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MECHANISMS AND GENETICS OF RESISTANCE TO BROWN PLANTHOPPER, *NILAPARVATA LUGENS* (STAL) IN RICE, *ORYZA SATIVA* L. - A REVIEW

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ABSTRACT

Plant resistance has been recognised as the most desirable and economic tactic in the management of rice brown planthopper, *Nilaparvata lugens* (Stal). Three modalities or mechanisms of resistance has been utilised well in breeding for resistance. The recent development in the use of molecular markers in QTL analysis facilitate easy manipulation of phenotypically complex traits. This paper reviews the studies of mechanisms biochemical bases and genetics of resistance to brown planthopper in rice.

The Brown planthopper, *Nilaparvata lugens* (Hemiptera : Delphacidae) (Stal) was formerly a minor pest of rice in South and South east Asia but now has become a major problem throughout these regions (Dyck and Thomas, 1979). The history of *N. lugens* as a pest of Green Revolution in Asian rice production has been well documented (Heinrichs and Mochida, 1984; Gallagher *et al.*, 1994). Following the introduction of high yielding varieties and chemical insecticides the BPH has become serious constrain in rice production. Host plant resistance is a major economic and desirable practice for the management of BPH (Chelliah, 1985). Resistant rice varieties can play a complementary role in minimizing insecticide use and to promote biological control in tropical rice (Way and Heong, 1994). In many instances, resistant cultivars synergize the effect of biological control agents that suppress pest population. The release of resistant varieties by the International Rice Research Institute beginning with IR 26 in 1973 provided effective control of *N. lugens*. Since then large number of resistant sources have been identified for the planthoppers. Systematic evaluation of the world collection of *Oryza sativa* began in 1967 and by 1986, 400 accessions out of 50,000 accessions screened have been identified as having resistance to *N. lugens*. (Rapusas and Heinrichs, 1987). Most of the resistant accessions are from India and Srilanka. In addition, 132 wild *oryza* spp. accessions have been identified as resistant (Heinrichs, 1988). Breeding programmes for BPH resistance have been established in most of the Asian Countries. Gunathilagaraj and Ganeshkumar (1997) reviewed the sources of resistance to planthopper in India. The important BPH resistant varieties released in India *viz.*, Jyothi, CO 42, Sonasali, PY 3, Suraksha, Chandan, Vijram, Pavizham, MTU 4870 and Bhadra. But biotype selection in BPH has impeded the development of resistant varieties in many areas. Understanding the mechanisms and genetics of resistance is important before evolving resistant varieties. These are three mechanisms of resistance *viz.*, antixenosis, antibiosis and tolerance (Painter, 1958). Rice breeders identified ten major genes for conferring resistance to various populations of BPH. The resistance mechanisms are believed to be associated with minor genes which could be exploited in breeding for polygenic resistance to BPH. Khush (1979) viewed that varieties with more than one gene for resistance are expected to have a longer useful life as they slow down the development of biotype.

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Plant breeders and entomologists working on rice and other crops have long recognised that several traditional varieties have a rich source of minor resistant genes (Gallun and Khush, 1980; Thomas and Waage, 1996). Here, the different mechanisms of resistance and genetic aspect resistant breeding has been reviewed. Under genetics of resistance, major gene resistance and polygenic resistance are involved. In polygenic resistance the recent concept of Quantitative trait loci (QTL) analysis for BPH resistance has also been reviewed in the paper.

1. Mechanism(s) of resistance

The mechanisms of resistance need to be studied for ascertaining the degree of resistance among plants and it is essential for the development of durable resistant varieties. These resistant factors are heritable and they operate in a concerted manner to render plants unsuitable for insect utilization. The concept of resistance mechanisms could be useful to entomologists and breeders as they work together to develop varieties with most effective type of resistance against pest population (Heinrichs *et al.*, 1985). The main mechanisms of plant resistance to the BPH were identified as non-preference and antibiosis (Pongprasert and Weeraput, 1979).

1.1. Antixenosis

Antixenosis is non-preference type of resistance and found to be involved in most of the BPH resistant rice accessions (Song *et al.*, 1972; Pongprasert and Weeraput, 1979; Ho, 1981; Seetharaman *et al.*, 1984; Li *et al.*, 1995) (Table 1). Orientation response of insects is one of the important factor that determines the preference of food plant (Saxena *et al.*, 1974). The rice plant characters showed that the BPH was attracted to the plants by their green colour, humidity and odour (Saxena and Pathak, 1977). Antixenosis in resistant variety was suggested to be more due to gustatory rather than olfactory or visual influence (Sogawa, 1973; Pathak and Saxena, 1980). Though morphological characters may influence the alighting response of the hoppers, they were not considered as main source of non-preference because the hoppers could distinguish the resistant and susceptible varieties, when the plants were morphologically identical (Gunathilagaraj and Chelliah, 1985). The BPH showed no significant preference in alighting on different varieties, but the insect did not stay on resistant line for sustained feeding (Sogawa and Pathak, 1976).

1.2. Antibiosis

Antibiosis type of resistance disrupt the normal metabolic process of insects and affect their biology. Resistance is antibiotic when insect feed upon a resistant plant (Panda and Khush, 1995). Antibiosis mechanism in resistant varieties reduces pest population cumulatively by reduced rate of reproduction, length of reproductive life of adults by increasing developmental period and mortality of immature stages (Tingey, 1981). Antibiosis was expressed in terms of low population levels (Reddy and Kalode, 1981; Murugesan and Chelliah, 1982), reduced feeding and oviposition (Velusamy, 1982) and slower growth rates (Bharathi, 1982) when BPH was allowed to develop on resistant varieties. Soundararajan *et al.* (2002) described the antibiosis effect of rice double haploid lines on the population buildup, difference in wing form development and sex ratio.

The rate of population growth could be a reliable parameter in evaluating the degree of resistance (IRRI, 1980). In this studies the BPH population was allowed to develop on particular variety or accession to next generation. The population in the second generation was considered for evaluating the antibiosis for the development of BPH (Heinrichs *et al.*, 1985). It gives a cumulative antibiosis effect of particular rice variety. Low fecundity on resistant varieties was a potential

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Table 1. Varieties exhibiting antixenosis to *N. lugens*

Variety/accession	Reference
Andaragawewa	Cheng and Chang (1979)
ARC 5780, ARC 5988	Reddy and Kalode (1981)
ARC 5785, BKN 6809-74-40, HR 12, MCM 1, MCM 2, Ptb 20, XB 5	Pathak and Khush (1979)
Ptb 21, Ptb 33	Kalode and Krishna (1979)
ARC 6650, MR 1523	Pongprasert and Weeraput (1979)
ARC10550, ASD11	Bharathi (1989)
ASD 7, CO 22, Mudgo, Vellailangayan, SLO12	IRRI (1970)
ASD1 1, IET 6315, V.P. Samba	Velusamy (1982)
Babawee, Balamawee, Gangala, Hathiel, H 105, Kuruhondarawala, Murungakayang, Pannelti, Sudurvi 305, Thrissa	IRRI (1971)
CR 115-107	Dharmareddy and Misra (1995)
Dikwee	IRRI (1977)
EK 1263, Heenkhulama, Ptb 18, Rathu Heenati, Tibiriwewa, Sinnakayam	Cheng and Chang (1979)
Garunbaly	IRRI (1967)
IR 8, Shoa-hi-den, Panduruwee	IRRI (1967)
IR 26	Ho *et al.* (1982)
IR 64	Soundararajan *et al.* (2001)
Lin Shui 620	Yu *et al.* (1991)
MGL 2	Song *et al.* (1972)
O. officinalis	IRRI (1982)
Tibiriwewa	Cheng and Chang (1979)
TKM6	IRRI (1966)

antibiosis factor leading to considerable reduction in the population buildup of BPH with compared with that in a susceptible variety (Bharathi, 1982). A significant low BPH population was recorded on Ptb 33 followed by IR 64 and they were high in TN 1. Kim *et al.* (1982) reported that even the resistant varieties could support high population buildup and observed a decline in population levels when the plants matured.

Survival rate determines the effect of antibiosis factors on nymphal stage (Heinrichs *et al.*, 1985). Very low nymphal survival and higher nymphal mortality of BPH were observed in resistant varieties (Misra *et al.*, 1986). Higher nymphal mortality caused lower rate of adult emergence in the resistant varieties (Choi *et al.*, 1973; Lee and Park, 1976). Pathak (1971) concluded that varieties which permitted the least survival of nymphs were truly resistant. Nymphal survival also depends on age of the plant. Nalini and Gunathilagaraj (1992) reported low survival of first instar WBPH, *Sogatella furcifera* H. nymphs on resistant rice accessions. The rate of survival reduced progressively with the increase in plant age. Forced feeding of hoppers on resistant accessions containing certain toxic or deterrent substances had detrimental effect on survival rate. The essential nutrients required for normal growth could not be obtained as ingestion period was short or the plant itself lack that particular nutrient. The adverse effect on nymphal survival indicated operation of antibiosis factor. (Heinrichs and Rapusas, 1983).

The nymphal development period was prolonged in resistant varieties than in susceptible ones (Pongprasert and Weeraput, 1979). Sogawa and Pathak (1976) suggested that prolonged nymphal period on resistant accession 'Mudgo' might be due to reduced

ingestion of adequate quantities of nutrients required by BPH or due to lack of vital nutrients required by the insect or due to the toxic substances in the plants. The developmental time of BPH was mainly affected by the increase in the length of nymphal stage (Cheng and Sun, 1992). Velusamy (1989) reported that differences in nymphal growth were significant among resistant wild rices. The nymphs never became adults on *Oryza officinalis* Wall. The insects probed readily and fed for longer period on susceptible plants, on resistant varieties the insect made brief and repeated probes that reduced the effective ingestion period and assimilation of food in the body or the varieties had inadequate or unsuitable nutrients for nymphal development which would have prolonged the nymphal duration (Koyama, 1985). Painter (1953) suggested that in some instances, the resistance might be attributed to the complete absence of specific nutrients required by the insect. Although no evidence could be presented to support this view, that the resistant varieties are inadequate or unsuitable for nymphal development is not ruled out. Such adverse effects on resistant varieties on the biology of *N. lugens* were reported by Sogawa and Pathak (1970).

Measuring honeydew excretion is a tool for assessing antibiosis on feeding activity of sucking insects on resistant and susceptible varieties (Auclair, 1958). Several methods *viz.*, filter paper method (Paguia *et al.*, 1980), bromocresol green indicator method (Pathak and Heinrichs, 1982), parafilm sachet method (Pathak *et al.*, 1982) and P^{32} radio active method (Velusamy, 1982) have been developed to assess honeydew excretion of *N. lugens*. Low honeydew excretion was related to BPH resistance in rice varieties (Sogawa and Pathak, 1976). Filter paper method for measuring honeydew is simple and can substitute for time consuming population buildup studies (Soundararajan *et al.*, 2001). In filter paper method, the honeydew excreted by hoppers, dropped directly on filter paper and measured. Feeding activity of *N. lugens* was high on susceptible and reduce or nil feeding was noticed on resistant varieties (Paguia *et al.*, 1980).

The varieties or accessions exhibited different types of antibiosis parameters were listed in Table 2.

1.3. Tolerance

The term tolerance is different from resistance in the aspect that the latter stems from insect response to certain host plant characteristics and former expressed from a plant's response to insect attack (Ho *et al.*, 1982). Tolerance is highly attractive concept possibly being superior to specific resistance as means of protecting plants from pest damage (Browning and Frey, 1969). The tolerant cultivars have little selective advantage on the host to develop new biotypes (Panda and Heinrichs, 1983). Tolerant plants support large insect population with little damage or yield loss and have value in maintaining predator and parasite population (Horber, 1972). The mechanisms of resistance to *N. lugens* in the rice lines bred from the *indica* cultivar Mudgo were determined by Hirao and Todoroki (1975). The result of greenhouse and field tests indicated that non-preference and tolerance played important role in resistance. Ho *et al.* (1982) reported that the cultivar Triveni possesses tolerance to *N. lugens* damage both at the vegetative and manture growth stage. Yield reduction caused by feeding of *N. lugens* was about 40% on 35, 50 or 75 days old plants when infested with 400 member of *N. lugens*, whereas it was almost 100% on the susceptible cultivar TN 1. Panda and Heinrichs (1983) determined the levels of tolerance and antibiosis to *N. lugens*. Tolerance was measured as plant weight loss caused by *N. lugens* feeding. The detailed methodology

Table 2. Varieties exhibiting antibiosis effect on *N. lugens*

Varieties/accessions	Type of antibiosis expression	References
ARC 5988, ARC 7080, Sinna Sivappu	Low population buildup	Seetharaman *et al.* (1984)
ARC 6650	Low population buildup	Ramaraju and Sundarababu (1991)
ARC 10550, CO 42	Low population buildup	Murugesan and Chelliah (1982)
ASD 7, IR 56	Low population buildup	IRRI(1988)
ASD 11, IET 6315, T7, V.P. Samba	Low population buildup	Velusamy (1982)
Gambada, Gangala, Heenhoranamawee Hong Yuan, Horanamawee, Muthumanikam Samba	Low population buildup	Velusamy and Saxena (1991)
Garunbalay, Shoa-hi-den, Ski Skrivimankoti	Low population buildup	IRRI (1967)
H 105, IR 9-60	Low population buildup	Cheng and Chang (1979)
HR 12, MCM-1, Ptb 20, XB 5	Low population buildup	IRRI (1976)
HR 98, Murunga 137, Sudurvi 306	Low population buildup	Pathak and Khush(1979)
IR 32, SLO 13, RH 1	Low population buildup	IRRI (1978)
IR 62	Low population buildup	Cook *et al.* (1987)
Babawee, Balamawee, Dikwee, Kuruhondarawala, Seruvellai, Thirissa	Low population buildup	IRRI (1971)
Bing 88122	Low population buildup	Xilin *et al.* (1995)
HR 529-42-5-2, HR 529-45-3, HR 632-9-4, KR 78-87-4, KR 87-564, ER 108-335-6, YR 901-16-1	Low population buildup	Lee and Park (1976)
IR 22	Low population buildup	Medina *et al.* (1996)
IR 64, Xiushui 620	Low population buildup	Gao *et al.* (1990)
IR 64	Low population buildup	Senguttuvan *et al.* (1991)
IR 72	Low population buildup	IRRI (1996)
IR 1402- 38038, IR 1514A-E 597-2, IR 1514A-E 666-7, IR 1541-76-3-3	Low population buildup	IRRI (1974)
Kang You 80	Low population buildup	Xiang *et al.* (1996)
MR1523, Ptb33	Low population buildup	Kalode (1976)
Mudgo	Low population buildup	IRRI (1968)
Ptb 20, Ptb 21, XB 5	Low population buildup	IRRI (1976)
Rathu Heanati	Low population buildup	Pathak and Khush (1979)
ARC 5188, ARC 5560, ARC 5754, ARC 5157, ARC 5764, ARC 5780, ARC 5838, ARC 5917, ARC 5973, ARC 5981, ARC 12864, ARC 13854	Prolonged development period	Reddy and Kalode (1981)
ARC 5785, BKN 6809, HR 12, MCM 1, Ptb 18, Ptb 20, Ptb 21	Prolonged development period	IRRI (1976)
ARC 10550	Prolonged development period	Bharathi (1989)
ARC 14529, CR 57-1 1-2, Sinna sivappu	Prolonged development period	Samal and Misra (1990)
ASD7	Prolonged development period	Song *et al.* (1972)
Babawee	Prolonged development period	IRRI (1977)
Balamawee, Dikwee, Kuruhondarawali, Seruvillai, Thirissa	Prolonged development period	IRRI (1971)
IET 5741, IET 6315, V.P. Samba	Prolonged development period	Velusamy (1982)
IR 22, IR 26	Prolonged development period	Alam and Cohen (1998b)

(Contd.

Varieties/accessions	Type of antibiosis expression	References
IR32, IR 34, Ptb 33, W 1256	Prolonged development period	Pongprasert and Weeraput (1979)
IR 56	Prolonged development period	IRRI (1987)
IR 64	Prolonged development period	Senguttuvan *et al.* (1991)
IR 72	Prolonged development period	IRRI (1996)
MCM 12, MR 1523	Prolonged development period	IRRI (1975)
Mudgo	Prolonged development period	Sogawa and Pathak (1976)
Triveni	Prolonged development period	IRRI (1988)
ARC 5918, ARC 10443, ARC 13984, ARC 14529, ARC 14864, ARC 10443, ARC 13984, ARC 14529, ARC 14864	Low Feeding rate	Reddy and Kalde (1981)
ARC 5973, ARC 5988	Low Feeding rate	Seetharaman *et al.* (1984)
ARC 6650, MR 1523, Ptb 21, Ptb 33	Low Feeding rate	Kalode and Krishna (1979)
ARC 10550	Low Feeding rate	Bharathi (1989)
ASD 7, Babawee	Low Feeding rate	IRRI (1978)
ASD 11, V.P.Samba	Low Feeding rate	Velusamy (1982)
Dhouri 1043, Dhouri 1163, EB 17, Ganja Kali, Hinge, Hiranki, Jay Bay Rang, Kanak, Kappe Khatia pari	Low Feeding rate	Pophaly and Rana (1993)
Hong Yuan, Tai Nuo Xuan	Low Feeding rate	Zhang *et al.* (1994)
HR 529-42-5-2, HR 529-45-3, KR 87-56-4, KR 108-335-15	Low Feeding rate	Lee and Park (1976)
IR 32, IR 36, IR 38, IR 42	Low Feeding rate	IRRI (1979)
IR 46, Utri rajappan	Low Feeding rate	IRRI (1981)
IR 64, Kencana	Low Feeding rate	Chelliah *et al.* (1981)
Mudgo	Low Feeding rate	IRRI (1969)
O. latifolia, O. nivera, O. rufipogan	Low Feeding rate	IRRI (1983)
O. punctata	Low Feeding rate	IRRI (1982)
Rathu Heenati, Triveni	Low Feeding rate	IRRI (1980)
Vellailangalayam	Low Feeding rate	Song *et al.* (1972)
Xiu Shui 620	Low Feeding rate	Gao *et al.* (1990)

for evaluating tolerance to *N. lugens* under greenhouse conditions is described by Heinrichs *et al.* (1985). Velusamy and Heinrichs (1988) reported the variety Utri Rajapan as tolerant and IR 46, Kencena and Triveni as moderately resistant due to low levels of antibiosis and tolerance. Panda and Heinrichs (1983) studied in a field microplot that IR 26 plants had a damage rating of 9 and were completely hopper burned resulting in 100 per cent yield reduction. Nair *et al.* (1978) reported that a breeding line 57-5-1 from a cross of IR 8 x Ptb 20 was tolerant to *N. lugens* and gave higher yields in spite of supporting a heavy population which caused hopper burn in susceptible cultivars.

The major components of moderate level of resistance in rice to BPH was reported to be tolerance (Ho *et al.*, 1982; Bharathi, 1982) (Table 3).

2. Biochemical bases of resistance mechanisms

BPH resistance could not be traced to any morphological or anatomical characteristics

Table 3. Varieties tolerant to *N. lugens*

Variety/accession	Reference
ARC 10550, ASD 11	Chelliah *et al.* (1981)
Bao Xuan 2, Zhong shan Long	Li *et al.* (1991)
Bathurst	Karim (1975)
Chianug, Chianung Yu 10, L 602104, Mudgo, Shen yu 9	Cheng and Chang (1979)
CO42, Ptb 18	Bharathi (1982)
Garunbalay	IRRI (1966)
Garunbalay, TKM 6	Bae and Pathak (1970)
IR 8	IRRI (1967)
IR 32, IR 34, IR 36, IR 1628-632-1	Stapley *et al.* (1979)
IR 46, Triveni	IRRI (1981)
IR64	Cohen *et al.* (1997)
Kencana, *O. nivara*, *O. rufipogon*	IRRI (1982)
Line 57-5-1 (IR 8 x Ptb 20)	Nair *et al.* (1978)
Lung-Yu, Pelopar, Peta, Thirissa	Cheng (1973)
Utri Rajapan	Panda and Heinrichs (1983)

of rice plants and is usually attributed to either a lack of phagostimulants or to the presence of antifeedants (Saxena, 1986). Low concentrations of amino acids especially the sucking stimulants, asparagine was considered to impart resistance to BPH in Mudgo (Sagawa and Pathak, 1970). Koyana (1985) reported that arnino acids *viz.*, arginine, histidine, theionine, tryptophan and valine are essential for nymphal growth of leaf and planthoppers.

Sucking inhibitors such as soluble silicic acid and oxalic acid were reported on resistant rice plants. Shigematsu *et al.* (1982) identified β-Sitosterol is a strong BPH sucking inhibitor and Kaneda (1982) reported that low asparagine content intensifies the inhibitory effect of β-Sitosterol. Volatile chemicals such as terpenoids, aldehydes, fatty acids, esters, waxes extracted as steam distillates have been shown to affect the behaviour and biology of the BPH (Saxena and Okech, 1985). Cook *et al.* (1987) suggested that the surface of the rice plants play a role in food plant selection by BPH. Surface waxes have been shown to affect BPH behaviour. Reduced settling and probing of the plant surface after the exploration and movement off of the stem on to the leaves results from chemical cues in the wax. Chemical cues received by the BPH from the plant surface originate from the alkanes or carbonyl compounds of the epicuticular wax and vary among cultivars. Analysis indicated that the chemical differences between waxes are due to the higher ratio of long to short carbon chain compounds in resistant cultivars. The enhanced surface activity and BPH dispersal from IR 46 (Woodhead and Padjham, 1988) may account for the field resistance of this cultivar (Heinrichs, 1986).

3. Genetics of BPH resistance

3.1. Major gene resistance

Resistance to BPH in rice is a classic example of major gene resistance (Panda and Khush, 1995). Rice breeders have identified atleast ten major genes conferring resistance to various populations of BPH (Table 4). Resistance conferred by five genes Bph 1, Bph 3, Bph 6, Bph 9 and Bph 10 are inherited with dominance, others bph 2, bph 4, bph 5, bph 7 and bph 8 are inherited recessively. Generally, major gene resistance expresses high level of resistance but not always and it is considered less stable (Gunathilagaraj and Ganeshkumar, 1997).

3.2. Polygenic resistance in rice to BPH

Van der Plank (1968) coined the term horizontal resistance to denote the resistance governed by polygenes. In polygenic resistance,

Table 4. Major genes identified for *N. lugens* resistance

Resistant gene	Variety/accession	Reference
Bph 1	Mudgo, CO 22, MTU 15	Athwal *et al.* (1971)
	IR 747-B 2-6	Martinez and Khush (1974)
	IR 34, IR 30	IRRI (1976)
	Tibiriwewa, Balamawee, CO 10, Heenakkulama,MTU 1 9, Sinnakayam, SLO12, Sudhubalawee, Sudurvi 305	Lakshminarayana and Khush (1977)
	Mudgo, MTU 15, CO 22	IRRI (1978)
	Andaraghawewa, RP 9-6	Verma *et al.* (1979)
	Norin PL 3	Nemato *et al.* (1989)
	IR 64	Khush (1989)
Bph 2	ASD 7	Athwal *et al.* (1971)
	Ptb 18	Athwal and Pathak (1972)
	H 105, IR 1154-243	Martinez and Khush (1974)
	H 5, IR9-60, Kaosen-yu 12	Cheng (1975)
	IR 32, IR 36	IRRI (1976)
	ASD 9, Anbaw, C 7, Dikwee 328, Hathiel, Kosatawee, Madayal, Mahakdikwee, Malkora, M.I. 329, Murungakalayam 302, PK 1, Ovarkaruppan, Palasithari 601, Seruvellai, Sinnakaruppan, Vellailangayan	Lakshminarayana and Khush (1977)
	IR 2863-38-1-2, IR 4432-52-6-4, IR 30, IR 36, IR 42, IR 38	IRRI (1978)
	CR 94-13, H 5, Murungakanyani 3, Palasithari 601, Murungakayan 101B, Murungakayan 303B, C 62- 1-230	Pathak and Lal (1976)
	Norin PL 4	Nemato *et al.* (1989)
	ASD 7, Ptb 18, H 105, ASD 9, Palasithari 601, H 5	IRRI (1978)
Bph 2 and Bph 3	Ptb 33	Khush (1979)
	Hondarawala	Shrestha and Adhikary (1987)
Bph 4	Babawee, Gambada, Samba, Heenhoranamawee, Hotel Samba, Khata Samba, Kidukuruwee, Lekam Samba, Senawee, Sulai, Thirissa, Vellai Illankali	Lakshminarayana and Khush (1977)
	IR 13240-81-1, IR 13240-83-1	IRRI (1978)
	Lekamsamba, Sulai	Verma *et al.* (1979)
	Norin PL 7	Nemato *et al.* (1989)
Bph3 and Bph 4	Ptb 21	Ikeda and Kaneda (1981)
Bph 5	ARC 10550	Kabir and Khush (1988)
Bph 6	Swarnalatha	Kabir and Khush (1988)
Bph 7	T 12	Kabir and Khush (1988)
Bph 8	Col. 15 Thailand, Col. 11 Thailand	Nemato *et al.* (1989)
	Thai col. 11	Ketipearchchi *et al.* (1998)
Bph 9	Kharamana, Balamawee, Pokkali	Nemato *etal.* (1989)
	Pokkali	Ketipearchchi *et al.* (1998)
Bph 10 (t)	Introgression line from *O. sativa* and *O. officinalis*	Jena and Khush (1990)

each of the minor genes involved exerts a limited effect which is not specific to the insect strain and is expressed quantitatively and cumulatively. It provides low to moderate levels of resistance (Harris, 1975). Moderate resistance, otherwise called field resistance is incomplete resistance and involves tolerance as a major component (Ezuka, 1972; Robinson,

1976). The concept of moderate resistance as a means of slowing or preventing bio-type selection and stability of resistance is increased in tolerant varieties (Saxena and Barrion, 1985).

Khush (1979) reported the possibility of incorporating minor genes for resistance into desirable agronomic background. It has long been proposed that moderate or polygenic resistance to insect pest including BPH is often more durable than monogenic resistance (Johnson, 1983; Heinrichs, 1986; Kennedy *et al.*, 1987; Bosque-Perez and Buddenhagen, 1992). Complexes of minor genes may confer durable resistance by providing several resistance factors that act on different aspects of pest physiology (Kennedy *et al.*, 1987). Brown planthopper virulence to major resistance genes has a polygenic basis (Roderick, 1994) and continuous variation in adaptation to various major genes is observed among individuals and populations (Gallagher *et al.*, 1994; Cohen *et al.*, 1997).

Several minor genes in the varieties derived from *O. officinalis* provide enhanced resistance (Luong and Luong, 1997). BPH resistance in IR 64 confers moderate resistance by several minor genes or quantitative trait loci that in various combinations contribute to antixenosis, antibiosis and tolerance (Cohen *et al.*, 1997; Alam and Cohen, 1998a). IR 36, another popular variety appears to have minor resistance genes in addition to a major gene (Khush, 1989). Reduced preference of BPH for orientation, feeding, oviposition and an increased antibiosis effect in several varieties indicated the presence of modifiers or minor genes besides the single dominant gene in the rice accessions (Bharathi and Chelliah, 1991).

3.3. QTL analysis for insect resistance

The development of crop varieties with polygenic insect resistance has been hindered by the added expense and difficulty of breeding for quantitative traits. The use of molecular marker techniques in Quantitative Trait Loci (QTL) analysis has opened new opportunities. The advent of molecular markers such as Restriction Fragment Length Polymorpism (RFLP) facilitated the identification and easy manipulation of polygenes (QTL) to improve phenotypically complex traits (Beckmann and Soller, 1986). Use of RFLP markers on all chromosomes enabled to determine the location of Bph 1 on chromosome 12 (Hirabayashi and Ogawa, 1996).

QTL analysis of insect resistance has been conducted on tomato (Maliepaard *et al.*, 1995; Mutschlor *et al.*, 1996), potato (Bonierbale *et al.*, 1994; Yencho *et al.*, 1996), maize (Schon *et al.*, 1993; Byrne *et al.*, 1996; Bohn *et al.*, 1996) and barley (Mohanramipour *et al.*, 1997), besides rice.

The qualitative assessment of resistance will not help in identifying individual components of resistance and in turn the genes concerned. Several methods were developed to understand the nature of individual mechanisms. The measurement of antibiosis and tolerance in each line can be estimated based on the quantitative measurement of both plant and insect components. The quantitative data can be directly used to fix the number of genes by adopting the QTL mapping technique (Kadirvel, 1998).

The rice double haploid population derived from a cross between an improved *indica* variety IR 64 and a traditional tropical *japonica* variety Azucena has been used for mapping and analyzing major genes and QTLs for numerous agronomic characters and insect resistance (Huang *et al.*, 1997; Yadav *et al.*, 1997). A total of 7 QTLs associated with resistance to BPH was identified in the double haploid population derived from IR 64 and Azucena. The QTLs were located on 6 of the 12 rice chromosomes. Two QTLs were predominantly associated with a single resistance mechanism; one with antixenosis and

one with tolerance. Most of QTLs were derived from IR 64 which has been shown to have a relatively durable level of moderate resistance under field condition (Alam and Cohen, 1998a). Soundararajan *et al.* (2001) identified seven significant QTLs for resistance to BPH in the same double haploid lines but at different linkage group. The identified QTL spread over 4 linkage group. In addition, 16 probable QTLs also identified for various parameters under three different mechanisms of resistance. The probable QTLs spread over 8 linkage groups. In case of whitebacked planthopper (WBPH) *Sogatella furcifera* (Horvath), the tolerance parameter plant dry weight loss was found to be useful in detecting the QTL on chromosome 11 and two more QTLs one for functional plant loss index and other for mass screening were identified. The analysis on tracing allelic contribution of IR 64 and Azucena towards resistance to WBPH indicated that IR 64 contributed more than Azucena (Kadirvel *et al.*, 1999).

A total of 10 QTLs for ovicidal response against WBPH was detected with 292 RFLP markers in a set of 71 rice recombinant inbred lines derived from a cross of *japonica* cultivar Asominori and *indica* cultivar IR 24. The QTL on chromosome 8 was identified as important region for the ovicidal response and accounted for a large part of the phenotypic variance. One suggestive region on chromosome 10S and three suggestive QTLs were detected repeatedly and this may control the biosynthesis of antibiotic substances (Yamasaki *et al.*, 1999).

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