

Brown planthopper: A genetic marvel*

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Abstract

Rice planthoppers have again attained a major pest status in this century causing enormous yield losses through direct feeding and transmission of pathogenic viruses. Consequently, there has been increased focus of research on their biology, genetics and molecular biology in search of alternative methods to manage them. This review highlights main findings of these studies to reveal how genetic plasticity of the brown planthopper (BPH) has equipped the species to fight back adversities and pose challenges for its effective management. Genome of BPH with size of 1141 Mb spread across 30 chromosomes is predicted to have 27,571 genes. Salivary glands, first line of offense, secrete proteins that trigger either susceptibility (ETS) or immunity (ETI) reaction in the host plant. Fat bodies, spread all over the body, are sites of primary lipid metabolism, endocrine regulation, systemic immunity, vitellogenesis, and housing of microbial symbionts. BPH harbours yeast like symbionts (YLS) in its fat bodies that play critical role in insect survival. BPH populations across Asia have acquired resistance against almost all classes of insecticides which has been attributed to neofunctionalization of duplicated P450 genes. So far about 40 major host plant resistance genes and 72 QTLs have been reported from cultivated rice and its wild relatives but BPH has ability to quickly evolve virulent populations. Role of cytochrome P450 enzymes and of symbiotic YLS in this ability has been shown. Several studies have focused on the reproductive physiology of BPH and identified key genes that can be target for RNAi mediated silencing as novel strategy for pest management. Several recent studies have also covered genetic and molecular basis of wing polymorphism and adaptation for long distance migration in this insect. Other recent studies on effect of climate change on BPH incidence and its genetic ability to adapt to the changes in the weather and climate have cautioned that this insect is likely to continue to be a major problem in days to come. On a larger perspective, this rapidly expanding knowledge is providing us with novel approaches and tools to contain the pest and stay a step ahead of it in the evolutionary race.

Key words: BPH, biology, host plant resistance, insecticide resistance, climate change

Introduction

Rice brown planthopper (BPH), *Nilaparvata lugens* (Stal), along with the other two sympatric species whitebacked planthopper (WBPH), *Sogatella furcifera* (Horvath) and small brown planthopper (SBPH), *Laodelphax striatella* (Fallen), has again attained a major pest status in this century (Bentur and Viraktamath, 2008; Bottrell and Schoenly, 2012). Despite 46 species of planthoppers being reported to

feed on rice, these three species, especially BPH, have challenged rice production in intensive rice cultivation belt across Asia. It especially causes direct damage in all stages of life cycle, particularly nymph and adult stages, by direct feeding on phloem sap and by transmitting ragged stunt virus and grassy stunt virus diseases. Prior to 1980s BPH was not even reckoned as a pest of rice. This phenomenal evolutionary success, as it is now emerging through intensive studies, is

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attributed to its genetic plasticity and adaptability. Due to its high economic impact on rice production, a large number of researcher groups across the world have been engaged in intensive studies during the past five decades. This has resulted in explosion of over 770 research publications during last five decades (Figure 1). The major focus of these studies has been on insecticide resistance related (30%), insect-plant interactions (22%) and reproduction (19%). There have been excellent reviews published recently (Fujita *et al.*, 2013; Ling and Weillin 2016, Du *et al.*, 2020, Haliru *et al.*, 2020) covering specifically insect-plant interactions. However, no comprehensive review is available. An attempt is made here to briefly review the broad progress in our understanding of BPH biology, genetics and its interaction with host plant.

Genome of BPH has been sequenced (Xue *et al.*, 2014) and noted with size of 1141 Mb spread across 30 chromosomes. Relatively, BPH genome size is the largest in comparison with those of WBPH (720 Mb, Wang *et al.*, 2017) or SBPH (541 Mb, Zhu *et al.*, 2017). In all, 27,571 genes have been predicted; of which 10,245 have been assigned gene ontology while 16,330 genes are noted to be specific to BPH. BPH is monophagous with its feeding confined to rice (*Oryza*), having shifted its host from *Leersia* over the past 0.25 million years (Sezer and Butlin, 1998).

Salivary Glands

Salivary glands are the first line offense of BPH while attempting to feed on rice plant. These produce two types of secretions: a coagulating gelling secretion that quickly hardens to form salivary sheath around the probing stylets consisting of polyphenol oxidase and peroxidase enzymes, and a watery secretion that contains digestive enzymes like alkaline phosphatase, esterase, amylase, beta glucosidase as well as other components mainly secretory salivary gland proteins (SSGPs). These SSGPs are main class of effectors that trigger susceptibility (ETS) or immunity (ETI) depending on the rice genotype BPH is attempting to feed upon (Huang *et al.*, 2017; Ji *et al.*, 2017; Ye *et al.*, 2017). Of the 352 reported genes encoding putative secreted proteins of salivary gland, 67 genes are differentially expressed in TN1 and Mudgo reared insects (Ji *et al.*, 2013). Rao *et al.*, (2019) characterized six of the effector proteins. A mucin-like protein is required for feeding by BPH but it also induces immunity response in plants acting like an effector (Shangguan *et al.*, 2018). Application of salivary gland extract to rice plants induces systemic host mRNA patterns associated with nutrient remobilization (Petrova and Smith, 2015). Thus, salivary gland of BPH has a repertoire of effector proteins which can evolve rapidly to overcome host mediated resistance.

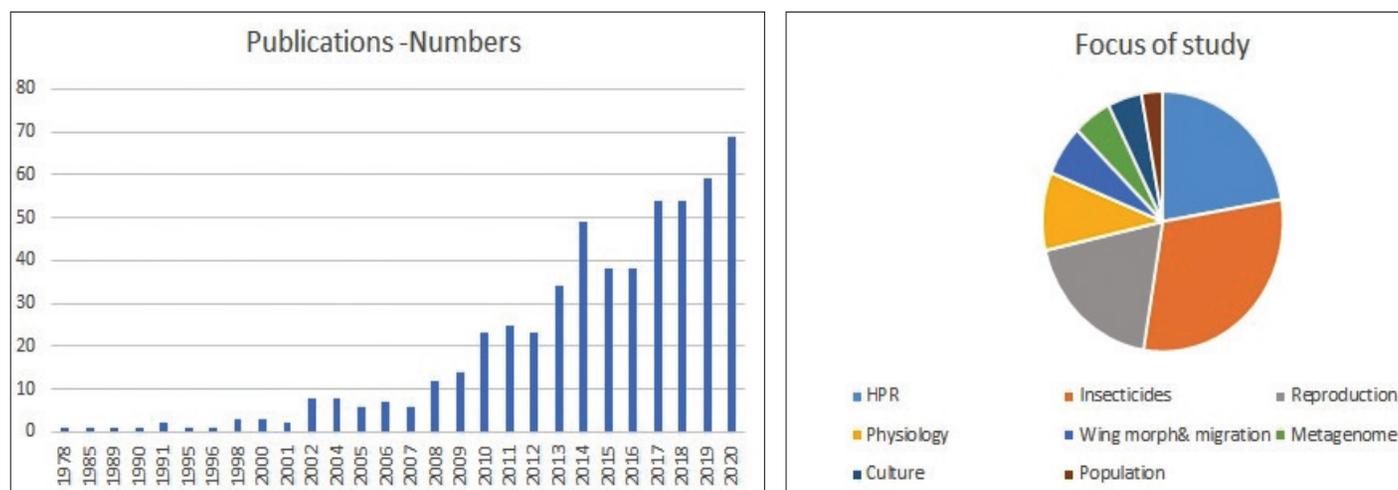


Figure 1: Number of publications on BPH appearing year-wise and the focus of the study (Source: Pubmed)

Fat Bodies

Insect fat body is a highly dynamic tissue composed primarily of storage cells. It is distributed throughout the insect's internal body cavity; the haemocoel, near the epidermis, digestive organs and ovaries. Akin to the combination of liver and adipose tissue in mammals, fat bodies are site of primary lipid metabolism, endocrine regulation, systemic immunity, vitellogenesis, and housing of microbial symbionts. BPH harbours yeast like symbionts (YLS) in its fat bodies that play critical role in insect survival. While the insect can degrade seven of the amino acids independently, six of these are catabolised exclusively by YLS while seven more of these are degraded by both (Wan *et al.*, 2015). Impaired lysine degradation by YLS negatively affects the survival and development of *N. lugens*. Transcriptome analysis of fat bodies from two BPH populations with different virulence levels revealed that these are sites of intermediate metabolism, immunity and detoxification of xenobiotics (Yu *et al.*, 2014). Expression of several of the genes in BPH population reared on Mudgo rice differed significantly from those reared on TN1 rice. Lipid, amino acid and xenobiotic metabolism related genes were significantly upregulated in the Mudgo population. Protein transport related genes in YLS, and cell division and ribosome assembly related genes in another symbiont *Wolbachia* were upregulated in this population. These studies highlight the critical role of the symbionts in BPH virulence on resistant genotypes.

Insecticide Resistance

BPH populations across Asia have acquired resistance against almost all classes of insecticides (Matsumura *et al.*, 2009; Garrood *et al.*, 2015; Wu *et al.*, 2018). There have been intensive studies on evolution and mechanism of insecticide resistance. Role of P450 genes, a family with 54 genes, in insecticide resistance in BPH has been extensively documented. Neofunctionalization of duplicated P450 genes drives the evolution of insecticide resistance in the insect (Zimmer *et al.*, 2018). Garrood *et al.*, (2015) studied field-evolved resistance to imidacloprid and ethiprole in populations of BPH collected from across South and East Asia. Association of overexpression

of CYP6ER1 gene with resistance to imidacloprid, thiamethoxam and buprofezin was noted. RNA interference of this CYP6ER1 gene resulted in susceptibility (Garrood *et al.*, 2015; Pang *et al.*, 2016). However, P450 CYP6AY1 was over expressed in one of the Indian populations. Synergistic and compensatory effects of two- point mutations in the insect GABA receptor RDL confer resistance to fipronil (Zhang *et al.*, 2015). Carboxyl esterase gene (*NlCarE*) plays an important role in chlorpyrifos detoxification and its overexpression may be involved in chlorpyrifos resistance in *N. lugens* (Lu *et al.*, 2017). RNA interference of NADPH-cytochrome P450 reductase (CPR) increases susceptibility to insecticides including buprofezin (Liu *et al.*, 2015).

Host-plant Resistance

Major emphasis of BPH management is on development of resistant rice varieties exploiting host plant resistance (Brar *et al.*, 2009). So far about 40 major genes and 72 QTLs conferring resistance to BPH have been reported from cultivated rice and its wild relatives (Fujita *et al.*, 2013, Ling and Weillin 2016, Du *et al.*, 2020, Haliru *et al.*, 2020). A major limitation here is the ability of BPH to quickly evolve virulent populations, often referred to as biotypes, capable of overcoming host resistance. Recent studies have been aiming to understand genetic and molecular basis of such virulence in BPH. Role of cytochrome P450 enzymes in virulence was studied by Peng *et al.*, (2017) who noted that among the 21 Cyp genes CYP4C61 gene expressions was more in virulent biotype Y than in biotype 1. They suggest that duplication of P450 genes in BPH genome is likely contributing to adaptation to host plant resistance, as in case of insecticide resistance noted above. Role of symbiotic YLS in metabolic response of BPH while feeding on resistant rice has been studied (Liu *et al.*, 2017). The study showed significant metabolic differences between BPH nymphs feeding on the resistant NIL-BPH15 and susceptible TN1 rice. To survive on this resistant rice, BPH nymphs probably ingest more sap and/or get necessary nutrients from their yeast-like symbionts at later feeding stages. Jing *et al.*, (2014) and Kobayashi *et al.*, (2014) have attempted to map virulence loci that break down host



resistance on BPH genome using molecular markers. Over 860 markers including 125 gene specific markers have been reported and used in mapping three virulence loci Qhp7, Qgr5 & Qgr14 (Jing *et al.*, 2014). Kobayashi *et al.*, (2014) mapped the virulence gene *vBph1* located in the 1.8 cM genomic region flanked by SNP markers VLS01 and VLS05 of linkage group 10.

Reproductive Physiology

Another feature of the brown planthopper that has enabled its evolutionary success is its reproductive potential. Several studies have focused on the reproductive physiology of BPH. Role of Broad-Complex (Br) and Krüppel homolog 1 (Kr-h1), two transcription factor genes downstream of juvenile hormone and ecdysone pathways in the ovary development was noted by Jiang *et al.*, (2017). An adenyl cyclase like-9 gene (NIAC9) influences growth and fecundity in BPH (Ge *et al.*, 2017a). PHF7, a novel male gene influences female fecundity and population growth through secretion of accessory gland and transferred to female through mating (Ge *et al.*, 2017b). This can be a target gene for RNAi mediated gene silencing to reduce population growth of the insect. Ge *et al.*, (2016) have also shown that suppressing male spermatogenesis-associated protein 5-like gene expression reduces vitellogenin gene expression and fecundity. Yu *et al.*, (2016) identified 94 seminal fluid proteins in the male accessory glands of BPH of which four were unique to this insect. Forkhead box transcription factor L2 activated follicle cell protein gene *NIFcp3C* to regulate insect chorion formation (Ye *et al.*, 2017). Role of juvenile hormone (JH) secreted by corpora allata has been studied intensively. TOR pathway-mediated JH synthesis regulates nutrient-dependent female reproduction (Lu *et al.*, 2016), while nutritional signaling also regulates vitellogenin synthesis and egg development through JH (Liu *et al.*, 2016). Silencing a sugar transporter gene *Nlst6* reduces growth and fecundity. Several agro-chemicals like antibiotics or even insecticides stimulate BPH reproduction. Adipose triglyceride lipase (Atgl) mediates the antibiotic jinggangmycin-stimulated reproduction (Jiang *et al.*, 2015). Sub-

lethal doses of triazophos and fenvelrate insecticides also induce reproduction (Bao *et al.*, 2008).

Wing Polymorphism and Migration

A special trait of interest for BPH is its ability to migrate long distance being carried by the wind currents (Otuka *et al.*, 2008). To suit to this adaptation, the insect has wing dimorphism involving short winged brachypterous forms with high fecundity and long winged macropterous form suited to long distance migration. Several recent studies have covered genetic and molecular basis of wing polymorphism and adaptation for long distance migration. There is an ovarian diapause in macropterous females prior to migration and TOR (target of rapamycin) genes are shown to be involved in this diapause (Liu *et al.*, 2016). Zhou *et al.*, (2017) showed that transformer-2 (*NItra-2*) determines sex in nymph and wing shape of the progeny. They also suggested the important role of *NIJHEH* (juvenile hormone epoxide hydrolase) gene in determining the wing morph. Higher levels of JH in V instar nymph lead to development of short wings. Xu and Zhang (2017) explained the molecular basis by which two insulin receptors (InR1 and InR2) act as switches to determine alternative wing morphs in the BPH.

Climate Change Adaptation

There have been several recent studies on effect of climate change on BPH incidence and genetic ability of the insect to adapt to the changes in the weather and climate. Pandi *et al.*, (2018) studied impact of elevated CO₂ and temperature on BPH in rice ecosystem. They observed that increased CO₂ and temperature resulted in escalated BPH multiplication through increase in both fecundity and number of adults, thus inflicting higher yield loss in rice. Similar study in Bangladesh by Ali *et al.*, (2014) showed months or areas characterized by a climate that is either cold and dry or hot and wet that are likely to experience higher levels of BPH due to climate change. At high temperature (37 °C), heat shock protein (HSP) genes were the most co-regulated (Huang *et al.*, 2017). Macropterous are more heat resistant than brachypterous adults. Up-regulation of *NIHsc70* gene provides more thermal tolerance/resistance in macropterous adults (Lu *et al.*, 2016a, b).

Perspectives

This rapidly expanding knowledge on BPH and other related planthoppers of rice has not only given us an insight into its evolutionary superiority but also has revealed several ‘weak points’ that can be tweaked to our advantage from pest management point of view. RNAi based approach and the key target genes identified can be used for the purpose. Genome editing aiming at susceptibility genes is another promising alternative. Resequencing of scores of rice genotypes and the emerging identification of superior haplotypes of the known and unknown resistance genes can widen our choice in host-plant resistance deployment approach. It is thus probable that we may stay a step ahead of it in the evolutionary race.

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