74	Philippines	<i>Bph3</i> ^{36,37}	Widespread in some regions ³⁶	10
IR66	Philippines	<i>bph4</i> ^{36,37}	Localized ³⁶	11

1: Athwal et al., 1971; 2: Sidhu et al., 2005; 3: Sun et al., 2006; 4: Angeles et al., 1986; 5: Jairin et al., 2007a; 6: Lakshminarayana and Khush, 1977; 7: Jairin et al., 2007b; 8: Sun et al., 2005; 9: Kawaguchi et al., 2001; 10: Khush et al., 1985; 11: Kabir and Khush, 1988; 12: Qiu et al., 2010; 13: Qiu et al., 2014; 14: Nemoto et al., 1989; 15: He et al., 2013; 16: Murata et al., 2000; 17: Iishi et al., 1994; 18: Jena et al., 2006; 19: Rahman et al., 2009; 20: Hernandez and Khush, 1981; 21: Myint et al., 2012; 22: Liu et al., 2009; 23: Srinivasan et al., 2015; 24: Yamasaki et al., 2003; 25: Sidhu et al., 1979; 26: Angeles et al., 1981; 27: Chelliah, 1986; 28: Padmavathi et al., 2007; 29: Wu and Khush, 1985; 30: Min et al., 1991; 31: Ho et al., 1982; 32: Panda and Heinrichs, 1983; 33: Velusamy et al., 1986; 34: Saxena, 1989; 35: De Datta, 1981; 36: Khush and Virk, 2005; 37: Brar et al., 2009; 38: Cohen et al., 1997

Table 3 Preferences by *Nilaparvata lugens* populations from India, Bangladesh and Myanmar among 39 rice accessions. **Numbers are ranks (SEM in parentheses)**

Variety or breeding line	India – Hyderabad 2010 ¹	India – Hyderabad 2007 ¹	India - Maruteru ¹	India - Llundhiana ¹	Bangladesh ¹	Myanmar ¹	Affected populations (tested populations)
IR71033-121-15	-	6.8 (2.0)†	19.5 (3.5)†	2.3 (0.0)†	12.7 (0.7)†	-	4 (4)
MOI	2.2 (0.3)†	11.6 (1.9)†	2.0 (0.4)†	6.7 (0.5)†	3.6 (1.3)†	-	5 (5)
Rathu Heenati	16.2 (7.0)	2.4 (0.2)†	7.4 (0.7)†	9.2 (0.0)†	12.7 (0.7)†	15.5 (3.7)†	5 (6)
ADR52	1.5 (0.5)†	4.5 (2.0)†	13.7 (4.0)†	6.1 (0.4)†	27.0 (2.2)	-	4 (5)
PTB33	3.7 (0.4)†	2.4 (0.2)†	4.9 (0.9)†	1.2 (0.0)†	30.4 (1.8)	-	4 (5)
IR74	20.9 (6.5)	9.6 (0.8)†	-	3.4 (0.0)†	5.8 (3.0)†	-	3 (4)
Balamawee	19.7(6.8)	7.4 (2.7)†	14.6 (8.2)†	24.5 (4.7)	30.4 (1.8)	15.5 (2.4)†	3 (6)
Mudgo	16.7 (6.4)	16.9 (4.2)	10.1 (0.7)†	9.2 (1.1)†	9.9 (2.5)†	27.0 (2.2)	3 (6)
ARC 6650	11.0 (2.3)	20.7 (5.4)	18.8 (6.05)†	23.3 (5.1)	12.7 (0.7)†	-	2 (5)
IR24	31.5 (8.6)	20.8 (6.4)	15.9 (4.2)†	30.2 (6.5)	12.7 (0.7)†	-	2 (5)
IR62	19.6 (5.3)	32.3	33.2 (1.8)	4.6 (0.0)†	9.8 (2.7)†	-	2 (5)
IR72	27.5 (7.1)	24.9 (4.3)	20.2 (2.8)†	10.9 (1.7)	12.7 (0.7)†	-	2 (5)
N'Diang Marie	24.0 (6.9)	27.8 (4.7)	3.4 (1.0)†	18.2 (2.0)	4.1 (0.8)†	-	2 (5)
ASD7	15.2 (4.6)	24.8 (2.6)	13.5 (1.8)†	27.1 (3.1)	9.9 (2.5)†	25.3 (2.5)	2 (6)
Babawee	17.2 (5.4)	17.7 (4.6)	14.3 (3.1)†	10.7 (0.4)	2.7 (1.0)†	21.3 (3.8)	2 (6)
IR65482-7-216-1-2	18.6 (5.4)	21.0 (1.5)	-	-	9.9 (2.5)†	-	1 (3)
IR70	19.8 (4.4)	24.9 (4.3)	-	35.6 (1.1)	7.0 (2.2)†	-	1 (4)
ARC 11367	27.6 (7.6)	9.6 (0.8)†	23.3 (0.9)	28.3 (4.4)	23.5 (1.9)	-	1 (5)
IR22	25.7 (6.7)	25.5 (4.3)	25.1 (4.5)	29.1 (2.1)	12.7 (0.7)†	-	1 (5)
IR65482-4-136-2-2	33.8 (8.8)	17.5 (7.7)	23.3 (0.9)	12.6 (1.1)	9.8 (2.7)†	-	1 (5)
IR66	14.4 (4.1)	20.7 (5.4)	29.1 (2.7)	25.2 (5.0)	12.7 (0.7)†	-	1 (5)
Jia Nong 66 (T12)	28.5 (7.4)	37.3	-	23.9 (1.3)	30.4 (1.8)	6.2 (0.5)†	1 (5)
Utri Rajapan	9.9 (2.0)	18.7 (5.7)	26.2 (7.8)	35.6 (1.1)	12.7 (0.7)†	-	1 (5)
Yagyaw	12.0 (3.7)	16.6 (6.6)	4.9 (0.5)†	26.7 (1.9)	27.0 (0.0)	-	1 (5)
ARC 10550	14.3 (3.1)	24.8 (2.6)	21.5 (1.6)	12.6 (0.7)	30.4 (1.8)	4.4 (0.5)†	1 (6)
Chinsaba	33.8 (8.8)	20.7 (6.8)	20.8 (2.2)†	25.2 (4.1)	30.4 (1.8)	27.0 (2.2)	1 (6)

Swarnalata	16.8 (7.1)	16.9 (4.2)	21.7 (1.4)	22.9 (3.5)	30.4 (1.8)	30.6 (2.0)	0 (6)
Da Hua Gu	30.4 (7.8)	19.9 (6.8)	33.2 (1.6)	19.3 (1.0)	27.0 (2.2)	-	0 (5)
IR40	25.9 (6.9)	28.7 (2.8)	34.7 (1.2)	21.0 (6.1)	27.0 (2.2)	-	0 (5)
N22	9.4(1.8)	36.0 (1.6)	31.8 (1.8)	32.9 (3.8)	23.5 (1.9)	-	0 (5)
Triveni	18.9 (4.7)	31.7 (0.9)	21.1 (2.0)	29.6 (5.4)	33.9 (2.0)	-	0 (5)
ARC 10239	23.1 (5.3)	36.0 (1.6)	-	34.0 (1.4)	23.5 (1.9)	-	0 (4)
Pokkali	23.0 (8.2)	28.7 (2.8)	-	29.8 (2.0)	27.0 (2.2)	-	0 (4)
Asiminori	30.2 (8.5)	-	-	22.9 (4.3)	30.4 (1.8)	-	0 (3)
IR64	33.8 (8.8)	-	37.7 (0.0)	-	30.4 (1.8)	-	0 (3)
T65	-	32.87	-	-	33.9 (2.0)	30.6 (2.0)	0 (3)
IR56	-	24.8 (2.6)	-	-	30.4 (1.8)	-	0 (2)
IR60	-	12.8 (2.8)	-	-	33.9 (2.0)	-	0 (2)
TN1	33.8 (8.8)	36.0 (1.6)	39.0 (0.0)	27.5 (2.0)	30.5 (4.2)	30.6 (2.0)	
Df	34	32	28	33	38	10	
Error df	68	67	58	68	76	33	
F-value	4.223***	5.680***	10.950***	12.126***	28.077***	16.223†***	

1: *** = $P \leq 0.005$; bold font (with daggers) indicates significantly lower damage than TN1 **at** $\alpha = 0.05$ (Dunnett's test); '†' = variety/line not tested

Table 4 Preferences by South East Asian *Nilaparvata lugens* populations among 39 rice accessions. **Numbers are ranks (SEM in parentheses)**

Variety or breeding line	China	Taiwan	Vietnam	Indonesia	Philippines - Laguna	Philippines - Mindanao	Affected populations (tested populations)
Rathu Heenati	3.3	10.6 (2.6)†	6.7 (3.3)†	6.5 (3.3)†	4.0 (0.7)†	11.0 (4.8)	4 (5)
Balamawee	3.3	10.6 (2.6)†	10.0 (2.3)	14.0 (3.3)†	8.9 (2.0)†	9.8 (3.1)	3 (5)
Swarnalata	27.1	12.1 (7.4)†	7.2 (2.9)†	2.0 (0.2)†	12.8 (1.5)	19.2 (7.4)	3 (5)
PTB33	3.3	10.6 (4.2)†	1.3 (0.2)†	21.5 (2.3)	5.5 (1.2)†	4.8 (1.4)	3 (5)
ARC 6650	27.1	13.9 (1.0)†	21.0 (5.6)	2.0 (0.2)†	26.4 (1.3)	14.4 (4.1)	2 (5)
Babawee	8.1	3.9 (1.0)†	21.0 (5.6)	17.1 (2.1)	8.9(2.0)†	9.6 (3.4)	2 (5)
IR65482-4-136-2-2	27.1	19.9 (6.8)	25.4 (3.2)	13.6 (2.6)†	8.9 (1.8)†	16.5 (5.6)	2 (5)
IR71033-121-15	8.1	13.9 (1.0)†	12.8 (4.2)	10.4 (1.3)†	11.6 (3.0)	20.0 (9.1)	2 (5)
MOI	3.3	7.2 (2.6)†	14.9 (2.6)	5.2 (2.2)†	11.3 (2.5)	14.4 (4.1)	2 (5)
Triveni	13.0	13.9 (1.0)†	34.4 (1.7)	10.4 (1.3)†	15.8 (5.1)	14.6 (8.4)	2 (5)
IR60	27.1	10.6 (3.5)†	14.5 (5.7)	-	18.5 (2.7)	29.7 (1.8)	1 (4)
IR64	-	22.5 (3.5)	10.0 (2.3)	-	10.2 (3.1)†	9.6 (3.4)	1 (4)
ADR52	10.8	10.6 (2.6)†	12.8 (4.2)	30.1 (2.1)	18.0 (2.1)	13.2 (6.5)	1 (5)
IR22	27.1	34.7 (0.8)	34.4 (1.7)	13.6 (2.6)†	32.7 (1.5)	21.4 (7.4)	1 (5)
IR62	8.1	3.9 (1.0)†	14.5 (5.7)	25.8 (6.4)	10.7 (1.5)	4.8 (1.4)	1 (5)
IR65482-7-216-1-2	8.1	31.6 (3.3)	25.4 (3.2)	13.6 (2.6)†	18.6 (4.1)	21.0 (2.8)	1 (5)
IR66	27.1	10.6 (2.6)†	19.3 (3.6)	21.7(5.5)	13.8 (4.0)	14.2 (4.4)	1 (5)
IR72	27.1	17.6 (3.8)	19.3 (3.6)	10.4 (1.3)†	19.8 (4.9)	26.0 (3.1)	1 (5)
IR74	3.3	10.6 (2.6)†	11.3 (5.2)	17.1 (2.1)	13.3 (3.4)	4.8 (1.4)	1 (5)
N'Diang Marie	27.1	18.2 (7.2)	12.8 (4.2)	10.4 (1.3)†	27.3 (3.6)	27.8 (5.8)	1 (5)
Pokkali	13.0	24.7 (5.7)	19.3 (3.6)	10.4 (1.3)†	14.4 (4.0)	22.6 (4.6)	1 (5)
ARC 10239	27.1	31.6 (2.4)	30.5 (2.9)	25.8 (6.4)	30.9 (1.8)	24.5 (8.9)	0 (5)
ARC 10550	27.1	34.7 (0.8)	24.3 (6.4)	32.0 (0.3)	22.3 (3.2)	27.8 (5.8)	0 (5)
ASD7	27.1	18.8 (4.0)	25.4 (3.2)	30.1 (2.1)	24.7 (2.6)	22.6 (4.6)	0 (5)
Chinsaba	27.1	31.6 (2.4)	34.3 (1.7)	32.0 (0.3)	31.3 (1.5)	29.1 (4.4)	0 (5)
IR24	27.1	28.4 (3.2)	29.3 (4.9)	21.3 (5.8)	20.0 (2.7)	26.3 (5.2)	0 (5)
IR40	27.1	31.6 (3.3)	25.4 (3.2)	32.0 (0.3)	30.9 (1.8)	31.6 (3.3)	0 (5)

IR70	13.0	20.4 (4.1)	14.9 (2.6)	17.1 (2.1)	19.8 (2.0)	21.3 (5.2)	0 (5)
Mudgo	27.1	17.6 (3.8)	14.9 (2.6)	26.0 (3.4)	27.0 (2.7)	17.6 (1.5)	0 (5)
N22	27.1	34.7 (0.8)	24.3 (6.4)	32.0 (0.3)	32.7 (1.5)	24.1 (5.8)	0 (5)
Utri Rajapan	27.1	23.6 (6.2)	25.4 (3.2)	30.1 (2.1)	29.4 (1.2)	26.0 (3.1)	0 (5)
Yagyaw	27.1	28.4 (3.2)	25.4 (3.2)	17.1 (2.1)	29.2 (2.0)	24.1 (5.8)	0 (5)
ARC 11367	27.1	25.3 (0.8)	-	17.1 (2.1)	33.6 (0.9)	33.4 (2.1)	0 (4)
Da Hua Gu	27.1	28.4 (3.2)	-	30.1 (2.1)	28.8 (3.3)	29.7 (1.8)	0 (4)
IR56	-	-	14.5 (5.7)	-	10.7 (1.5)	9.6 (3.4)	0 (3)
T65	27.1	-	34.4 (1.7)	-	28.8 (2.2)	32.8 (1.3)	0 (3)
Asiminori	-	-	-	-	30.6 (2.5)	31.6 (3.3)	0 (2)
Jia Nong 66 (T12)	27.1	-	-	-	-	-	0 (0)
TN1	27.1	34.7 (0.8)	30.5 (2.9)	30.1 (2.1)	26.9 (3.6)	23.3 (7.1)	
Df	36	34	34	32	37	37	
Error df	36	70	70	66	149	75	
F-value	NA	7.457***	5.174***	11.271***	8.930***	2.843***	

1: *** = $P \leq 0.005$; bold font (with daggers) indicates significantly lower damage than TN1 at $\alpha = 0.05$ (Dunnett's test); '-' = variety/line not tested

Table 5 Spearman correlations between rank resistance/tolerance of rice varieties according to SSST bioassays with 12 *Nilaparvata lugens* from South and East Asia

	Bangladesh	India - Lludhiana	India - Hyderabad 2010	India - Hyderabad 2007	India - Maruteru	Myanmar	Vietnam	Indonesia	China	Taiwan	Philippines - Laguna	Philippines - Mindanao
Bangladesh	-	0.235(33)	0.188(33)	0.124(36)	0.315(29)	0.444(10)	0.152(34)	0.256(33)	0.260(36)	0.276(35)	0.173(37)	0.328(37)
India - Lludhiana	0.181	-	0.193(33)	0.529(33)	0.390(28)	0.407(9)	0.646(30)	0.168(32)	0.497(33)	0.627(33)	0.562(33)	0.469(33)
India - Hyderabad 2010	0.281	0.281	-	0.362(33)	0.464(28)	0.525(9)	0.307(31)	0.016(32)	0.336(33)	0.391(33)	0.208(34)	0.388(34)
India - Hyderabad 2007	0.471	0.002	0.038	-	0.553(28)	0.425(10)	0.627(33)	0.237(33)	0.466(36)	0.542(34)	0.464(35)	0.379(35)
India - Maruteru	0.096	0.040	0.013	0.002	-	0.414(9)	0.331(27)	0.419(28)	0.424(28)	0.449(29)	0.281(29)	0.213(29)
Myanmar	0.198	0.277	0.146	0.220	0.269	-	0.393(10)	-0.068(9)	0.595(10)	0.243(9)	0.598(10)	0.426(10)
Vietnam	0.390	0.001	0.093	0.001	0.092	0.261	-	0.343(31)	0.561(33)	0.670(33)	0.675(34)	0.574(34)
Indonesia	0.151	0.358	0.930	0.185	0.027	0.862	0.059	-	0.339(33)	0.430(33)	0.461(33)	0.357(33)
China	0.125	0.003	0.056	0.006	0.025	0.069	0.001	0.054	-	0.609(34)	0.743(35)	0.728(35)
Taiwan	0.109	0.001	0.024	0.001	0.015	0.529	0.001	0.012	0.001	-	0.749(35)	0.681(35)
Philippines -Laguna	0.306	0.001	0.239	0.005	0.140	0.068	0.001	0.007	0.001	0.001	-	0.785(37)
Philippines - Mindanao	0.048	0.006	0.023	0.025	0.267	0.220	0.001	0.042	0.001	0.001	0.001	-

Numbers above the diagonal are Spearman's correlation coefficients with degrees of freedom indicated in parentheses; Numbers below the diagonal

are P-values; Bold font indicates significant correlations at $\alpha \leq 0.05$

FIGURE LEGENDS

Fig. 1. Location of **the** participating institutes that screened *Nilaparvata lugens* populations for virulence against resistant rice varieties (see Table 1 for details).

Fig. 2. Dendrogram indicating degree of pair-wise similarity among 12 *Nilaparvata lugens* populations from South and East Asia based on standardized screening of rice varieties for ranked preferences. Similarities were calculated based on correlation coefficients (see Table 4).

Figure 1

Figure 2