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REVIEW ARTICLE

Identical threats of rice: Insights into biotypes of brown planthopper (*Nilaparvata lugens* stal)

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Abstract

By continuous feeding, insects tend to overcome the host resistance. As the plant resistance mechanism gets upgraded in due course of time, the monophagous insects co-evolve as a means of adaptation, which includes biotype formation. A biotype is morphologically identical to its original form, primarily based on the selection pressure exerted by the host. Brown Planthopper (BPH) is a major rice pest in Asia, which could able to cause 60 % of yield loss under severe pest outbreak. This Brown planthopper exhibits multiple biotypes distinguished by their ability to overcome specific host resistance genes. Four original biotypes have been identified, withbiotypes 1 and 2 being prevalent in Southeast Asia and East Asia. Biotype 3 developed under laboratory conditions on resistant varieties whilebiotype 4 is native to the Indian Subcontinent. These biotypes differ in virulence, feeding behaviour and overcoming resistant genes in rice cultivars. Understanding the genetic basis of biotype differentiation and host resistance mechanisms is crucial for durable, broad-spectrum BPH resistance in rice. Though more than 46 resistance genes/QTLs have identifies so far, long-term management depends on combining genetic strategies such as gene pyramiding by utilizing multiple genes at a time along with regional monitoring of biotypes and area-wide IPM programs which can slow down the adaptation by the pest. These strategies balance resistance durability with lower pest selection pressure, for better pest management and increased rice yields.

Keywords: biotypes; BPH; gene pyramiding; host adaptation; resistant genes; rice

Introduction

Rice is one of the important staple crops in the world, which is cultivated over 168.36 million hectares and yields almost 799 million metric tons (1). Of the biotic and abiotic stresses affecting crop productivity, the damage caused by Brown planthopper (BPH) (*Nilaparvata lugens* Stal.) is critical. The BPH feeds on the phloem sap, resulting in 'hopper burn'-distinguished by wilting, yellowing and death of the plant (2). Both nymphs and adults infest the crop and cause heavy losses. It is also a vector of viral diseases like rice ragged stunt virus (RRSV), rice wilted stunt virus (RWSV) and rice grassy stunt virus (RGSV), which were widely prevalent during the mid to late 1970s. With the introduction of the Green Revolution in the 1960s, large-scale and frequent infestations of the BPH have emerged as a significant threat to rice production. These infestations have been linked with the use of high-yielding, semi-dwarf types of rice, characteristic of the new era and intensive fertilizer application by farm producers. Later, excessive pesticide application was identified as a major cause of many of the outbreaks (3). In India, large- scale damage in connection with BPH was first reported in Kerala in 1973. Later it extended to other states like Andhra Pradesh, Bihar, Haryana, Odisha, Punjab, Tamil Nadu and Uttar Pradesh. Although BPH outbreaks had reduced during the 1990s, resurgence was observed post 2005 across major rice-growing belts in South and Southeast Asia. Combined with advancements in agricultural research, the resurgence has resulted in the identification of novel resistance genes from various sources and introgression into existing rice varieties (4). To date, more than 46 genes and several QTLs have been linked to resistance against planthoppers in rice. Several resistant modern rice varieties have also been developed and released through national breeding initiatives (5, 6). Several works on molecular breeding, omics studies, molecular mechanism of resistance and gene discovery of rice against BPH are available, but the problem of virulence adaptation by BPH to resistant rice genotypes are not sufficiently explored, though it is a major threat to the durability of novel resistant sources (7, 8). The outbreaks of native populations and the altered populations of BPH in the recent past, emphasize the need to carry out extensive research on host plant resistance. The knowledge of mechanism underlying the formation of biotypes and their adaptation towards resistant hosts, can provide durable resistant sources at both regional and international level (9) Studies on insect biotypes is therefore essential to study the insect-host relationships and its co-evolution.

Origin of insect biotypes

Benjamin Walsh is the first entomologist to work on "phytophagic varieties," which refers to the insect population having similar morphological traits but different biological traits. He documented 15 similar species of gall wasps that preferred different variants of the same host plant (10). A biotype possesses genetic homogeneity but has differential virulence characters. Phytophagous insects attempt to overcome every management measure, forcing the insect to develop some counter strategies and also evolve to biotypes that are morphologically similar but functionally different from the original forms (11, 12). Biotypes are considered to be an intraspecific category that have similar genetic composition for a biological attribute (13). Hessian fly is one of the early organisms to be studied for the existence of races among its populations. Earlier, the terms "biotypes" and "races" were used interchangeably. But later it was understood that they are distinct from each other: "biotype" refers to a population with similar phenotypic traits but whose behaviour and physiology are distinct and are specifically adapted to a host variety; "race" refers to the population that is geographically or even reproductively isolated and have sometimes distinct physical traits (14). Phenotypic and genotypic studies suggest that the biotypes are transitory variants during the primordial stages of speciation (15). Differentiation among the biotypes may be due to a spatial or temporal allopatric variation (geographical variation) or sympatric (local variation) or parapatric with other compatible populations (13). Phenotypic variations are naturally present in the populations (16). To interpret this feature, genetic variations through the structure of genes within individuals or within populations and alleles within loci are to be elucidated. Either genetic or environmental factors or both, might be the reason for the evolution of biotypes. An undetected existing biotype may evolve into a more virulent biotype (17, 18). The development of the biotype concept can be explained by gene-for-gene relationship between the genotype responsible for virulence in insect pest and presence of major/vertical genes in the host plant responsible for resistance in host plant (10). In the two stages of biotype development, initially the sudden change was induced by host defence system which is responsible for fitness of the surviving genotypes regardless of resistance by host. Later, these survived genotypes become the best fitted genotypes among the pre adapted individuals in existing ecosystem (16). This concept can be explained with biotypes of brown planthopper. The biotype 1 survived in varieties with no resistance genes. The biotype 2 survived in varieties having bph1 resistant gene while biotype 3 survived on varieties having *bph2* resistant gene (19). The genes responsible for virulence against resistant varieties were already present in biotype 1 of BPH but in lower concentrations. The variants escaped from the resistance mechanism of host had undergone interbreeding and formed new biotypes (13). As of now, biotypes are documented from 50 insect species belonging to 20 families from 7 orders. Aphids accounts for half of the documented biotypes (20).

Factors influencing biotype development

A number of factors play a role in the biotype evolution, such as host plant resistance, gene-mediated selection pressure, genetic mutation, pre-existing variation in virulence and sexual recombination events (21). However, the degree and persistence of virulent gene expression are ultimately controlled by the initial allele frequency of virulent alleles, host plant resistance mechanism type and complex interactions among the pest genotype, host plant and environment (20). Biotypes can be instigated due to the widespread cultivation of host range which are susceptible to the insects. This problem is made worse by improper insecticide use, poor crop rotation, bad farming practices and unmanaged weed hosts. Sap-feeding insects like aphids feed on plant phloem and their saliva triggers predictable reactions in the plants (22). The evolutionary significance of salivary glands in biotype development has been proven, with some salivary proteins identified to be important in host adaptation (23). Environmental processes like the incidence of natural enemies, endosymbionts, the insects' ability to adapt to host plants and resistance to insecticide, contribute to the development of biotypes. The short generation cycles of aphids allow them for the quick fixation of adaptive characteristics developing during asexual reproduction(18). Endosymbionts have also been found to be associated in development of biotypes. For instance, BPH harbors a large diversity of bacterial symbionts which are responsible for biotypes (24). Agricultural ecosystems largely favour biotype formation. In Southeast Asia, the widespread monoculture of genetically uniform rice cultivars and indiscriminate use of insecticides have led to the emergence of BPH biotypes (20). Biochemical basis of resistance has been previously proven. In sorghum, increased pectin methylase activity in the saliva of *Schizaphis graminum* biotypes has been observed (10). An analogous adaptation in biotypes with salivary proteins has been reported in *Diuraphis noxia* in wheat (25). Recent omics research greatly enhanced our knowledge of resistance mechanisms in rice against the brown planthopper (BPH). Transcriptomics research has revealed dynamic gene expression changes in resistant varieties, indicating important genes such as Bph30, which reduces amino acid metabolism but enhances flavonoid biosynthesis pathways, thereby enhancing plant defence (26). Metabolomics research also highlights flavonoids, phenylpropanoids and alkaloids as important defence compounds, particularly in rice varieties with multiple resistance genes, such as BPH14 and BPH15, which establish sustainable resistance through enhanced metabolic fortification (27). Unlike aphid biotypes, the genetic mechanism of BPH biotype generation is not adequately explored because, many a time, the presence of a biotype, remain unnoticed due to the monophagous nature of the pest. However, many host plant interaction studies suggested that the virulence is due to absence or change in some effector proteins that used to be an indicate and defend in case of biotic stresses (28). Given the intricate interaction of insect-plant relationships, it would be prudent for the future resistance breeding programs to focus on the deployment of the most efficient and durable resistance genes, regardless of their expected impact on the genetic structure of pest populations.

Biology of brown planthopper

BPH is one among the insects under hemimetabolous group, because of which its life cycle comprises of egg, nymph and adult stages. The size of the adult BPH varies from 4-5 mm and is light brown to yellowish brown in colour. The presence of protuberant tibial spur in hind leg serves the taxonomical purpose to identify *Nilaparvata lugens*. Adults are seen in dimorphic forms *viz.,* macropterous and brachypterous forms

(29). Macropterous adults are long winged variants whereas brachypterous adults have reduced hind wings. Egg stage is about 7 to 11 days and has five nymphal stages with duration of 3 to 10 days (30). Long winged macropterous BPH have extensive flight capacity and are known to be responsible for hopper migration and colony initiation in the host fields (31). Adults start mating from the day of emergence (29) (Fig 1). Oviposition starts from second day of adult emergence and may extend up to 4 days. Females lay groups of eggs in leaf sheaths, sometimes in leaf blades, which are elongate and curved. Soon after hatching, nymphal stages move towards the culm region of the rice plant and starts sucking the sap (2). While growing, colour of instars changes from yellow to yellowish brown. Females of brachypterous form have brownish black scale like tegmina which are leathery without any clear venation and covers basal portion of the abdomen. Total lifecycle of BPH from egg to adult ranges from 19 to 23 days (32). Pre-oviposition period for macropterous forms is longer than the brachypterous forms which results in reproductive delay and lesser fecundity rate (31). The pest development is optimum at the temperature between 25 and 30 °C and humidity of 70-85 % (33). Increased temperatures and CO_2 concentrations may accelerate BPH growth and its reproduction rates, which results in higher population densities and potentially enhanced virulence. These climatic changes suggest that it can play pivoyal role in role expansion of biotypes and virulence of brown planthoppers (34). BPH have sucking type of mouthpart which sucks sap from the phloem in the stem of the plant. Vigorous sucking leads to symptoms like yellowish discolouration of leaves, rapid drying of leaves which results in the peculiar symptom called “hopper burn” (35) Fig. 1.

Biotypes of brown planthopper

BPH is one of the major key pests of rice crop. As it is monophagous in nature and undergoes heavy selection pressure, the pest develops resistance to the host defence mechanism and evolved different virulent forms which is documented as biotypes.

Evolution of BPH biotypes

BPH population acquires new virulence characters when exposed to resistant varieties having monogenic resistance. The evolution of biotypes is governed by genetic interactions, biological factors and cultural conditions (2). The first resistant rice variety IR-26 with *bph1* resistance gene was launched to control the attack of initially available BPH population, also referred as biotype 1 (36). This population could attack the host with no resistant genes. Due to the widespread cultivation of rice varieties possessing bph1 gene, biotype 2 has evolved which could infest a rice crop with bph1 gene. To tackle the infestation by BPH biotype 2, rice variety IR 36 with *bph2* gene was developed. The biotype 3 was developed in the laboratory by continuous feeding the BPH population on ASD7 variety which contains *bph2* gene (37). The rice variety IR 66 was launched in 1987 with *bph4* gene (35). Subsequently varieties with *bph3* gene namely, IR68, IR70, IR72 and IR74 were launched in 1988, all of which have conferred resistance against biotype 3. Distinguishable patterns of mortality were obtained among the biotypes 1,2 and 3 when exposed to steam distillate extracts or the oils extracted from the susceptible and resistant varieties

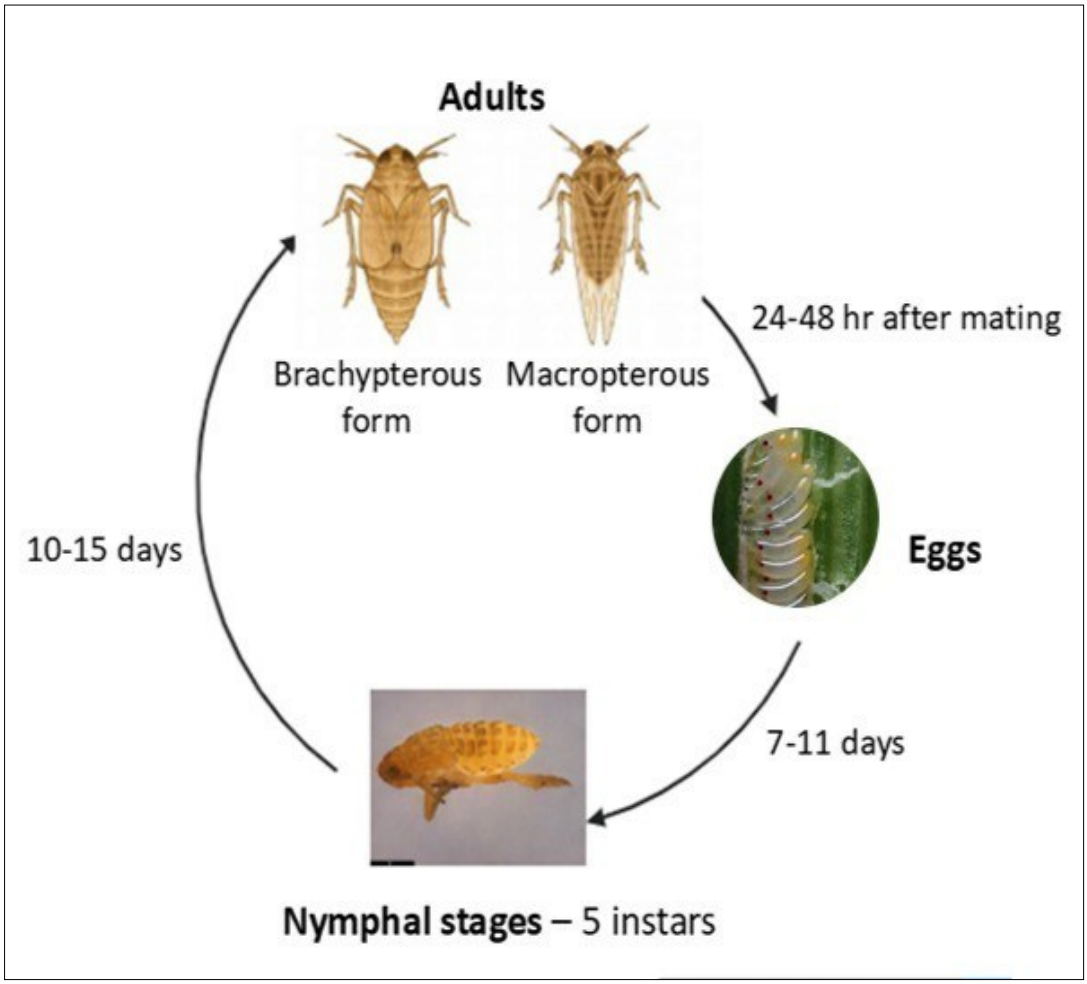

Fig. 1. Life cycle of brown planthopper.

(19). Biotype 4 or the south Asian biotype was evolved, when the improved cultivars having resistant genes *Bph1, bph2, Bph3* and *Bph4* were grown extensively in South Asia (35). Though IR 64 had the adequate amount of resistance against all available biotypes at that time, because of its repeated cultivation by farmers in Bali led to infestation of another evolved population of BPH which is designated as biotype Y (38). Biotype Y evolved from biotype 1 population that fed on a variety YHY15 containing Bph15 gene for 33 generations in two years' time (39). The laboratory reared biotypes are less stable than the other biotypes and they are much virulent on the host in which they are the reared (5). Virulence in the field population is variable and the insects evolve to attain resistance based on the host varieties grown in that particular area (40). The variations in the local populations occurred as a result of natural selection while breeding on a particular variety for several generations. Biotype can be formed when insects are adapted to a host and bred for several generations. The biotypes 2 and 3 were formed from original population when it was maintained in TN1 for eight generations (41).

Distribution of BPH biotypes

These biotypes are differentiated from other biotypes by non-morphological traits like feeding preference and adaptation to particular host or variety. BPH biotype 1 and 2 are distributed in Southeast and East Asia. While, the laboratory reared biotype 3 is distributed along rice growing areas of Japan and few parts of southeast asia (41). The fourth biotype, referred to Indian biotype or South Asian biotype, is distributed in South Asia especially among the Indian subcontinent (42). Whereas biotype Y is another laboratory reared BPH biotype developed on YHY15 variety. (38). This biotype is limitedly distributed on rice growing areas of China and Indonesia. Overall distribution of major BPH biotypes along the rice growing countries are depicted in Fig 2 and Table 1.

Table 1. Distribution of biotypes

Biotype	Distributed area	References
4	India, Bangladesh, Srilanka	(36, 43)
Y	China, Indonesia	(38, 39)
1	Southeast and East Asia	(40)
2	Indonesia, Vietnam and China	(44)
3	Japan	(41)

BPH resistant sources in rice

Athwal (45) identified two genes conferring BPH resistance, namely *Bph1* in Mudgo and *bph2* in ASD7 (Table 2). Eventually, the new recessive gene *bph2* was introgressed into IR26. The *bph2* resistance gene being durable is highly used in the breeding line and the cultivar IR36 possessing this gene is widely grown, which exerts tremendous pressure on the existing biotype (35). Subsequently resistance loci, *Bph3* and *bph4* were identified in two Sri Lankan varieties, *i.e.* Rathu Heenati and Babawee, respectively and were introgressed into many elite rice cultivars (37). These include IR56, IR60, IR66, IR68, IR70, IR72 and IR74. IR56 and IR60 contain the *Bph3* gene derived from the Rathu Heenati variety. IR66, released in 1987, has the *bph4* gene and IR68, IR70, IR72 and IR74, released in 1988, also carry the *bph3* gene. Later a new biotype 4 was identified which could feed on all those elite rice varieties having Bph3 and Bph4. Khush, Karim (36) identified a single recessive gene *bph5* with resistance to BPH biotype 4 in rice cultivar ARC10550, which segregated independently of *Bph1, bph2, Bph3* and *Bph4*. Genes

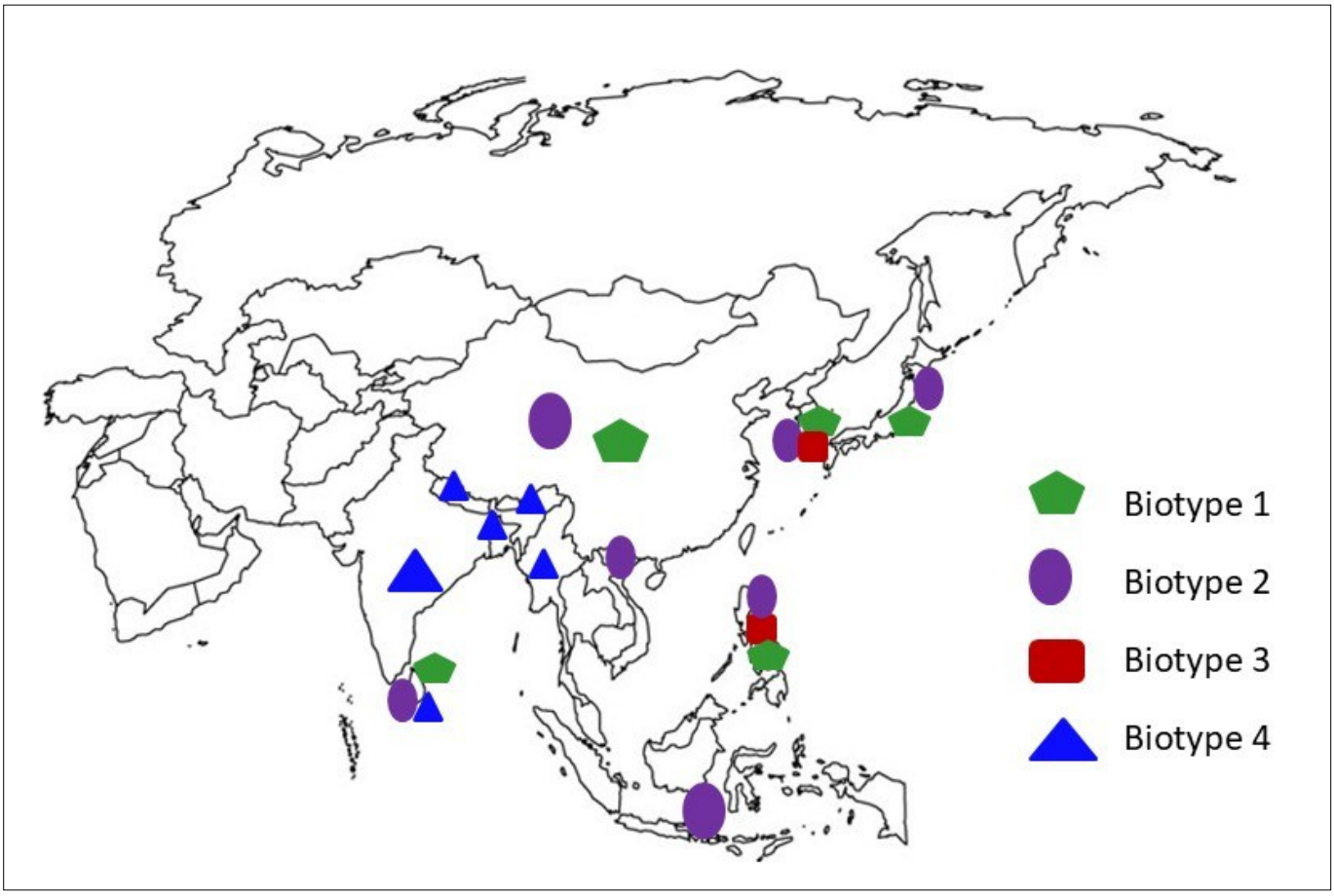

Fig. 2. Distribution of BPH biotypes across major rice growing regions of BPH.

Table 2. BPH genes/QTLs from rice genotypes showing resistance to different biotypes

Chr	Gene	Source	Resistant to biotype	HPR Mechanism	Reference
3L	*bph11(t)*	*O. officinalis*	-		(5)
6S	*Bph32*	Ptb33	4	Antibiosis	(5)
4S	*Bph33*	Poliyal	-	Antibiosis, Antixenosis	(5)
11L	*qBph11*	DV85	2	Tolerance	(6)
6S	*bph5*	ARC10550	4	-	(36)
12L	*Bph1*	Mudgo, TKM6	1,3	Antibiosis, Antixenosis	(45)
12L	*Bph10*	*O. australiensis*	1,3	-	(47)
12L	*bph2*	ASD7	1,2	Antibiosis, Tolerance	(48, 49)
4S	*Bph3*	Rathu heenati	1,2,3,4	Antibiosis	(48, 50)
6S	*Bph4*	Babawee	1,2,3,4	Antixenosis, Antibiosis	(48, 51)
4L	*Bph6*	Swarnalata	4	Antibiosis	(48)
12L	*Bph7*	T12	4	Antibiosis, Tolerance	(48, 52)
12L	*Bph9*	Pokkali	1,2,3	Antixenosis, Antibiosis,	(48)
1L	*Bph37*	IR64	-	Antibiosis, Tolerance	(48)
4L	*Bph17*	Rathu heenati, PTB33	1,2,3,4	Antibiosis, Antixenosis	(53)
4L	*Bph44*	Balamawee × PD601.	1	Tolerance	(53)
4L	*Bph22(t)*	*Oryza rufipogon*	1,2	-	(54)
8L	*Bph23(t)*	*Oryza rufipogan*	4	-	(54)
6S	*Bph29*	RBPH54	1,2	-	(54)
4S	*Bph30*	AC-1613	1,2,3	Antibiosis	(54)
6S	*qBph6*	IR71033-121-15	-	Antibiosis	(50)
12L	*bph8*	Chinsaba	1,2,3	-	(55)
4S	*Bph12*	B14	2	Antixenosis, Antibiosis	(56)
2L	*Bph13(t)*	*Oryza officinalis*	4	-	(57)
3L	*Bph14*	*Oryza officinalis*	1,2,3	Antibiosis	(58)
4S	*Bph15*	*Oryza officinalis*	1,2,3	Antixenosis	(58)
12L	*Bph18(t)*	IR65482-7-216	1,2	-	(59)
3S	*bph19(t)*	AS20-1	2	-	(60)
4S	*Bph20(t)*	*Oryza minuta*	1	-	(61)
12L	*Bph21(t)*	*Oryza minuta*	1	-	(61)
8L	*bph24(t)*	*Oryza rufipogan*	4	-	(62)
6S	*Bph25*	ADR52	-	Antibiosis	(63)
12L	*Bph26*	ADR 52	1,2	Antibiosis	(64)
4L	*Bph27*	GX2183	2	Antibiosis, Antixenosis	(65)
4L	*Bph27(t)*	Balamawee	1	Antibiosis, Antixenosis	(66)
11L	*Bph28(t)*	DV85		Tolerance	(67)
3L	*Bph31*	CR2711-76	4	Antibiosis, Antixenosis, Tolerance	(68)
1L	*Bph33(t)*	RP 2068	-	Antibiosis	(69)
4L	*Bph34*	IRGC104646	4	-	(70)
4	*Bph35*	RBPH660	-	-	(71)
4S	*Bph36*	*O.rufipogan*	1,2	Antibiosis, Antixenosis	(72)
1L	*Bph38(t)*	Khazar	3	-	(73)
4S	*Bph39*	RPBio4918-230S	4	Antibiosis, Tolerance	(74)
4S	*Bph40*	RPBio4918-230S	4	Antibiosis, Tolerance	(74)
4S	*Bph41*	SWD10	4	Antibiosis, Antixenosis	(75)
4S	*Bph42*	SWD10	4	Antibiosis, Antixenosis	(75)
11S	*Bph43*	IRGC 8678	3	Antibiosis, Antixenosis	(76)
4L	*Bph45*	IRGC 102165	4	Antixenosis	(77)
4L	*Bph46*	Landrace indica rice accession, CL45	4	Antibiosis	(78)
11L	*qBph11.3*	Landrace indica rice accession CL48	4	Antibiosis	(78)
3L	*qBph3*	IR02W101 (*Oryza officinalis*)	2	-	(79)
4S	*qBph4*	IR02W101 (*Oryza officinalis*)	2	-	(79)
4S	*qBph4.2*	IR65482-17-511 (*Oryza australiensis*)	2	Antibiosis	(79)
4S	*qBph4.3*	Salkathi	4	Antibiosis, Antixenosis	(80)
4S	*qBph4.4*	Salkathi	4	Antibiosis, Antixenosis	(80)
8L	*qBph8*	Swarnalata	2	Antixenosis	(81)

Chr- Chromosome; S- Short arm; L- Long arm

such as *Bph6* and *Bph7* identified from rice varieties Swarnalata and T12 respectively, also confer resistance to biotype 4 (46). Whereas *bph8* and Bph9, identified from South east Asian varieties, Chinsaba and Balamawee were resistant to Biotype 1, 2 and 3. In addition to this extensive search for resistance gene in cultivated varieties, new potential genes were searched in wild germplasms. *Bph10* is the first resistant gene to be reported in a wild relative (*Oryza australiensis*) of cultivated rice (47). Subsequently, bph11 and Bph12 were reported in the genetic background of wild rice *(Oryza officinalis*). Several genes were identified in both cultivated rice and wild relatives (5). Though several resistant genes have been explored over these many years, only very few genes confer resistance to all the four major biotypes (Fig. 3), while the remaining genes provide narrow resistance to either of the four biotypes or combinations of biotypes.

HPR mechanisms

Host plant resistance (HPR) is defined as "those characters that enable a plant to avoid, tolerate or recover from attacks of insects under conditions that would cause greater injury to other plants of the same species" (82). Mechanism of HPR to insect pests has been categorized into three types: antixenosis, antibiosis and tolerance. Antixenosis minimizes insect pest damage by deterring the pest or disrupting their behavior, leading to reduced colonization and oviposition on the host plant (83). Antibiosis is a resistance mechanism that impacts the biology of pests after infestation, negatively affecting their survival, feeding and reproduction (48). Above two mechanisms are extensively studied and exploited area in the field of host plant resistance (84). But the third mechanism *i.e.*, tolerance is one of the neglected yet still one of the crucial mechanisms which confers durable resistance against the faster rate of pest adaptation and loss of vigour of resistance genes. Unlike antibiosis or antixenosis, tolerance does not exert direct selection pressure on BPH populations, thereby minimizing the risk of biotype evolution (53).

BPH -Rice Interaction

Host searching behaviour and feeding behaviour are important processes to understand the Rice-BPH interaction and the resistance of rice against BPH. Host searching behaviour includes finding the location of the host and habitat, acceptance, suitability and then finally regulation of the process with metabolites playing a vital role in these processes (2). Higher levels of asparagine and lower levels of phytosterol are known to attract BPH (85). The process of insect feeding behaviour begins with careful observation of its landing place and saliva secretion while probing to find a suitable site for feeding. After finding the suitable site, BPH starts to insert its stylet and saliva flows continuously. This is followed by phloem cell ingestion and honey dew secretion (86). Feeding behaviour provides the clues for understanding resistance in rice. For instance, in the plant having bph14 and bph15 gene, probing by the BPH takes more time but contrastingly ingestion of phloem cells takes up less time (87). The interaction between rice and the BPH is process of co-evolution determining both resistance and susceptibility. Rice has evolved numerous defence mechanisms against BPH and other pests. The antibiotic and anti-xenotic effects observed in resistant varieties were also largely due to blockage of sucking (88). The process is known as sieve tube sealing, with callose deposition serving as a model for quantifying plant immunity to phloem feeders and pathogens (89). In rice plants with BPH resistance genes, callose builds up on the sieve plates, blocking the sieve tubes and directly hindering BPH feeding. Inhibition of the enzyme β-1,3-glucanase prevents the breakdown of callose, keeping the sieve tubes blocked and stopping the BPHs from continuously feeding on sap (86). In susceptible rice plants, the expression of β-1,3-glucanase genes increases after a BPH attack, leading to the breakdown of callose in phloem cells and allowing the pests to continue feeding (87). In susceptible plants continuous feeding

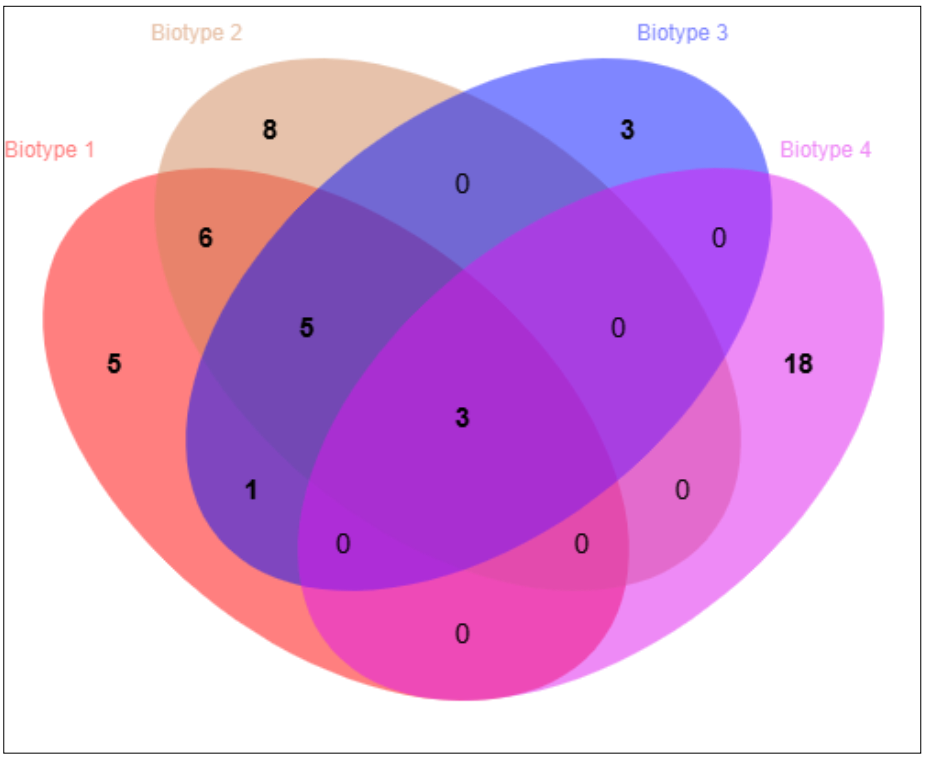

Fig. 3. Categorisation of genes conferring resistance to different biotypes.

by BPH and the ingestion of large amounts of phloem sap can quickly lead to a drop in sucrose levels. This triggers the expression of plant genes such as α-amylase, which catalyses the conversion of starch into sucrose to support normal growth. This process continues until the starch reserves are depleted (48). Additionally, prolonged BPH feeding inhibits photosynthesis, reducing the production and movement of assimilates. This diminishes the availability of carbohydrates necessary to sustain root activity, hindering nutrient uptake (90). Consequently, leaf senescence occurs, with more macromolecules in lower leaves breaking down to meet the plant's essential needs. In susceptible rice plants, these interconnected reactions are known as the BPH-feeding cascade (86). BPH have evolved such strategies to either evade detection by the rice plant or suppress its defence mechanisms.

Host adaptation by BPH

Presence of different alleles of virulence genes in a population, which is referred as phenotypic plasticity, enables the pest escape constantly from the host resistance mechanism (91). This character is associated with differential host adaptation (92). Phenotypic plasticity, along with short life cycle, high fecundity and high reproduction rate, helps the pest adaptation to host with several resistance genes (54). Virulence pattern differs in different geographical area with different environments and cross-breeding. In China, the biotype 2 has emerged in several provinces but only the virulent and high vigorous individuals were able to thrive. The population of biotype 2 was lower with increasing distance of migration (93). Earlier, it was assumed that the virulence of BPH is based on gene-for-gene concept but later crossing experiments of biotypes demonstrated that the virulence is inherited as a polygenic trait and is not governed by major genes (19). The newly formed biotype maintains the same virulence against previously existed non-resistant varieties, a proof of no loss of the redundant virulence in newer biotype during the evolution. The biotypes are virulent form of population due to natural selection from resistant varieties having population with continuous variation (12). Virulence pattern of different BPH population against several rice genotypes were studied by Horgan, Ramal (3) (Table 3). PTB33, one of the important resistant variety, confers resistance to most of the BPH populations but found to be susceptible to BPH populations from Bangladesh, Indonesia, China and Philippines (3). Meanwhile, Rathuheenati, another promising variety from Srilanka, is found to confer resistance against most of the BPH populations but susceptible to BPH population from India. Though this variety was once resistant to BPH populations of Maruteru and Punjab from India, later it became moderately resistant and sometimes even susceptible to most of the Indian BPH populations (3, 94). Similarly, some genotypes which are resistant against certain BPH population are found to be susceptible to BPH populations of other regions in India. It can be inferred that rice resistance to BPH, is a polygenic and continuously evolving trait. Eventually, the BPH population is also continuously adapting to resistance conferred by its host. This indicates that the biotypes cannot be demarcated easily and needs a thorough understanding of its evolution and genetic mechanism.

Diagnosing biotypes

Diagnosing different BPH biotypes is practically based on their

Table 3. Reaction of resistant rice genotypes against Asian population of BPH

S.No.	Genotypes	Corresponding Resistant gene	Indian Population of BPH					South Asian and South-East Asian Population of BPH						
			Aduthurai (Tamil Nadu)	Maruteru (Andhra Pradesh)	Gangavathy (Karnataka)	Cuttack (Orissa)	Ludhiana (Punjab)	Bangladesh	Myanmar	China	Taiwan	Vietnam	Indonesia	Philippines
1	IR 64	Bph1	S	S	S	S	S	S	-	S	S	S	-	**R**
2	ASD 7	Bph2	S	**R**	**R**	S	S	**R**	S	S	S	S	S	S
3	PTB 33	Bph2, Bph3, Bph 32	**R**	**R**	**R**	**R**	**R**	S	-	S	**R**	**R**	S	**R**
4	Rathu Heenati	Bph3, Bph17	S	S	**R**	S	S	**R**	**R**	S	**R**	**R**	**R**	**R**
5	Babawee	Bph4	S	**R**	**R**	S	S	**R**	S	S	**R**	S	S	**R**
6	ARC 10550	Bph5	S	S	S	**R**	S	**R**	**R**	S	S	S	S	S
7	Swarnalata	Bph6	S	S	**R**	S	S	S	S	S	**R**	**R**	**R**	S
8	Chinsaba	Bph8	S	S	**R**	S	S	S	S	S	S	S	S	S
9	Pokkali	Bph9	S	S	S	S	S	S	-	S	S	S	**R**	S
10	IR65482	Bph18(t)	S	S	**R**	S	S	**R**	-	S	S	S	**R**	S
11	IR71033	Bph20, Bph21	S	S	S	S	S	S	-	S	**R**	S	**R**	S

R- Resistant; S- Susceptible (Inferred from (3, 94))

virulence patterns on rice cultivars or genotypes. This is crucial for developing effective resistance strategies against BPH, due to the differential virulence expression of biotypes against the resistance genes. The phenotypic variation is negligible and could not be visibly observed though few earlier research has highlighted some variations.

Morphological variations among the biotypes: Minimal morphological differences have been recorded in the biotypes. The number of spines on the hind tarsus were significantly different among the biotypes. Biotype 1 and 2 had almost similar average spine for both female and male adults. But, the average number of spines was significantly lower in case of biotype 3. The distinct feature in wing venation among the biotypes is the loss of M2b vein and lack of fourth apical cell. Biotype 3 had this distinctness more than the other biotype (95). In Philippines, the three biotypes of the populations could be identified using the leg and antennal characters (96). However, no variations could be observed with the morphometric analysis of body parts, namely head width, length of hind tibia, length of ovipositor, width and length of tegmen, structures of female and male genitalia of both brachypterous and macropterous forms of three biotypes exhibited no distinctness among biotypes on basis of body dimensions

Physiological variations among the biotypes: Previous researchers analysed the relationship between the amount of honeydew excreted and the ability of each biotype population to infest specific resistant varieties (95). Significant individual variations in daily honeydew excretion existed within each biotype population and these variations overlapped considerably among the biotypes. Detailed chemosensory specificity bioassay using rice amino acids established the significant differences between the biotypes in their sucking response. Biotypes 2 and 3 consumed more of the solutions containing amino acids that are not typically major constituents in rice plants, compared to biotype 1 (Table 4). This suggests that biotypes 2 and 3 have a greater adaptability to unusual dietary substances than biotype 1. Additionally, biotypes 2 and 3 showed better tolerance to starvation and slightly longer survival on *Leersia hexandra*, which might also be attributed to this physiological trait. Interestingly the invertase activity in the salivary glands of biotype 1 is about twice as high as that in biotypes 2 and 3 (95). He further showed the differences among biotypes in amino acid production during the metaphase events (Table 4). Polymorphism of enzymes systems are considered to be first level of demographic speciation (97).

Genetic variation among the biotypes: Virulence of one biotype can be transferred to other biotype by rearing it in the resistant varieties up to eight generations (41). The genes conferring the ability to overcome host resistance are typically at low frequency in the natural population before the introduction of resistant varieties in the fields. This suggests that individuals carrying these genes are less fit from a survival perspective (98). Genetic fingerprints of BPH using RAPD-PCR, have shown that biotypes of BPH are not subspecific categories, rather are formed due to variance in virulence. RAPD bands produced in the experiment showed that the three biotypes of BPH are genetically homogenous and there are no specific bands for each biotype (99). However, the offsprings obtained from hybridisation of biotype 2 and 3 with biotype 1 have inferior characters than their parents. They exhibited lower honey dew excretion and ability to feed on resistant varieties, suggesting weaker host-resistance breaking capability (93, 95). Hybridization experiments in Taiwan and at IRRI showed that the Biotype I was more dominant than the others (96).

Molecular variation among biotypes: In a genetic analysis on four biotypes (1,2,3, Y) using EST-SSR markers, the mean values of alleles per locus and heterozygosity were lower in biotype 1 and higher in biotype Y. Similarity among individuals in the biotypes was higher in biotype 1 and least in biotype Y could be observed through phylogenetic tree construction. Thus, the genome level differentiation among the biotypes feeding different rice varieties was higher with the increasing genetic diversity within the single biotype populations. It was suggested that the genetic diversity of BPH can be positively correlated with their resistance against the host plants (39). Later, sequence -related amplified polymorphism (SRAP) markers, which are known to be effective than previously used markers, were used to declutter the virulence of the biotypes. The four biotypes categorised under two virulence groups (91).

Diversity of Indian biotype of BPH: The Indian biotype of BPH, is referred as biotype 4. It is designated as most destructive among all biotypes which is native to Indian subcontinent. Studies during the 1980s shown that the resistant gene *Bph3* (Rathu Heenati,), *bph4* (Babawee), bph8 (Chinsaba) and *Bph9* (Pokkali) conferred a broad-spectrum resistance to all the four biotypes while *bph5* (ARC 10550), *Bph6* (Swarnalata) and *bph7* (T12) conferred resistance to biotype 4 alone (19, 42). Later the genes such as *Bph13(t), Bph20(t), Bph21(t), Bph24(t), Bph34, bph39, bph40, bph42* and few QTLs identified from wild relatives of cultivated species *(Oryza officinalis, Oryza minuta, Oryza nivara and Oryza rufipogan)* were found to be resistant against biotype 4. Recently, *Bph 17-ptb* (PTB33), *Bph17* (Rathu Heenati), *Bph26* (ADR52), *Bph 31* (CR2711-76), *Bph32* (PTB33), *Bph33* (Poliyal), *Bph33(t)* (RP2068), *Bph39* and *Bph40* (RPBio4918-230s) have

Table 4. Differentiation of biotypes based on the amino acids

Biotype	Highly Phagostimulatory Amino Acids	Moderately Phagostimulatory Amino Acids	Metaphase Events	References
1	Asparagine Valine	Alanine Serine	Highest number of Metaphase Sex chromosomes are shorter in length The frequency of chromosomal aberrations is relatively high.	(95)
2	Alanine	Valine Serine Asparagine	Lowest number of Metaphase Sex chromosomes are shorter in length The frequency of chromosomal aberrations is relatively low	
3	Valine Serine	Asparagine Alanine	All the parameters are intermediate between Biotype 1 and 3	

shown resistance to this destructive biotype (6). However, the Indian population of BPH at different locations across the Indian country have shown differential response to these identified resistant genotypes (94) (Table 3).

Mitigating the formation of BPH biotypes

Breeding programs targeting development of insect-resistant crops with horizontal resistance and moderate resistance levels can delay the appearance of insect biotypes, complementing different pest management options effectively (20).

Identifying the resistant sources: A meticulous evaluation of BPH resistance in the available rice germplasms is important for identification and utilization of BPH resistance genes (35). The Standard Seed box Screening Test (SSST) evaluates the host resistance by measuring the degree of damage based on Standard Evaluation System (International Rice Research Institute-Standard Evaluation System, 2013). This proved to be very robust and convenient, to find resistant entry from a huge germplasm within short span of time and also to track the change in virulence. Major advantage of this type of screening method is that easy culling of highly susceptible entries. But still those entries selected from this method should not only be subjected to several tests to find its mechanism of resistance against the BPH but also should perform well in the field conditions (84). Collaborations between IRRI and researchers from across Asia facilitate the regular sharing of breeding materials like International Rice Brown Planthopper Nursery (IRBPHN) for specific field tests. These materials are supplied under the International Rice Testing Program (IRTP) and later through the International Network for Genetic Evaluation of Rice (INGER) (100). In India, Indian Institute of Rice Research (IIRR) and National Rice Research Institute (NRRI) conduct annual screening trials such as Planthopper Screening Trial (PHS), Planthopper Special Screening Trial (PHSS) for insect biotype studies and Planthopper Population Monitoring Trial (PHPM) to identify the resistant entries among the given germplasm (42).

Gene pyramiding: Rice breeders have mainly concentrated on broadening resistance sources (genes and mechanisms) and pyramiding two or more resistance genes or quantitative trait loci (QTLs) into high-yielding varieties through marker-assisted selection in order to decelerate pest adaptation and improve resistance longevity (101). Pyramiding major genes or QTLs can provide stable resistance to developing insect biotypes while enhancing yield potential. However, this aims at breeding for polygenic resistance or repeatedly discovering and introgressing new resistance genes into elite lines (35). Single resistance gene deployment (e.g., Bph1) offers narrow protection that frequently breaks down as pests evolve. Stacking several genes provides lasting and broad-spectrum resistance to all accessible biotypes. To slowdown biotype evolution, breeding programs ought to target cultivars with multiple resistance mechanisms that are stable across dominant biotypes (101). Resistance traits, however, might come at the expense of growth and yield due to resource limitation, prompting some studies to recommend partial resistance over complete resistance for long-term effectiveness (23). The conventional breeding practices obviously supports a tendency to inherit the genes with undesired qualities along with the desired ones. By contrast, the combination of multiple resistance genes provides wide-spectrum and durable resistance to novel biotypes through complementary and synergistic effects. Gene pyramiding is regarded as the effective approach to produce resistant rice varieties capable of tolerating both abiotic and biotic stresses.

Area-wide IPM: Tolerant rice varieties reduce reliance on insecticides by maintaining productivity under pest pressure, which also preserves natural enemy populations (102). While vertical resistance (controlled by single major genes like *Bph1*) often leads to biotype development when overcome, tolerance acts as a resilient secondary defence mechanism (53). For example, wild rice accessions like IRGC99577 and IRGC104646 demonstrate high tolerance through delayed hopper burn and minimal dry weight loss, providing durable protection even as new resistant varieties are developed (103). Studies confirm that tolerance mechanisms-such as callose deposition and glycine cleavage system upregulation-offer stable resistance without triggering virulence adaptations in BPH (87). Comprehensive and systematic monitoring and surveillance programs should be launched across regions to identify and map the presence of insect biotypes. The combination of digital pest monitoring with cultural control practices greatly enhances real-time monitoring and management of brown planthopper (BPH) biotypes. Cultural practices such as optimal planting times, use of resistant varieties in crop mosaics and effective water and fertilizer management decrease habitat suitability for BPH and ease pest pressure, thus lowering selective pressure for virulent biotypes (100). Remote sensing, drone photography and mobile apps facilitate rapid identification and spatial mapping of biotype-specific outbreaks at landscape scales, thus facilitating timely intervention (104).

Conclusion

BPH has been posing serious threat in rice which makes the conventional management strategies like chemical control ineffective and made it to cause resurgence and other problems. Extensive research on host plant resistance along with release of resistant/tolerant cultivars makes the management effective and economical. The development of highly virulent biotypes of BPH highlights the dynamic evolutionary arms race between BPH and rice. The resistance failure in major rice growing regions all over the world where resistant cultivars fell to newly adapted BPH populations is due to improper management, large scale cultivation of monogenic resistant rice and lapse in monitoring of biotypes. Increased knowledge of the molecular basis of rice-BPH interactions has shed light on the genetic and evolutionary basis of host adaptation, which allows the researchers to identify the mechanism of adaptation by BPH and formulate a resistant germplasm which could withstand the developing biotypes. To prevent biotype development, management strategies such as gene pyramiding, Integrated Pest Management practices like avoiding mono culturing of same variety in particular region and careful monitoring of biotype shifts after release of a resistant variety will be practical and effective. But still, technologies like CRISPR-Cas and functional validation of resistance at field level could effectively reduce time of resistant breeding programmes are yet to be implemented widely to tackle the present pace of the pest outbreaks. Through the integration of these proactive strategies, breeders and agronomists could be able to instil

durable resistance while limiting pest adaptation, ultimately protecting global rice productivity against the emergent threat of BPH biotypes.

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Authors' contributions

PSA and SV prepared the design of the study and drafted the manuscript. SJ, RS and JR participated in its design and coordination and reviewed the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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