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Antixenosis and Tolerance of Rice Genotypes Against Brown Planthopper

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Abstract: Nine genotypes were evaluated under greenhouse conditions for antixenosis and tolerance against brown planthopper (BPH, *Nilaparvata lugens* Stål). In antixenosis studies, proportion of insects settled on a test genotype in relation to the susceptible control TN1 was recorded, with significantly lower proportion of nymphs (55.22%–59.18%), adult males (60.33%–60.75%), and adult females (80.56%–79.26%) settled on RP2068-18-3-5 and Ptb33 in relation to those on TN1. Based on number of feeding sites, the test genotypes were ranked in order from the highest to the lowest as RP2068-18-3-5, Ptb33, MR1523, Rathu Heenati, Sinnasivappu, ARC10550, MO1, INRC3021 and TN1. The order was exactly reverse in terms of fecundity expressed as number of eggs laid per female. In tolerance studies, days to wilt, functional plant loss index and plant dry weight loss to BPH dry weight produced were recorded. RP2068-18-3-5, Rathu Heenati and Ptb33 performed better than the other test genotypes. These results helped in relative quantification of BPH resistance levels in the genotypes. RP2068-18-3-5, a new effective source of BPH resistance, can be used in resistance breeding after tagging of resistant genes/QTLs linked to different parameters of antixenosis and tolerance with selectable molecular markers.

Key words: antixenosis; molecular marker; *Nilaparvata lugens*; resistance breeding; rice; tolerance

Rice (*Oryza sativa* L.) is extensively cultivated under the most diverse ecosystems of tropical and sub-tropical regions of the world. With a projected increase in world population to 9–10 billion by 2050 along with the predicted water scarcity, decrease in arable land and the impending global climate change, it is a great challenge to meet the food requirements of these persons. Among various biotic constraints for rice production, insect pests are of prime importance (Heong and Hardy, 2009). Of over 100 species of insects reported as pests of this crop, 20 are of major economic significance (Prakash et al, 2007). The brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), is a typical phloem sap feeder that has remerged as the treat to rice production in Asia (Chen and Cheng, 1978; Normile, 2008; Heong and Hardy, 2009; Prasannakumar et al, 2013). The plant would suffer 40% to 70% yield loss if attacked by 100–200 first instar nymphs of BPH at 25 d after rice seedling transplanting (Bae and Pathak, 1970). The international conference held in 2010 exclusively on rice planthoppers analyzed the causes and consequences of BPH outbreak in many Asian countries (IRRI, 2010).

Both nymphs and adults of BPH suck sap from the lower portion of the plant, which results in yellowing leaves, reducing tillering number and plant height, and increasing in unfilled grains. Feeding also causes the reduction in chlorophyll and protein content of leaves and rate of photosynthesis, and even in case of severe attack, it causes extensive plant mortality referred to as ‘hopper burn’ symptom (Watanabe and Kitagawa, 2000; Liu et al, 2008; Horgan, 2009; Vanitha et al, 2011). BPH also transmits virus diseases like grassy stunt, ragged stunt (Ling et al, 1978) and wilted stunt (Chen et al, 1978). Monitoring of rice fields regularly helps in timely detection of its incidence and helps in effective pest management. Many insecticides are recommended for the pest control, but blanket application of these

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chemicals disrupts the natural balance of rice ecosystem (Sarao and Mangat, 2014). Cultivation of resistant varieties is the better and environmentally safe alternative (Song et al, 2002). Such varieties will also help in conservation of natural enemies, increasing their effectiveness (Gurr et al, 2011) and minimizing the pesticide applications (Panda and Khush, 1995; Sharma, 2007). Hence, breeding programme for development of BPH resistant varieties with different mode of host plant resistance is extremely important.

Screening rice germplasm at global level and breeding BPH resistant rice varieties were initiated during 1970s, and several resistant varieties have been released for cultivation (Khush and Brar, 1991; Jena et al, 2005; Sun et al, 2005; Chen et al, 2006; Brar et al, 2009; Kumar and Tiwari, 2010; Bentur et al, 2011; Li et al, 2011). However, resistance in many of these varieties has been overcome by virulent biotypes. Also, many of the 29 BPH resistance genes identified so far are not effective in India. No detailed studies have been conducted in India to evaluate relative performance of BPH resistant rice genotypes. These studies are especially valuable in resistance gene/QTL tagging and mapping (Fujita et al, 2013; Sai et al, 2013; Ali and Chowdhury, 2014). Keeping this objective in mind, present experiments were conducted to study antixenosis and tolerance levels in selecting rice genotypes with diverse genetic background.

MATERIALS AND METHODS

Insects

The source BPH population was collected from rice fields of Punjab Agricultural University, Ludhiana, India. Insects were collected during 2007 and continuously reared under greenhouse conditions on 30-day-old TN1 rice plants at the Rice Research Laboratories of Department of Plant Breeding and Genetics positioned at 30°54′ N and 75°48′ E at (28 ± 2) °Ċ, 75% ± 5% relative humidity and 14 h light/10 h dark photoperiod according to Heinrichs et al (1985).

Rice materials

The seeds of nine rice genotypes, RP2068-18-3-5, Rathu Heenati, Sinnasivappu, MR1523, MO1, ARC10550, INRC3021, Ptb33 and TN1, were received from the Indian Institute of Rice Research (formerly Directorate of Rice Research), Hyderabad, India. The pre-germinated seeds of the test genotypes were sown in pots or trays, depending on the experiment, containing well puddled soil during wet season in 2010 and 2011. All the test plants were raised in an insect-proof greenhouse. There were three replications of each genotype, and in each replication, there were five plants except for settling behavior studied. The mean of these five plants comprising one replication was used for data analysis.

Antixenosis studies

Settling behavior of nymphs

In this experiment, pre-germinated seeds of the test genotypes were sown in random rows, 3.5 cm apart, in a seed box (45 cm × 35 cm × 10 cm). Each row contained 10 seeds. The susceptible control TN1 was sown in two border rows and in the center of the box. The tray was kept in dark place to enhance seedling growth. The 10-day-old seedlings were infested with the 2nd–3rd instar hopper nymphs with 6–8 nymphs per seedling. The tray was covered with light-transmitting nylon mesh to prevent escape of nymphs. The number of nymphs settled on each seedling was counted at 1, 2 and 3 d after infestation. The seedlings were disturbed after each count for reorientation of the hopper nymphs.

Settling behavior of adults

The tested genotypes were grown in small plastic pots and kept in water trough. About 200 pairs of adults were released on 30-day-old seedlings under free choice test. Number of male and female adults alighting on different genotypes was counted at 4, 8, 12, 24, 48, 72 and 96 h after release. The seedlings were disturbed after each count for reorientation of the insects.

Feeding marks

In a separate experiment, the feeding marks were observed following the method of Natio (1964). To quantify the role of insects while feeding on different genotypes, a pair of newly emerged adults starved for 1 h was confined in mylar cage on 30-day-old caged uninfested plants of each tested genotype. The feeding marks were observed under microscope after 24 h of feeding by removing the plants from the pots and treated with 0.1% Rhodamine B Analytical Reagent dye for 15 min.

Number of eggs

Two pairs of newly emerged adult insects were released on caged uninfested plants. At 5 d after release, the adults were removed and eggs were counted according to the method of Khan and Saxena (1985).

Tolerance studies

To study the level of tolerance, 30-day-old seedlings of each genotype were covered with a mylar cage with well-ventilated windows. Twenty-five 2nd–3rd instar

hopper nymphs were introduced onto each plant. Similar set of uninfested plants were maintained. When plants started to wilt, planthoppers were collected, oven-dried for 48 h and weighed. Infested and uninfested plants were removed from the pots along with roots, washed properly to remove soil and oven-dried for 72 h to calculate functional plant loss index using the formula of Panda and Heinrichs (1983): Functional plant loss index (FPL, %) = (1 – Dry weight of infested plant / Dry weight of uninfested plant) × 100; Plant dry weight loss to BPH dry weight produced (PDWL, mg) = (Dry weight of uninfested plant – Dry weight of infested plant) / Dry weight of BPH progeny on infested plant.

Statistical analysis

The data obtained from various experiments were statistically analyzed in a completely randomized design using analysis of variance (ANOVA) with the help of IRRISTAT 4.0 developed by the Biometrics Unit of International Rice Research Institute, the Philippines. The different treatment means were separated by least significant difference test (LSD) at $P = 0.05$ (Gomez and Gomez, 1984). All the data were checked for normality before it was subjected to analysis. Data which lacked normality were transformed using arcsine and square root transformations.

RESULTS

Antixenosis studies

Settling behavior of nymphs

The settling behavior of nymphs on the first day after release differed significantly among the genotypes ($F_{8,18} = 213.77$, $P \leq 0.001$). Among different genotypes, the least number of nymphs settled on Ptb33, followed by RP2068-18-3-5 and Rathu Heenati (Fig. 1). Similarly, on the second day of observations, the settling behavior of nymphs differed significantly among different genotypes ($F_{8,18} = 154.79$, $P \leq 0.001$). The least number of nymphs settled on RP2068-18-3-5 and Ptb33. Likewise, on the third day of observations, the settling behavior of nymphs differed significantly among different genotypes ($F_{8,18} = 173.36$, $P \leq 0.001$). All most similar settling behavior of nymphs was observed on all the observation days. Overall, the number of nymphs settled 55.22% less on RP2068-18-3-5, 59.18% on Ptb33 and 49.73% on Rathu Heenati in relation to the susceptible control TN1 (Table 1).

Settling behavior of adult male

The settling behavior of adult male at 4 h after release differed significantly among different genotypes ($F_{8,18} = 60.80$, $P \leq 0.001$). The maximum number of adult males settled on susceptible control TN1, followed by INRC3021 and ARC10550. Significantly lower number of adult males settled on RP2068-18-3-5, Ptb33 and Rathu Heenati as compared with TN1 (Fig. 2). Likewise, the settling behavior of adult males at 8 h after release differed significantly among different genotypes ($F_{8,18} = 63.83$, $P \leq 0.001$). Similar trend was observed at 12 ($F_{8,18} = 40.48$, $P \leq 0.001$), 24 ($F_{8,18} = 38.02$, $P \leq 0.001$), 48 ($F_{8,18} = 25.24$, $P \leq 0.001$), 72 ($F_{8,18} = 16.79$, $P \leq 0.001$) and 96 h ($F_{8,18} = 19.30$, $P \leq 0.001$) after release. Mean of all the observations also differed significantly among different genotypes ($F_{8,54} = 53.33$, $P \leq 0.001$).

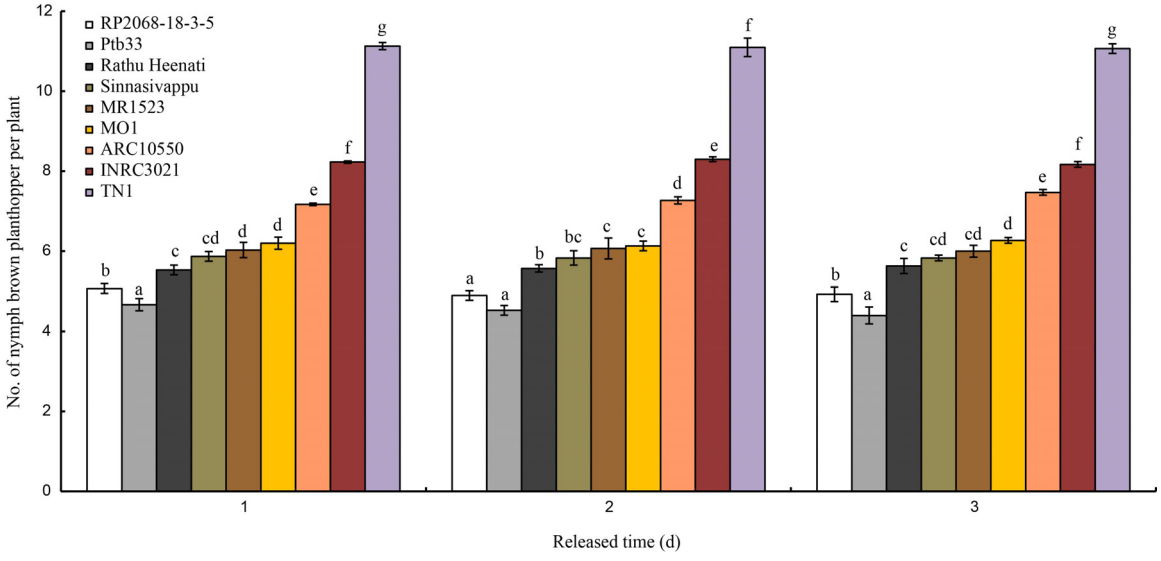

Fig. 1. Number of nymph brown planthopper per plant settled on different genotypes.

Different letters represent significant difference at the 0.05 level in each group. Bar represents the standard error.

Table 1. Reaction of rice genotypes to *Nilaparvata lugens*: Antixenosis.

Genotype	Gene	No. of nymph settled per plant	No. of adult males settled per plant	No. of adult females settled per plant	No. of feeding marks per plant	No. of eggs per plant
RP2068-18-3-5	Unknown	4.97 ± 0.05 b	4.71 ± 0.27 a	2.86 ± 0.14 a	20.00 ± 0.58 a	94.33 ± 0.88 a
Ptb33	*bph2* + *Bph3*	4.53 ± 0.08 a	4.76 ± 0.19 a	3.05 ± 0.13 a	18.67 ± 1.33 a	88.33 ± 1.45 a
Rathu Heenati	*Bph3* + *Bph17*	5.58 ± 0.03 c	5.33 ± 0.36 ab	3.00 ± 0.22 a	12.33 ± 0.88 b	109.67 ± 1.20 b
Sinnasivappu	Unknown	5.84 ± 0.01 d	5.86 ± 0.19 b	4.14 ± 0.37 b	11.33 ± 0.67 bc	123.33 ± 1.67 c
MR1523	Unknown	6.03 ± 0.02 d	7.57 ± 0.48 c	6.14 ± 0.12 c	13.33 ± 1.20 b	126.33 ± 1.33 c
MO1	*WbphO*	6.20 ± 0.04 de	8.09 ± 0.29 c	8.90 ± 0.17 d	8.67 ± 0.88 cd	149.33 ± 1.45 d
ARC10550	*bph5*	7.30 ± 0.09 f	9.28 ± 0.42 d	11.57 ± 0.17 e	6.33 ± 0.33 d	182.33 ± 1.76 e
INRC3021	Unknown	8.23 ± 0.04 g	9.71 ± 0.22 d	12.05 ± 0.26 e	7.33 ± 1.20 d	204.00 ± 1.53 f
TN1	None	11.10 ± 0.02 h	12.00 ± 0.50 e	14.71 ± 0.23 f	6.67 ± 0.67 d	221.33 ± 1.20 g
LSD ($P \leq 0.05$)		0.04	0.17	0.12	0.51	0.36

Data were shown as Mean ± *SE*; Data in the same column followed by different letters represent significant differences at the 0.05 level.

Overall, proportion of adult males settling on RP2068-18-3-5 (60.75%), Ptb33 (60.33%) and Rathu Heenati (55.58%) less in comparison with those on the susceptible control TN1 (Table 1).

Settling behavior of adult female

The settling behavior of adult females at 4 h after release differed significantly among different genotypes ($F_{8,18} = 122.35$, $P \leq 0.001$). Among different genotypes, significantly higher numbers of adult females settled on susceptible control TN1, followed by INRC3021. Significantly lower number of adult females settled on Rathu Heenati, followed by RP2068-18-3-5 and Ptb33 (Fig. 3). The settling behavior of adult females at 8 h after release differed significantly among different genotypes ($F_{8,18} = 93.49$, $P \leq 0.001$). Similar trend was observed at 12 ($F_{8,18} = 87.30$, $P \leq 0.001$), 24 ($F_{8,18} = 212.37$, $P \leq 0.001$), 48 ($F_{8,18} = 85.75$, $P \leq 0.001$), 72 ($F_{8,18} = 107.13$, $P \leq 0.001$) and 96 h ($F_{8,18} = 49.67$, $P \leq 0.001$) after release (Fig. 3). Overall, number of adult females settling on different genotypes differed significantly ($F_{8,54} = 345.26$, $P \leq 0.001$) (Table 1).

Feeding marks

Number of feeding marks produced by the insect also differed significantly among different genotypes ($F_{8,18} = 16.25$, $P \leq 0.001$). Based on the number of feeding marks, the test genotypes were ranked in order from the highest to the lowest as RP2068-18-3-5, Ptb33, MR1523, Rathu Heenati, Sinnasivappu, MO1, INRC3021, TN1 and ARC10550 (Table 1).

Fecundity

The fecundity differed significantly among different genotypes ($F_{8,18} = 258.60$, $P \leq 0.001$) (Table 1). It was significantly lower on RP2068-18-3-5 and Ptb33, followed by Rathu Heenati and Sinnasivappu in comparison with that on TN1 (Table 1).

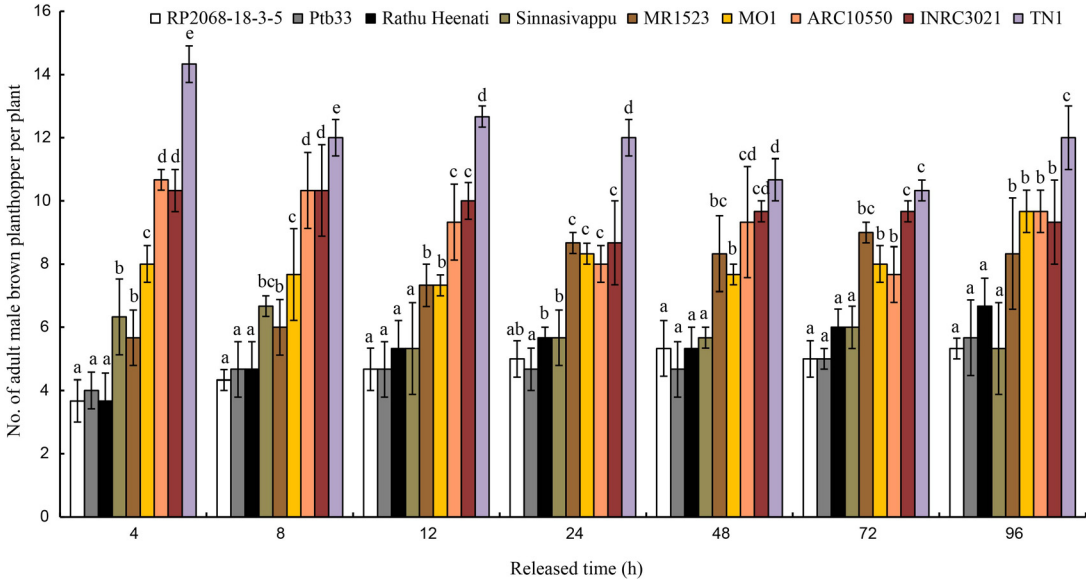

Fig. 2. Number of adult male brown planthopper per plant settled on different genotypes.
Different letters represent significant difference at the 0.05 level in each group. Bar represents the standard error.

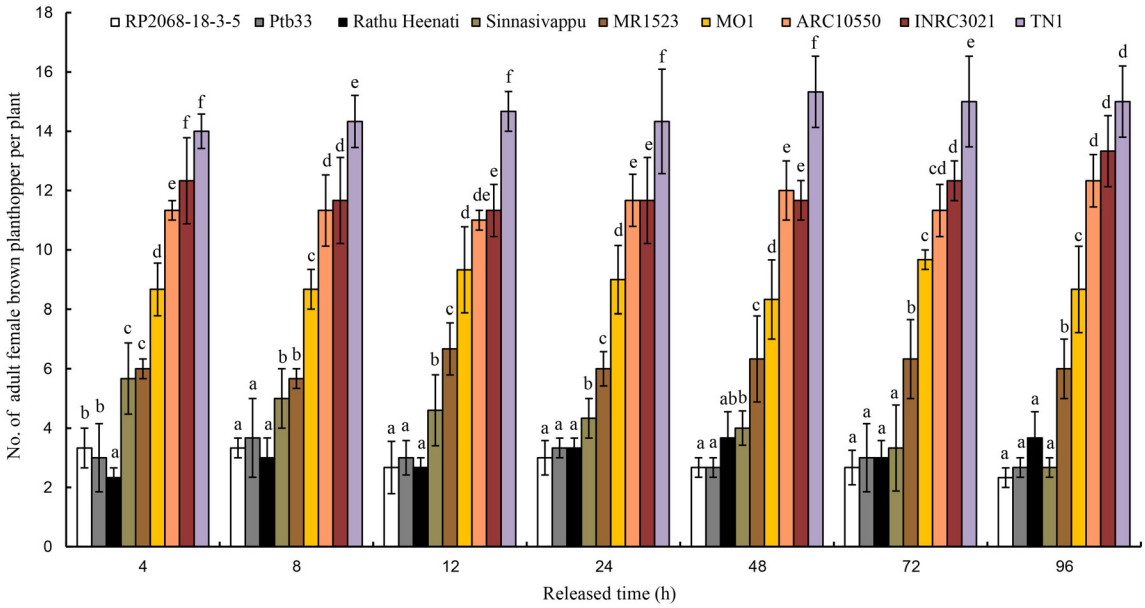

Fig. 3. Number of adult female brown planthopper per plant settled on different genotypes.
Different letters represent significant difference at the 0.05 level in each group. Bar represents the standard error.

Tolerance studies

The test genotypes differed significantly in respect of days to wilt under constant pest pressure (Table 2, $F_{8,18}$ = 277.00, $P \leq 0.001$). Ptb33 and RP2068-18-3-5 wilted significantly later compared to TN1.

The functional plant loss indices differed significantly among the test genotypes ($F_{8,18}$ = 855.62, $P \leq 0.001$). It was the lowest in Ptb33 and RP2068-18-3-5, followed by Rathu Heenati, but the highest in TN1 (Table 2).

The plant dry weight loss to BPH dry weight produced differed significantly among the genotypes ($F_{8,18}$ = 509.21, $P \leq 0.001$). It was the least in Ptb33 and RP2068-18-3-5, followed by Rathu Heenati (Table 2).

DISCUSSION

Host-plant resistance is the core of pest management system because it is specific to the target pest and has no adverse effect on the non-target organisms. To evaluate germplasm, host choice test is an indicator of the antixenotic factor. Several reports suggest higher number of BPH settling on susceptible genotypes compared to resistant ones (Samal and Misra, 1990; Qiu et al, 2012; He et al, 2013), and also in case of whitebacked planthopper (WBPH) (Shukla, 1984; Bhattal, 1992; Ramesh et al, 2014). Time series of observations suggest that nymphs or adults tend to move to the susceptible plants with increasing exposure. Thus, it appears that antixenosis is more guided by feeding response rather than olfactory or tactile stimuli. Some studies involving steam distillation of resistant plants being sprayed on susceptible plants suggested role of volatile chemicals or surface wax in determining insect preference (Horgan, 2009), though more studies

Table 2. Effect of *Nilaparvata lugens* on rice genotypes: Tolerance.

Genotype	Days to wilt (d)	FPLI (%)	PDWL (mg)
RP2068-18-3-5	13.58 ± 0.29 a	19.17 ± 0.60 a	10.50 ± 0.29 a
Ptb33	13.87 ± 0.24 a	17.29 ± 1.15 a	9.16 ± 0.42 a
Rathu Heenati	8.80 ± 0.20 b	25.67 ± 0.58 b	14.00 ± 0.39 b
Sinnasivappu	7.27 ± 0.07 c	31.51 ± 0.72 c	25.21 ± 1.27 c
MR1523	8.27 ± 0.18 b	38.23 ± 0.39 d	26.76 ± 0.74 c
MO1	7.53 ± 0.35 c	61.81 ± 0.79 f	32.79 ± 0.77 d
ARC10550	6.40 ± 0.12 d	66.59 ± 0.77 g	66.50 ± 1.42 f
INRC3021	5.40 ± 0.23 e	56.27 ± 0.85 e	51.30 ± 0.68 e
TN1	5.13 ± 0.07 e	85.37 ± 0.56 h	113.53 ± 1.60 g
LSD ($P \leq 0.05$)	0.09	1.49	0.32

FPLI, Functional plant loss index; PDWL, Plant dry weight loss to BPH dry weight produced.
Data were shown as Mean ± *SE*; Data in the same column followed by different letters represent significant differences at the 0.05 level.

are needed to confirm these observations. Defense responses in the form of physical barriers that impede insect-pest access to plant tissues affect the insect feeding (Hedin, 1983). These results were corroborated by the findings of Samal and Misra (1990), who reported that more adults of BPH settled on susceptible variety than resistant one. Likewise, Alagar and Suresh (2007a) observed that the settling response of nymphs was more apparent at 24 h after infestation on all the tested genotypes. The average number of nymphs was lowest on KAU1661 (4.3 per plant) than susceptible control TN1 (7.7 per plant), while on Basmati 370, the highest per cent of unhatched eggs (25.4%) and the lowest number of total eggs laid (130.8 per plant) were recorded. Shukla (1984) and Bhattal (1992) also reported that WBPH female adults show distinct preference for the susceptible rice varieties than the resistant ones.

Genetic basis of antixenosis is just emerging. Only several QTLs linked to different parameters of antixenosis against both BPH and WBPH are reported in rice (Fujita et al, 2013). Qiu et al (2013) reported a QTL *Qbph8* along with the major gene *Bph6* in rice variety Swarnalata accounting for antixenosis in BPH. Average number of BPH settled on the *Qbph8* plants is less than 93-11 plants over the 24–120 h observation period. Further, less BPH insects were observed on *Bph6*+*Qbph8* plants compared to the *Bph6* or *Qbph8* plants alone, indicating a stronger antixenotic effect in pyramided plants. A gene coding for sesquiterpene synthase (STPS) in Rathu Heenati is reported to influence antixenosis during the first 120 h of BPH interaction with the rice (Kamolsukyunyong et al, 2013). Interestingly, our results showed significantly different settling pattern between males and females. It is possible that preference by adult females for settling also reflects preference for oviposition.

Feeding varied from genotype to genotype and it determined insect food intake. It includes probing response, or the application of proboscis and introduction of stylets into the food source and duration of feeding. In our observations, we found more restless behavior of BPH on RP2068-18-3-5 and Ptb33 as insects moved all over the leaf sheath to find suitable feeding site. It suggested that the test plants presented some mechanical barrier to penetration for probing or plant sap was not palatable to the insects. These differences were reflected due to genetics of the genotypes (Heinrichs and Rapusas, 1983; Shukla, 1984; Gunathilagaraj and Chelliah, 1985; Bhattal, 1992; Du et al, 2009). These results are also supported by Bhattal (1992), who reported that the adult WBPH makes significantly higher number of feeding probes on NCS2041, ARC11367 and PR109 than TN1. These observations have been further substantiated with electropenetrogram studies (Ghaffar et al, 2011).

Summary of the antixenosis studies showed that among genotypes, Ptb33 with *bph2*+*Bph3* performed better than RP2068-18-3-5 only in terms of settling of nymphs, while it was on par with it in the rest of four tests. Rathu Heenati with *Bph3*+*Bph17* was on par with these two genotypes in settling of male and female tests while being significantly poor performer in the other three tests. Significantly more males settled on the resistant genotypes than susceptible ones, while more females settled on the susceptible genotypes. In contrast, the susceptible control TN1 with no resistance gene performed significantly poor in four of the five tests in comparison with all the other eight test genotypes. However, in terms of number of feeding marks, MO1 and INRC3021 with unknown BPH resistance genes, and ARC10550 with *bph5* were on par with TN1, but were significantly different with most of the other genotypes. In overall performance Sinnasivappu, MR1523 and MO1 with unknown BPH resistance genes were observed to be intermediate.

Tolerance is the capacity to produce a variety of high quality and yield despite insect infestation and this component of host plant resistance is less exploited. Panda and Heinrichs (1983) developed elaborate FPLI method and identified rice varieties like Triveni, Kanchana and UtriRajapan with tolerance as predominant component of BPH resistance. Alam and Cohen (1998) refined the tolerance parameter as PDWL per unit dry weight of insect produced. Chen et al (1978) reported that BPH population caused the reduction in plant dry weight. Likewise, Geethanjali et al (2009) proposed a simple test of day to wilt for tolerance parameter, which is being rapidly accepted (Alagar and Suresh, 2007b; Ramesh et al, 2014). Alagar and Suresh (2007b) reported that 30- and 60-day-old plants of ARC10550, KAU1661 and ARC6650 take significantly longer period for wilting than TN1. Similarly, Qiu et al (2014) submitted *Bph7* in rice variety T12 to mainly account for tolerance component of resistance against BPH. Likewise, Ramesh et al (2014) suggested a major dominant gene *Wbph12*(t) to confer tolerance to WBPH in Sinnasivappu. Since tolerant trait is believed to exert less selection pressure on the insect, such gene may contribute to durable resistance.

Summary of tolerance studies showed that

performance of RP2068-18-3-5 and Ptb33 was on par in all the three parameters while that of Rathu Heenati was followed. The susceptible control TN1 performed distinctly different from all the other genotypes except INRC3021 in respect of days to wilt test. This test grouped all the test genotypes into five distinct groups, RP2068-18-3-5 and Ptb33 in the first group, Rathu Heenati and MR1523 in the second group, Sinnasivappu and MO1 in the third group, ARC10550 alone in the fourth group, and INRC3021 and TN1 in the fifth group. From these experiments, it can be concluded that host selection can affect BPH settling and feeding. The restless behavior of BPH on the resistant varieties also increases their vulnerability to the natural enemies. Rice genotypes RP2068-18-3-5 and Ptb33 both displayed high levels of antixenosis and tolerance to BPH. This will provide better option for plant breeders and biotechnologists to develop suitable varieties to combat BPH. It is apparent from our study that development of a variety which can disrupt the settling and feeding of BPH as well as low plant biomass loss could play a pivotal role in pest management strategies.

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