

Chapter 2

Planthopper Outbreaks in Different Paddy Ecosystems in Asia: Man-Made Hopper Plagues that Threatened the Green Revolution in Rice

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Abstract The brown planthopper (BPH), *Nilaparvata lugens* (Stål), and white-backed planthopper (WBPH), *Sogatella frucifera* (Horváth), are the rice monophagous species, which are inevitably associated with rice agriculture in Asia. In the 1970s, BPH suddenly occurred as the most preeminent insect pest of rice and threaten the green revolution in the tropical Asia. The BPH outbreaks in Southeast Asia were caused by disruption of ecological balance between BPH and natural enemies by insecticides, which were accepted as a technical component to ensure the high-yielding output of high-yielding varieties (HYVs) in the tropical paddy ecosystems. The outbreaks in India are primarily attributed to disruption of coevolutional interactions between BPH and local rice plants in the monsoon-prevailing paddy ecosystems by abrupt replacement of BPH-resistant traditional rice varieties with susceptible exotic HYVs by the high-yielding varieties program. Unsuccessful deployment of BPH-resistant IR varieties was critically reviewed in relation to the standardized seedbox screening test (SSST), which had been exclusively used to breed BPH-resistant IR varieties. Sixteen of 19 IR varieties incorporated with the *Bph1* and *bph2* genes were easily defeated with emergence of adaptive BPH biotypes so that their sequential releases could not stop BPH outbreaks. Only a few varieties such as IR36 and IR64 were found to have durable field resistance to BPH even after breakdown of their monogenic resistance. Field performance of IR36 and IR64 indicated that they have some other resistance traits that cannot be evaluated by the SSST. Incapability to evaluate field resistance traits commits a risk of insidious erosion of those traits during the process of SSST-dependent breeding. That could be a reason for a tentative resistance in most of the BPH-resistant IR varieties. WBPH outbreaks in Punjab plain, prevalence of WBPH and WBPH-vectored new virus disease in China and Vietnam, and ovicidal resistance to WBPH in *japonica* rice were referred with special reference to the wind-borne massive displacement biology of WBPH in the active monsoon rice areas.

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2.1 Introduction

There is a small stone image of Buddha in Fukuoka, a northern city of Kyushu, Japan. It was enshrined for mourning a million farmers perished with historical famine caused by an outbreak of the brown planthopper (hereafter BPH), *Nilaparvata lugens* (Stål), devastated over the western part of Japan in 1732 (Suenaga and Nakatsuka 1958). Because BPH is rice monophagous and potentially outbreak-prone for its *r*-strategic biology, it has inevitably been associated with rice agriculture. Since the remote past, such sporadic BPH outbreaks were a catastrophic natural disaster in the traditional rice farming in Japan. The outbreaks were not related to any technical innovations in rice farming, but were caused by unpredictable massive overseas invasions of the pest.

In the tropical Asia, BPH was only a minor rice herbivore before the advent of the green revolution in rice in the 1970s. However, it dramatically came out as the most preeminent insect pest of high-yielding varieties (HYVs) of rice (Dyck and Thomas 1979). Insecticides and resistant rice varieties were thought to be essential means to ensure the high-yielding output of HYVs by suppressing the pest infestations.

However, prophylactic insecticide applications rather encouraged BPH to upsurge population density and plunged into a vicious spiral of BPH outbreaks and insecticide sprays in the tropical paddies (Kenmore et al. 1984; Heong and Schoenly 1998). Deployment of BPH-resistant IR varieties was neither a simplistic solution of the problems. Sequential releases of BPH-resistant IR varieties incorporated with different resistance genes were easily defeated with successive emergences of adaptive BPH biotypes (Sogawa 1982; Gallagher et al. 1994).

Persistent BPH outbreaks in the tropical Asia once declined and were put under control by the IPM extension projects by FAO and IRRI (Pontius et al. 2002). However, BPH is once again threatening the rice farming in Asia at far more serious scales than previous outbreaks under intensified cropping patterns, recovery of prophylactic insecticide applications, extension of hybrid rice, and changes in socio-economic and political situations surrounding the rice agriculture (Bottrell and Schoenly 2012). At present, it is intended to reconfirm the root causes of BPH outbreaks and the problems of BPH-resistant IR varieties in order to cope more rationally with the revival of the BPH problems.

2.2 Insecticide-Induced BPH Outbreaks

1. Initiation of BPH outbreaks at IRRI

BPH outbreaks in the tropical Asia started from the experimental farm of International Rice Research Institute (IRRI). The first infestation of BPH was

found at IRRI in 1964 (IRRI 1964). It was only two years after inauguration of the institute and two years before release of IR8. BPH emerged soon after insecticides were used to control the rice stemborers in 1962. Population density of BPH increased quickly beyond its economic injury level under the routine applications of diazinon. Major outbreak of BPH occurred on diazinon-treated IR8 (IRRI 1971). Eventually, uncontrollable outbreaks continued from 1971 to 1976 (Pathak and Dhaliwal 1981).

Around 30 years later, hopperburn disappeared completely from the IRRI farm after drastic reduction ($\geq 90\%$) of insecticide use with adoption of IPM. When biodiversity restored in the IRRI farm, coincidentally BPH infestation declined below sub-injurious levels as it used to be. The beginning and ending of the BPH events at IRRI implicate a big instruction about the genesis of BPH outbreaks in the tropical paddies (Heong et al. 2007).

BPH was previously a minor rice herbivore, but emerged soon as a pest form by prophylactic chemical control of the endemic rice stemborers. Insecticides were rationally applied following the most advanced technologies at the IRRI research farm. Therefore, the BPH outbreaks at IRRI cannot be attributed neither to misuse of insecticides nor to inadequate application practices. The BPH outbreaks terminated when prophylactic insecticide usages were restrained by the implementation of IPM practices without any other changes in the crop managements. Therefore, it is apparent that fertilization and susceptibility of paddy plants were not the primary causes of BPH outbreaks. The BPH history at IRRI indicates undoubtedly that insecticides are the ultimate cause of the BPH outbreaks. So that the BPH history at IRRI is the epitome of the BPH outbreaks, which had prevailed in the green evolution era and which is once again threatening the rice farming in the tropical Asia.

During the process of BPH outbreak at IRRI, diazinon lost its effect to BPH in 1969 after three years of its routine use. Reproduction of BPH was rather stimulated and hopperburn appeared in the diazinon-treated fields (IRRI 1970). It was the first sign of BPH resurgence induced by insecticides in the tropical paddies. However, little attention was paid yet to the ecological disorders of paddy ecosystems treated with insecticides. The population upsurge of BPH was attributed to a side effect of diazinon at sublethal dosages, microbial degradation of diazinon applied to submerged paddy soil, and development of insecticide resistance in BPH (IRRI 1970).

In 1980, Kenmore (1980) has first demonstrated evidently by his credible on-farm experiments such as life table analysis of BPH and natural enemy exclusion experiments that disruption of natural biological control functions by insecticides is the root cause of BPH outbreaks in the tropical paddies adopted the green revolution package technology. After that, BPH resurgence was reported not only with diazinon but also with various broad-spectrum organophosphorous and synthetic pyrethroid insecticides (Reissing et al. 1982a, b; Chelliah and Uthamasamy 1986; Heinrichs 1994). Some resurgence-inducing insecticides were ironically recommended as a tool to generate BPH population in field screening of resistant rice varieties against BPH (Heinrichs et al. 1978). It was also pointed out that resurgence-causing insecticides could accelerate biotype selection on resistant varieties (Aquino and Heinrichs 1979).

The outbreaks of BPH could be attributable to its potentially outbreak-prone r -strategic biology. However, its high intrinsic fecundity is usually poised with high mortality due to biological control by natural enemies. Such ecological balance between BPH and natural enemies is, however, highly vulnerable to broad-spectrum insecticides, because of their non-selective toxicity to natural enemies, non-ovicidal activity, and shorter residual period than the egg period of BPH. As the consequences, the BPH populations emerged from survived eggs enable to reproduce exponentially in the natural enemy-eradicated habitats. That is the basic mechanism of BPH resurgence in the paddy fields treated with insecticides. Harmful effects of pesticides on the balance of arthropod community in different agro-ecosystems were already been pointed out as early as in the 1950s (Ripper 1956). It has been criticized that the lack of an ecosystem concept in the main disciplines rendered the BPH phenomena unintelligible until the discovery of the rich and complex relationship between natural enemies and rice pests was beginning to unfold at IRRI in the 1980s (Anderson et al. 1991).

2. Devastation of BPH outbreaks in Indonesia

Indonesia is a prime example of the nations, which adopted the green revolution package technology to achieve rice self-sufficiency (Oka 1979). It is also said that Indonesia was a prime example of a country, which adopted the pesticide-dependent pest management systems developed in Japan (Soenardi 1972; Soekarna and Sundaru 1983; Sogawa et al. 1994). Insecticides were invested as an essential means to increase rice production. BPH was a minor rice pest before the advent of operational chemical control in the rice intensification programs (BIMAS/INMAS) in 1970 (Soenardi 1972; Yazawa 1987). The first large-scale chemical control was carried out in 0.8 million ha of paddies in Java to control the rice stemborers by aerial applications of phosphamidon, an organophosphorous insecticide (Singh and Sutyoso 1973). Since then, an agricultural air force played a major role in operational control of rice pests over the program areas. The plant protection brigades in each province also took charge of operational controls on the ground. The pesticide cost was subsidized at 85 % by the government and allocated to the program areas through the BIMAS authority, a government channel.

Hopperburn began to appear in HYVs sprayed with insecticides from 1972 onward (Mochida et al. 1977b; Mochida 1979). Coincidentally, BPH-vectored grassy stunt and ragged stunt virus diseases also became epidemic. In spite of intensive aerial applications of diazinon, hopperburn spread rapidly over the major rice areas in the period from 1975 to 1979. BPH infested 350,000 ha of rice areas in Java and caused yield losses of 350,000 tons in the 1976/77 wet season. During those crop seasons, about 6,000 tons of organophosphorous insecticides, mainly diazinon, fenitrothion, chlorpyrifos, isoxathion, and dichorvos, were applied. Nevertheless, persisted BPH outbreaks inflicted serious damages on rice production, which was stagnated losing 0.4–0.5 million tons of rice. Indonesia became the world's largest rice importer in the BPH outbreak period (Whitten et al. 1990).

Fortunately, BPH populations declined on the new BPH-resistant variety IR36, which was introduced in 1978. IR36 was then compulsively planted in the BPH-epidemic areas and became the most popular rice variety in Indonesia in the early 1980s. More than 70 % of total rice areas were planted with only IR36. Rice production increased at average annual rate of 6.6 % from 1979 to 1983. The rice self-sufficiency was eventually attained upon IR36 in 1984.

It should be pointed out that insecticides supplied by the BIMAS authority increased steeply even after depression of BPH outbreaks and achievement of rice self-sufficiency upon IR36. More than 60,000 tons of diazinon, chlorpyrifos, fenitron, monocrotophos, and phenthoate were supplied for preventing possible pest infestations in 1986. Besides, IR36, which was efficient to suppress BPH infestations, was quickly replaced with IR42 and allied national HYVs such as Krueng Aceh and Cisadane after attainment of rice self-sufficiency, because the rice price of IR36 tumbled due to poor quality and over production (Mizuno 1987). Although the substituted new varieties possess the same BPH resistance gene as that of IR36, they were easily defeated with development of new virulent biotypes unlike IR36. In North Sumatra, IR42 was defeated by a new biotype in 1982 (Sogawa et al. 1984a, b). By 1986, over 70 % of paddy fields in Java were planted with Krueng Aceh and Cisadane and exposed to the newly developed virulent BPH biotypes (Sogawa et al. 1987). The rice areas infested by the new biotypes spread from 80,000 ha in 1985 to 200,000 ha in 1986 in Central Java in spite of maximized operational control with insecticides.

Government faced with resurrected BPH menace and bankruptcy of newly achieved rice self-sufficiency, and a special task force affiliated to the National Development Planning Board (BAPPENAS) urgently conducted field inspections and disclosed that massive provision of subsidized insecticides through the government channel was the root cause of the BPH problems. Based on this assessment, Presidential Decree No. 3 was issued on November 5, 1986, by which the national crop protection policy was drastically shifted from unilateral dependence upon insecticides to ecosystem-orientated IPM, and 57 broad-spectrum insecticides were immediately banned from using in paddy fields (Southern 1987). Subsidies for insecticides were completely removed by 1989. The agricultural air force was also disorganized. This paradigm shift broke the vicious spiral of insecticides and BPH outbreaks. An insect growth regulator buprofezin extinguished hopperburn, which acts selectively to BPH and is safe to natural enemies (Sogawa 1989, 1993). After that, Indonesian National IPM program was launched with technical and funding supports by the FAO rice-IPM program in 1989 (Oka 1991; FAO-IPM Secretariate 1993; Oka 1996). BPH outbreaks were suppressed by a new variety IR64 with durable field resistance to BPH under restrained insecticide use with implementation of IPM.

3. Set back of IPM and revival of BPH outbreaks

Thirty years ago, we have learned serious ill effects of insecticides to paddy ecosystems from unanticipated BPH outbreaks happened in the green revolution schemes during the 1970s–1980s. However, our previous lessons have not been properly exploited to the management of tropical paddies.

In Indonesia, for example, BPH outbreaks were once suppressed by IPM. However, IPM declined due to the change in the rice policy from self-sufficiency to free trade after the Asian economic crisis in 1997 and subsequent political power shift in the early 2000s. The Presidential Decree was substantially castrated. According to the FAO statistics, insecticide imports increased more than 30-folds after shifting the rice policy and are still increasing at higher rates. Insecticides for rice pest control were once restricted to only a few chemicals such as buprofezin by the Presidential Decree, but now, more than 130 insecticides are registered (Trisyono 2012). IPM was merged into integrated crop management (ICM) or crop total management (CTM) as a tactical tool of crop management with insecticides, in which the ecosystem-based strategies of IPM became vague and routine prophylactic sprayings of insecticides designed by pesticide dealers were recommended to rice farmers.

Besides, hybrid rice was politically introduced so as to revitalize rice agriculture in 2005. Cost of hybrid rice seeds was subsidized (GRAIN 2007). Heavy inputs of insecticides and fertilizers are essential for its high-yielding cultivation. When hybrid rice areas expanded to 650,000 ha in 2009, the BPH plague came back to Indonesia together with prophylactic insecticide sprays (Baehaki 2009; Cabunagan et al. 2010; Muhsin 2010; Heong 2011; Horgan 2011a, b; Winarto et al. 2011a, b; Baskoro and Winarto 2012). Hopperburn appeared in IR64 with field resistance indicates serious disruption of paddy ecosystem functions by indiscriminate insecticide applications.

4. Repeated BPH outbreaks by insecticides in Thailand

Quality rice has been an important export commodity in Thailand, where BPH broke out twice in the past. The first outbreak happened on BPH-susceptible Thailand varieties in 1980–1981, after sudden upsurge of pesticide use in 1978–1979 (Kenmore 1991). After that, resistant varieties such as RD21 (with *Bph1* gene from IR26) and RD23 (with *bph2* gene from IR32) were released in 1981 and planted widely. However, those varieties became susceptible by 1986. New resistant variety Suphan Buri 60 (with *bph2* gene from IR48) was then released in 1987. Because of its high-yielding ability and excellent grain quality, Suphan Buri 60 became the most popular rice variety in the central plain. The second outbreak happened mostly on Suphan Buri 60 in 1989–1990, within two years after its release (den Braber and Meenakanit 1992). The outbreak was closely associated with intensive use of synthetic pyrethroid, deltamethrin, which is well known as a typical insecticide to induce BPH resurgence.

In 1991, soon after the second outbreak, a neonicotinoid insecticide, imidacloprid (admire), was introduced to control BPH. Imidacloprid did not induce BPH resurgence, because of its long-lasting (more than 40 days) systemic toxicity. Its residual period is enough long to cover a whole life cycle of BPH and did not allow resurging the BPH populations from survived eggs. As the results, BPH was well controlled for a first few years. However, it was not a long-lasting solution of BPH problems. BPH became resistant to imidacloprid (Fabeller et al. 2010; Gorman et al. 2008; Harris 2006). Decline of control effect of imidacloprid to BPH was first reported in 2003. After that, the imidacloprid-resistant BPH spread

in the central plain during the mid-2000s. Infestations by the imidacloprid-resistant BPH became serious in the paddies, where natural enemies were eradicated by its long-lasting toxicity of imidacloprid.

Abamectin, cypermethrin, and chlorpyrifos substituted for imidacloprid to control imidacloprid-resistant BPH (Luecha 2010a). Those substituted insecticides, which have not long-lasting residual toxicity, readily induced resurgence of imidacloprid-resistant BPH. Eventually, the third BPH outbreaks started in the Thai rice-bowl at far more serious scales than previous outbreaks in the period from 2009 to 2012 (Thongdeethae 2009; Wattanesk 2010; Luochoa 2010b; Soitong et al. 2011; Chaiyawat 2011; Rattanakarn et al. 2012a, b). Repeated BPH outbreaks induced by insecticide-dependent pest managements in Thailand warn us that insecticides cannot solve the BPH problems in the tropical paddies.

2.3 BPH Outbreaks Induced by Exotic HYVs

BPH outbreaks also happened in South Asia in the green revolution era. However, those were different from the insecticide-induced outbreaks in Southeast Asia. BPH, which was recorded as *fulgorid* hopper or rice *fulgorid*, had already been an endemic pest of rice in the irrigated double-cropping rice areas in Orissa, Andhra Pradesh, Tamil Nadu, and Kerala along the coastal tract of the Bay of Bengal in the period from 1920 to 1970 (Gorman 1974; Israel and Rao 1954; Rao 1961). For example, BPH occurred in a pest form in Andhra Pradesh as early as in 1927. In Tamil Nadu, the rice farmers have long known the BPH infestations as “pugayan.”

BPH became very rapidly a major rice pest in India since around 1970. Light trap data from several AICRIP (All-India Coordinated Rice Improvement Project) centers recorded massive upsurges of the BPH population in 1971–1972 (Kalode 1976). BPH began to occur in an epidemic scale, particularly in the eastern coastal tracts and southern India since around 1972. Although hopperburn damages by BPH were also recorded in the single cropping areas in the central and northern parts of India as well, the infestations were rather sporadic and localized.

The HYVs program, which was launched in India in 1965, is greatly responsible for the change in the pest status of BPH in the double-cropping rice areas. A number of semidwarf HYVs such as TN1 and IR8 were introduced on a large scale in 1966 and 1967. Simultaneously, AICRIP bred locally adapted HYVs such as Jaya and Padma using IR8 as a parent. All those varieties were highly susceptible to BPH. BPH began to occur in an epidemic scale in the exotic HYVs since around 1972, while indigenous local varieties suffered only slightly (Das et al. 1972; Gopalan 1974; Kulshreshtha 1974; Abraham and Nair 1975; Prakasa Rao et al. 1976).

The BPH-epidemic areas in India belong to an active Indian monsoon region. Monsoon influences greatly the BPH ecology, which assists long-range and massive displacements of BPH between remote rice areas. Sudden massive invasions of BPH could be a serious threat to the traditional rice farming in the

monsoon-prevailing regions (Fig. 2.1). It is relevant to the evidence that most of the resistant rice germplasm were found among traditional *indica* landraces in South India and Sri Lanka (Ikeda et al. 1993; Khush 1979). BPH resistance could

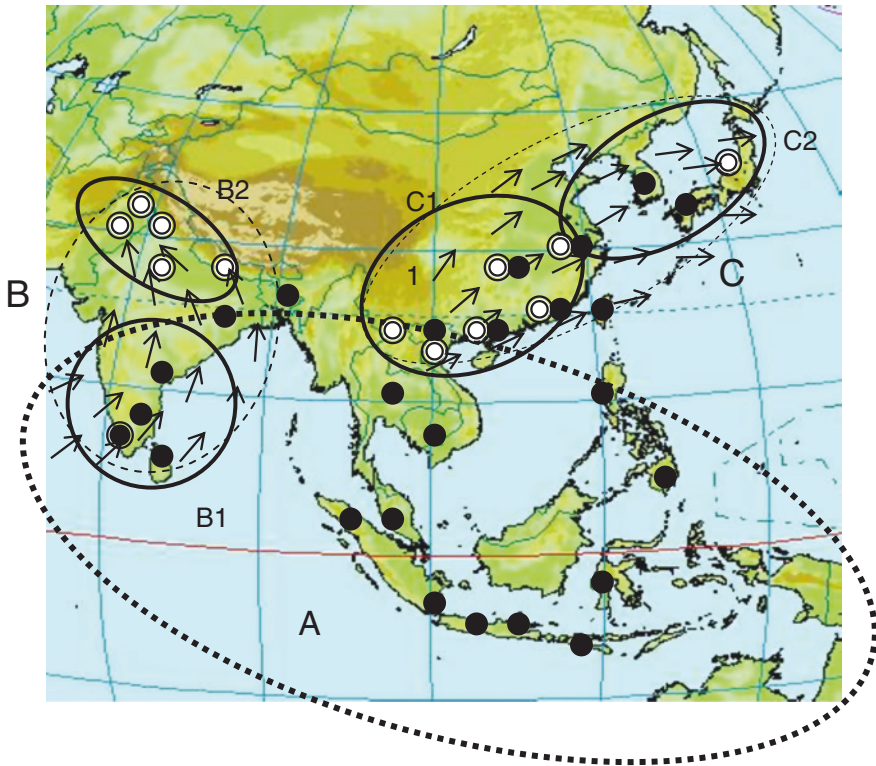


Fig. 2.1 The rice planthopper epidemic areas in different paddy ecosystems in Asia. Closed (●) and open double spots (⊙) indicate the areas where the outbreaks of BPH and WBPH were recorded, respectively. A: Tropical paddy ecosystems, where the BPH is endemic, has a non-voltine life cycle and reproduces perennially if host plants are available. BPH outbreaks in Southeast Asia were induced by prophylactic insecticide investment into the paddy fields as a packaged technology for the Green Revolution. B: Indian monsoon-dependent paddy ecosystems. The BPH-resistant rice landraces distributed abundantly in South India (B1), while most of the WBPH-resistant genes came from the northern parts of Indian subcontinent (B2), where WBPH invades into the summer rice by the aid of monsoon, but cannot over winter there. Outbreaks of BPH and WBPH in these paddy ecosystems were primarily caused by the careless introduction of susceptible exotic HYVs for the Green Revolution. C: East Asian monsoon-dependent paddy ecosystems, in which both the BPH and WBPH make long ranged migrations from the northern part of Indochina Peninsula to the Far East Asia by the predominant monsoon and reproduce some generations in the spring and summer paddy fields, but cannot survive in winter. C1 indicates the Chinese hybrid rice-prone areas, where WBPH shifted from a minor to the pre-eminent insect pest of rice, and new viral disease SRBSDV vectored by WBPH became epidemic. The *japonica* rice is planted in the C2 areas, where the *japonica* rice evolved ovicidal resistance to cope with massive monsoon-borne invasions of WBPH

be an indispensable self-defense trait of the local rice plants to cope with monsoon-borne massive invasions of BPH and to complement to biological control by indigenous natural enemies.

It has also been known the BPH populations in India are originally more virulent than those in Southeast Asia. The BPH-resistant IR varieties with the *Bph1* and *bph2* genes were susceptible to the Indian populations (Verma et al. 1979a, b; IRPS 1982; Velusamy et al. 1984). Sympatric distribution of BPH-resistant rice germplasm and virulent BPH biotypes in South India indicates that there had been long coevolutional interactions between rice plant and BPH. Easy replacement of indigenous BPH-resistant local varieties with exotic susceptible HYVs disrupted genetic balance (or coevolutional interactions) between paddy plants and BPH populations and caused BPH outbreaks. Insecticide-induced resurgence was not the primary cause of BPH outbreaks in South India.

In Godavari area in Andhra Pradesh, for example, the locally improved MTU and SLO varieties were commonly planted in the period from the 1930s to 1960s. The MTU and SLO varieties were selected from predominated native rice landraces. Complicated genetic resistance to BPH in the MTO and SLO varieties was indicated by their variable responses to the IRRI biotypes of BPH (Sogawa 1979). This is an example of genetic diversity of BPH resistance retained in the local rice germplasm in South India.

There are another examples of resistant and tolerant local rice varieties to BPH and other insect pests and diseases that are commonly available and recommended in the pesticide-free SRI (system of rice intensification) paddies in the coastal states of the eastern India (SDTT 2010). The multiple resistances to rice pests in the local rice varieties could be evolved through intensive tritropic interactions among rice plants, pests, and natural enemies in the monsoonal Indian paddy ecosystems. Those local rice varieties are the good materials to understand the actual properties of intrinsic BPH resistance in rice evolved in the paddy ecosystems.

2.4 Deployment of Host Plant Resistance in BPH Management

1. Breeding of BPH-resistant HYVs

Host plant resistance and biological control are ecological approaches to manage crop pests (Kennedy et al. 1987). These are also compatible components of IPM strategies. IRRI started screening of insect-resistant rice germplasm in 1966 by imitating a seedling plant method, which was originally used to evaluate resistance to small sucking insects in crop plants by Painter (1951). After the first BPH-resistant traditional *indica* variety Mudgo was discovered in 1967, the seedling plant method was established as standardized seedbox screening test (SSST) (Heinrichs et al. 1985). The SSST-based resistance breeding for BPH had started without any ecological aspects on the host plant resistance to BPH in rice plants.

In the SSST, BPH resistance was instantly evaluated based on relative damage scores of the seedlings submitted to a side-by-side sucking preference response by newly emerged BPH nymphs. Such behavioral response of newly emerged BPH nymphs does not represent holistic ecological interactions between BPH and rice plants in the paddy ecosystem. The SSST is, however, technically elegant and has a great advantage in screening a large number of materials, and it was exclusively adopted to screen BPH-resistant germplasm and to breed BPH-resistant IR varieties at IRRI and other Asian countries.

By the mass screening of rice germplasm, several BPH resistance genes were identified by the SSST. All the planthopper resistance genes are of monogenic and are designated by numerical codes with prefix *Bph* (Khush and Brar 1991), which were easily manipulated in conventional breeding programs.

2. Tentative vertical resistance in IR26 and IR42

The BPH resistance genes identified by the SSST were incorporated into IR varieties as an essential trait to cope with the BPH outbreaks. The BPH-resistant IR varieties were widely introduced into the BPH-epidemic tropical paddies since the first BPH-resistant IR26 with *Bph1* was released in 1973. However, those IR varieties were not the panacea for the BPH problems. Most of them were easily defeated with prompt emergence of adaptive BPH biotypes (Sogawa 1982).

The resistance genes *Bph1* and *bph2* were incorporated into 19 IR varieties by 1980, but 16 were readily defeated by virulent BPH biotypes. For instances, IR26 with *Bph1* and IR42 with *bph2* were highly resistant to BPH when they were released. However, within a few years, they lost genetic resistance with emergence of matching virulent biotypes (Gallagher et al. 1994). Consequently, sequential release of IR26 and IR42 failed to stop the outbreaks of BPH.

The resistance genes *Bph1* and *bph2* are monogenic factors to disrupt sustained BPH sucking from the phloem of rice plants (Sogawa 1982). On the other hand, the BPH populations retain polygenic flexibility to modify their biotype compositions to overcome the sucking blockage by *Bph1* and *bph2* (den Hollander and Pathak 1981; Roderick 1994; Tanaka 1999). Accordingly, IR26 and IR42 showed only temporary vertical (resistance gene and biotype specific) resistance until a BPH population adjusts their biotype makeup so as to feed on those resistant varieties.

3. Varietal resistance-breaking planthopper biotypes

The BPH populations, which have differential ability or inability to infest rice varieties with specific BPH resistance genes identified by SSST, are commonly referred to as biotypes, although there are some controversies about genetic status and nomenclature of biotype populations (Claridge and den Hollander 1982).

Mass-rearing inbred BPH populations established on TN1, Mudgo, and ASD7 were designated as biotypes 1, 2, and 3 at IRRI (IRRI 1976; Pathak and Heinrichs 1982). So far as these biotypes 1, 2, and 3 concern, they show phenotypically a vertical virulence specific to the BPH resistance genes *Bph1* and *bph2*, as if there were a gene-for-gene relationships between the virulence of biotypes and host

plant resistance conferred by each BPH resistance gene (Gallun and Khush, 1980). However, naturally developed field populations of biotypes do not exist as genotypically uniform variants. Therefore, the nomenclatures of IRRI biotypes cannot be applied to the field populations (Clarige and den Hollander 1980, 1983).

In Southeast Asia, sequential releases of IR varieties with different BPH-resistance genes (e.g., IR26 with *Bph1* and IR42 with *bph2*) led significant changes in varietal resistance-breaking performance in the BPH populations (Feuer 1976; Varca and Feuer 1976; Huynh 1977; Mochida et al. 1977a; Aquino and Heinrichs 1979; Staplay et al. 1979; Medrano and Heinrichs 1980; Sogawa et al. 1984a, b; Ho 1985; Sogawa et al. 1987; Huynh and Nhung 1988; Chau 1990; Pathak et al. 1990; Chau 1992; Thuat et al. 1992; Chau et al. 1993). Present BPH populations in Southeast Asia exhibit complicated variations in their virulence patterns depending upon the history of rice variety shifts in each locality, where gene-for-gene patterns are no longer recognized between the BPH populations and rice varieties (Claridge and den Hollander 1982).

Majority of the BPH resistance genes are originated in the southern parts of Indian subcontinent. This indicates that there have been more intensive coevolutional interactions between BPH and rice landraces in South Asia than in the rest of distribution areas in Southeast Asia. As the results, the BPH populations in South India and Sri Lanka are virulent to the IR varieties with *Bph1* and *bph2* (Velusamy et al. 1984).

4. Genetic flexibility in the BPH biotype populations

Local BPH populations from different rice varieties in the different places in Sri Lanka showed different virulence patterns and specific adaptation to the respective local host rice plants, on which they fed and reproduced (Claridge and den Hollander 1982). Interestingly, a perennial wild rice *Oryza rufipogon* is universally susceptible to all the local BPH populations. Several other studies also showed considerable variations among local BPH populations in fitness or performance to different host varieties even among populations that were in close geographic proximity (Claridge and den Hollander 1982; Gallagher 1988; Huynh and Nhung 1988). These field evidences indicate that the natural BPH populations retain highly diversified genetic pool to maximize their fitness to the locally available host plant resources.

Selection experiments revealed that BPH populations could easily adapt to the resistance varieties carrying the *Bph1* and *bph2* genes within 5–10 generations under continuous inbred conditions (Clarige and Den Hollander 1982; Pathak and Heinrichs 1982; Sogawa and Kilin 1987). Heritability for BPH biotypes is estimated based on the data of selection experiments. The estimated heritability is sufficiently high to suggest that significant amounts of genetic variation exist in the BPH populations for survival on rice varieties containing different genes for resistance (Roderick 1994).

In a similar manner, the BPH biotypes developed repeatedly in the irrigated tropical rice areas, where IR varieties with different BPH resistance genes were sequentially planted. Newly gained virulence is generally persistent in the local BPH populations for considerably long period. For example, the BPH populations in the Philippines retain the ability to infest the rice varieties with *Bph 1* gene,

which had not been planted for many years after emergence of virulent biotypes. Previously and newly gained virulence are retained independently in the same populations. A significant portion of BPH individuals also was found to have dual virulence against the both *Bph1* and *bph2* genes in North Sumatra, Mindanao, and South Vietnam, where IR varieties with the *Bph1* and *bph2* genes were sequentially released (Sogawa et al. 1984a, b; Medrano and Heinrichs 1985; Huynh and Nhung 1988). Recent field BPH populations in South Vietnam show very wide cross-virulence to the *Bph5*, *bph6*, *Bph7*, *bph8*, and *Bph9* genes, which are not yet deployed in the breeding programs (Phuong et al. 1997). Another experiments further demonstrated that BPH could adapt simultaneously to 2–3 genes for BPH resistance (Nemoto and Yokoo 1994).

All these experimental and field evidences indicate that the biotype shift is not achieved by a simple replacement of genotypes, but progressed by a modification of genotypic composition and combination within each reproductive populations under a selection pressure by genotypic variations in the host plants. Highly diversified polygenic adaptation to the BPH resistance genes indicates that the BPH populations enable to overcome any modes of usage of the BPH resistance genes identified by the SSST, such as pyramiding or sequential release and also rotation, mixing, or mosaic cultivation. Moreover, it is noteworthy that BPH populations have abilities to defeat even some exotic resistance factors derived from the non-host plants like *Oryza officinalis* by the SSST. Breakdown of BPH resistance in MTL98 in Vietnam is an example (CLRRI 1997, personal communication).

5. Durable horizontal resistance in IR36 and IR64

Easy breakdown of BPH resistance posed serious distrust to BPH-resistant IR varieties for controlling BPH. However, we found a few IR varieties such as IR36 and IR64 possessed remarkable field resistance to BPH. Even after breakdown of its *bph2*-resistance, IR36 showed a durable field resistance to BPH and effectively curbed its outbreaks. Rice self-sufficiency was temporarily attained upon IR36 in the Philippines and Indonesia through its field resistance.

When IR64 was released in 1985, its *Bph1*-resistance had already been useless, because it was defeated by adaptive biotypes long before. Nevertheless, IR64 was accepted widely for its stable field resistance to BPH. BPH did not break out on IR64 for more than two decades in the Philippines and Indonesia (Medina et al. 1996; Cohen et al. 1997; Alam and Cohen 1998a). IR36 and IR64 showed durable horizontal resistance to different biotypes.

IR64 indicates that some unidentified genes, which are independent from the BPH resistance genes identified by the SSST, play significant roles in the expression of field resistance to BPH (Alam and Cohen 1998b). However, the genetic background and mechanisms of field resistance have been poorly understood.

6. Field resistance to BPH in rice

Herein, the term “field resistance” is tentatively used to describe various rice plant traits to reduce fitness of BPH, which are conferred by other than the BPH resistance genes identified by the SSST. Field resistance is conceivable as a common

and basic self-defense mechanism in wild host plant and traditional crop cultivars to coexist with the associated herbivores.

IR26 and IR64 have the same *Bph1* gene for BPH resistance from TKM6 and Mudgo, respectively, but their performance against the *Bph1* resistance-breaking biotypes is distinctive. IR26 became highly susceptible when its *Bph1* resistance was defeated by virulent biotypes emerged, while IR64 retained remarkable moderate resistance to the IR26-defeated biotypes. It has been shown that IR64 has several QTLs that impart slight to moderate levels of antibiosis, antixenosis, and tolerance, and their combinations confer the durable and horizontal field resistance. Overall field resistance has only been assumed as different levels and combinations of resistance components, antixenosis, antibiosis, and tolerance (Panda and Heinrichs 1983; Cohen et al. 1997). Diversified parentages of IR64 could be the source of those QTLs for durable field resistance. IR64 is a descendant of 20 traditional local varieties from 8 countries.

IR36 and IR42 are the sister varieties shearing the *bph2* gene for BPH resistance from the same sources of PTB18 and PTB21. Within 5 years after their release, BPH populations that are able to feed on IR36 and IR42 appeared. However, IR36 retained moderate resistance against the IR42-defeated BPH biotypes. The population growth of IR42-defeated biotype was strongly suppressed on IR36 (Sogawa et al. 1984a, b). It is also evident that the BPH populations that fully adapted to IR36 have not evolved for long years in the IR36 monoculture areas. Selection experiments showed that BPH populations could readily adapt to IR42 within 5 generations under isolated inbred condition (Sogawa and Kilin 1987), while fully adapted population hardly developed on IR36 even after continuous selections for more than 30 generations (Sogawa unpublished data). Some extra genes other than the *bph2* gene confer the durable field resistance to BPH in IR36, which are not inherited to IR42.

From the above-mentioned examples, it is evident that the BPH-resistant IR varieties could be divided into two categories with special reference to their differences in the genetic background of BPH resistance (Fig. 2.2). One is the IR varieties that have only the resistance genes identified by the SSST, but field resistance traits were lost during the process of breeding. IR26 and IR42 are the examples of this category. They show temporary vertical resistance. The other one is the IR varieties retain field resistance traits to BPH in addition to the resistance genes identified by the SSST such as IR36 and IR64. They show durable and horizontal resistance to different biotypes of BPH.

Traditional cultivars such as Kenchana, Utri Rajapan, Triveni, Wagwag, and Baosyan 2, which are moderately resistant to BPH and had ever been widely grown by farmers, will provide us with precious aspects on the intrinsic nature of durable field resistance to BPH in paddy fields (Mochida et al. 1979; Ho et al. 1982; Panda and Heinrichs 1983; Wu et al. 1984; Velusamy et al. 1986). The local varieties that are recommended to plant in the pesticide-free SRI paddies in the eastern coastal tracts in India are also interesting materials to study the practical field resistance to multiple pests and diseases (SDTT 2010). Those local varieties are expected to have unknown resistant and tolerant traits that cannot be evaluated by the SSST.

Although field resistance is generally not so strong as varietal resistance conferred by the resistance genes identified by the SSST, it would be durable and act across all biotypes, and combinations with natural enemies in the IPM context will provide sustainable rice planthopper management in the tropical paddy ecosystems (Kartohardjono and Heinrichs 1984; Way and Heong 1994; Cuong et al. 1997). Instead, IPM practitioners argued that high level but temporary resistance conferred by the genes identified by the SSST is not necessary to manage BPH in the rice areas, where insecticide use is low and natural enemies are well conserved (Medina et al. 1996). A special emphasis has been placed on durable horizontal resistance to preclude upsurges of highly mobile insect pests that are already present in the crop ecosystem, and host plant resistance is considered as the basic foundation on which all elements of integrated control strategy are built (Buddenhagen and de Ponti 1983; Maxwell 1991).

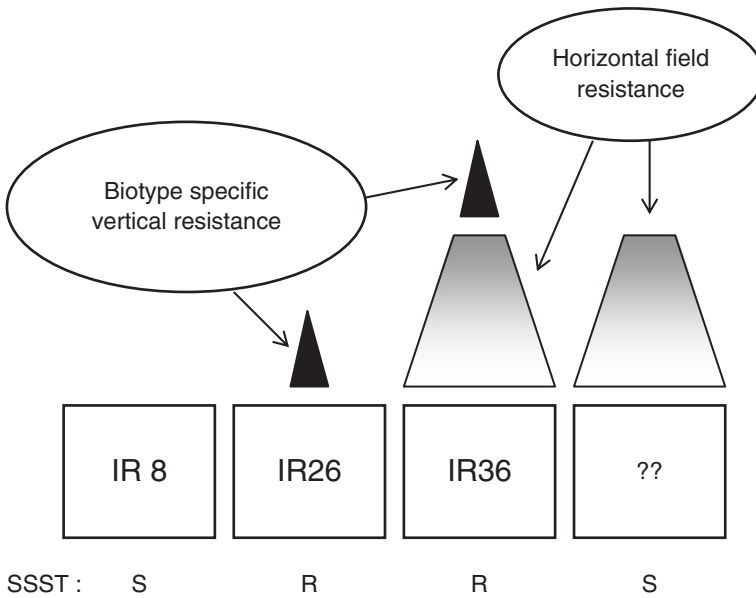


Fig. 2.2 IR varieties with different genetic backgrounds for BPH resistance and their responses to BPH by the SSST (R: resistance, S: susceptibility). Square base of each figure indicates high-yielding genetic domain of selected IR varieties and Hypothetical varieties having only field resistance. Triangular tips indicate the BPH-resistant genes identified by the SSST. The trapezoid portions indicate the traits (or QTLs) for field resistance to BPH, which cannot be evaluated by the SSST, and mostly eroded insidiously during the process of the SSST-dependent resistance breeding. The hypothetical varieties have equivalent field resistance to BPH to the IR36 and IR64, but they were eliminated as susceptible plants by the SSST

7. Erosion of field resistance in SSST

One of the decisive defects of SSST is incapacity to evaluate field resistance to BPH, which in turn commits a great risk of insidious erosion or decline of useful field resistance traits from rice plants. This defect of SSST is homologous to the “Vertifolia effect,” which means insidious loss or decline of field resistance during the breeding for a particular vertical resistance (van der Plank 1984).

The resistant crop varieties suffered “Vertifolia effect” from their breeding process become highly susceptible when their particular genetic resistance is defeated with the emergence of virulent biotypes of BPH as in the cases of IR26 and IR42. In those varieties, field resistance traits of their ancestral traditional rice varieties were completely eroded during the process to incorporate the *Bph1* and *bph2* genes by the SSST. In particular, when large amounts of breeding lines are submitted to the SSST at the earlier stages of breeding, the field resistance traits will be massively eroded, because the breeding lines having only field resistance traits will be eliminated as susceptible ones in the SSST (Fig. 2.2).

Modern breeding of high-yielding IR varieties has been successful in the improvement of high-yielding capacity, quality of rice grain, and agronomic suitability and also to incorporate the monogenic BPH resistance genes identified by the SSST. On the other hand, the levels of field resistance decline insidiously to a dangerous low level in some IR varieties. High vulnerability to BPH infestations in some IR varieties could be attributed to the decline of field resistance. Degradation of field resistance traits from rice varieties perturbs the tritrophic balance among the host plants, BPH and its natural enemies in the tropical paddy ecosystems and will trigger the eruptive population growth of *r*-strategic BPH. That is a possible reason why most of the BPH-resistant IR varieties did not succeed in sustainable BPH management. Buddenhagen and Ponti (1983) has emphasized the preventive breeding, which means breeding a crop so as to prevent the increase of minor pests and pathogens already present in the crop ecosystem in the tropics.

8. Evaluation of field resistance

Varietal resistance in IR varieties with the *Bph1* and *bph2* genes is expressed by the blockage of sustainable phloem sucking of BPH (Sogawa 1982). In this regard, the *Bph1* and *bph2* are the sucking-inhibitory genes to confer antixenotic resistance to BPH. The SSST is able to evaluate preferential sucking response of BPH by the subsequent damage scores of rice seedlings, but unable to evaluate neither antibiotic resistance nor tolerance that are expressed through the post-feeding interactions between BPH and rice plants.

Field resistance to BPH in rice plants must be evaluated from more holistic and ecological viewpoints based on the population dynamics of BPH in relation to the phenology of paddy plants in the paddy ecosystems. The interactions between BPH and rice plant can be divided into the following three major events.

- (a) Immigration and host plant selection: Colonization of BPH in a paddy field starts with random immigrations of macropterous adults (Kuno 1968). After

alighting on a plant, the planthopper commences stylet probing to discriminate host plants (Sogawa 1982). At this process, antixenotic factors in host plants, which act via insect sucking, play a key role in the expression of varietal resistance in the paddies. Honeydew excretion by macropterous female and the density of macropterous immigrants in the field plants are the parameters to evaluate host plant antixenosis.

- (b) Reproduction: Population growth of BPH depends largely upon the brachypterous females emerged from the progeny of macropterous immigrants (Kisimoto 1965), while the macropterous adults emigrate out from the breeding habitats and do not contribute to the subsequent population growth in the original habitat. Therefore, the host plant traits, which affect the ratio of brachyptery, fecundity of brachypterous females, egg mortality, etc., will act as important antibiotic factors for varietal resistance during the process of insect reproduction.
- (c) Infestation: Established BPH colonies function as an “extra sink” affiliated to the host plants, which intercept translocation of photosynthates and vital metabolic substances in the sieve elements of host plants (Sogawa 1994). The population density decides the size of the extra sink. Density of nymphal population is a powerful parameter to indicate the overall levels of antibiosis. Functional biomass interactions between the insect population and host plant decide plant damage intensity and yield losses, which is also a useful parameter to indicate the level of host plant tolerance (Panda and Heinrichs 1983; Reese et al. 1994).

Recent advance of QTL-based analyses of genetic traits as well as gene-tagging and marker-assisted selection (MAS) technologies offer us more efficient approach for analyzing the complex and quantitative field resistance traits (Mohan et al. 1997; Alam and Cohen 1998b; Yencho et al. 2000). Both monogenic and polygenic traits are equally analyzed in this approach. The QTL-based approach requires a well-saturated molecular marker map, appropriate recombinant inbred rice populations, and ecologically significant phenotyping procedures. Comparisons of the QTLs detected by ecological phenotyping methods suggest directly ecological mechanisms of field resistance. Until now, most of the gene mappings for planthopper resistance traits have been undertaken by using the SSST. The SSST may detect some traits, which are strongly associated with the insect feeding. However, SSST-dependent phenotyping does not detect field resistance traits, because those traits mostly operate in the post-feeding ecological and physiological interactions between the grown host plants and the insect populations.

2.5 Whitebacked Planthopper and Host Plant Resistance

1. The whitebacked planthopper (WBPH)

There is another rice planthopper, the whitebacked planthopper (WBPH), *Sogatella frucifera* (Horváth). WBPH and BPH are equally rice monophagous

r-strategists and sympatric to each other. However, their population ecologies are distinctive due to their differential feeding behavior. BPH can utilize rice plants throughout the cropping season and reproduces continuously 3–4 generations. On the other hand, WBPH prefers to feed on fresh leaves of rice plants at tillering stage and reproduces only one or two generations in a crop cycle. WBPH emigrates from the paddy fields at reproductive growth stages. WBPH has a macroptery-biased wing dimorphism to facilitate frequent habitat shifts. Because of this biology, WBPH usually dominates in the monsoon-prevailing rice areas outside of its tropical endemic habitats (Fig. 2.1).

2. Outbreaks in Punjab

Punjab is famous for successful green revolution in both wheat and rice. WBPH was not an important rice pest before 1965 when farmers grew traditional tall *indica* local varieties in Punjab, the northwestern segment of the Indo-Gangetic plain in India. Rice is a summer crop planted in the monsoon season (kharif) from June to December. WBPH began to cause serious damages to rice in Punjab, when the HYVs program was launched with the introduction of exotic semi-dwarf HYVs.

The first outbreak of WBPH was recorded in 1966, which coincided with the introduction of TN1. Since then, the outbreaks of WBPH occurred in 1972, 1975, 1978, and 1981 on the HYVs derived mainly from TN1 and IR8 (Kulshreshtha et al. 1970; Dhaliwal and Singh 1983; Dhaliwal et al. 1985). In 1983 kharif season in the Punjab, the population density of WBPH reached to 200–500 insects per hill and eventually caused hopperburn over 1,000 ha of paddy fields (Saini 1984). PR106 was most seriously damaged, which was expected to be less susceptible to WBPH when introduced in 1976.

In the Punjab plain, WBPH infestations usually start at 15–25 days after transplanting. WBPH populations increase on the paddy rice during the mid-tillering stage in September to October (Sehgal et al. 2001). Incidence of BPH also increased in the same period, but the population density of WBPH outnumbered that of BPH. Simultaneously, WBPH became a major insect pest of rice after introduction of HYVs in the hilly tracts of Haryana, Madhya Pradesh, and Uttar Pradesh adjacent to Punjab (Petel 1971; Verma et al. 1979a, b; Kushwaha et al. 1982; Shukla et al. 1986). In Uttar Pradesh, WBPH has attack rice regularly since 1969. Infestation was severe in 1972 and 1977, when typical hopperburn occurred in the paddy fields at late tillering stage (Verma et al. 1979a, b). In 1982, more than 3,000 ha of paddy fields in the Kathmandu Valley, Nepal, were seriously infested with WBPH (Pradhan et al. 1983).

Since then, WBPH has continuously been one of the major insect pests of rice in the rice–wheat cropping system in the Indo-Gangetic plain (Sehgal et al. 2001). Since insecticide use was very minimal, outbreaks cannot be attributed to the insecticide-induced resurgence. Concentrated distribution of WBPH-resistant rice germplasm in the northern corridor of Indian summer monsoon indicates that WBPH resistance was an important self-defense trait of summer rice to cope with massive monsoon-borne invasions of WBPH. Abrupt outbreaks of WBPH were

caused by careless replacement of indigenous WBPH-resistant local rice with WBPH-susceptible exotic HYVs by the HYVs program.

3. Varietal resistance to WBPH in rice

Based on the SSST, several WBPH resistance genes were identified among *indica* rice varieties. All the WBPH resistance genes identified by the SSST are of monogenic and are designated by numerical codes with prefix *Wbph* (or *Wph*) (Khush and Brar 1991).

Of 48,554 accessions of traditional cultivars from the IRRI world collection of rice, 401 (0.8 %) were selected for resistance to WBPH by the SSST at IRRI (Romena et al. 1986). About 10, 3, and 2 % of the resistant accessions selected came from Pakistan, Nepal, and India, respectively, which occupied about 88 % of the total resistant accessions selected (Romena et al. 1986). Almost 70 % of WBPH resistant traditional rice varieties in India distribute in the northwestern semiarid areas of Uttar Pradesh, Rajasthan, Gujarat, Madhya Pradesh, and Punjab and 15 % in the northeastern hilly tracts of Assam and Meghalaya. On the other hand, the WBPH-resistant traditional varieties are not found among the accessions from Kerala, Andhra Pradesh, and Tamil Nadu in South India, from which most of the BPH-resistant germplasms were found. Likewise, the accessions from Philippines, Laos, Vietnam, and Cambodia were all susceptible to WBPH (Romena et al. 1986). It seems to indicate that majority of WBPH-resistant *indica* rice was originated in the northern corridor of Indian summer monsoon, the northern periphery of the Indian subcontinent.

Distinct difference in the virulence to rice varieties was found between the Southeast and South Asian populations of WBPH. Forty of 118 varieties were resistant to the WBPH population at IRRI, but susceptible to the population in Hyderabad, India. On the contrary, nine varieties were resistant at Hyderabad, but susceptible at IRRI (IRRI 1978). The WBPH population in Punjab was further virulent to 8 of 17 varieties that were resistant to both the Hyderabad and IRRI populations, and the varieties with the *Wbph1* gene were mostly susceptible to the Punjab population (Gupta and Shukla 1986). Likewise, N22 with the *Wbph1* gene was not resistant at Pantnagar, Uttar Pradesh (Lal et al. 1983).

These reports indicate the WBPH populations in South Asia are more virulent than the Southeast Asian populations. Particularly, the Punjab population in the northwestern part of India is the most virulent. Coincidental distribution of virulent WBPH populations and WBPH resistant rice germplasm indicates that there has been an intensive coevolutional interaction between WBPH and *indica* rice landraces in the northern parts of South Asia.

The mechanism of WBPH resistance in the local rice in Punjab has not been known except for their possible sucking-inhibitory properties indicated by the SSST. However, the resistance genes identified by the SSST could not be responsible for all of their resistance traits. So far, five genes for WBPH resistance have been identified by the SSST at IRRI, but none of them were incorporated into the IR varieties. Therefore, 27 IR varieties from IR5 to IR62 are all susceptible to WBPH in the SSST. However, of them, 16 varieties were found to be moderately

resistant in the modified SSST, where 20-day-old seedlings are used instead of 7-day-old ones in the SSST. Furthermore, population growth of WBPH was adversely affected by IR5, IR36, IR56, IR60, and IR62 (Velusamy and Heinrichs 1985). In addition, IR48, IR52, IR60, and IR62 were found to be moderately resistant to WBPH in the Indo-Gangetic plain (Sehgal et al. 2001). The above information indicates that there are some other host plant traits confer WBPH resistance in IR varieties, which cannot be identified by the SSST.

4. Prevalence of WBPH in Chinese hybrid rice

Hybrid rice boosted rice production in China. However, it is also evident that it caused pest outbreaks. Of them, WBPH became the most preeminent insect pest of hybrid rice (Hu et al. 1992; Sogawa 2001). WBPH was only a secondary insect pest of rice before the 1970s in China. However, immediately after release of hybrid rice in 1976, the first WBPH outbreak happened on a hybrid rice Nanyou 2 in Hunan Province in 1977 (Tan 1987). In 1982, about 1,600 ha of Shanyou 6 fields were severely infested with WBPH, and of 80 ha were completely destroyed in the hybrid rice pilot areas in Guangdong Province, South China, where Shanyou 2, Shanyou 6, and Weiyou 6 were introduced deliberately (Feng and Huang 1983). Field density of WBPH in Fujiang Province increased significantly for the period from 1978 to 1987. Before 1980, the average field density was below 5 insects per hill, but increased up to 40 insects per hill in 1987 (Lin 1989). Frequency of WBPH outbreaks was positively correlated with the expansion of hybrid rice areas in the period from 1980 to 1990 in Guangdong Province and similarly in Hunan and Guangxi Provinces (Hu et al. 1992). Light trap catches of WBPH exceeded those of BPH at Shantou, Guangdong Province by 1985, and became the most predominant insect pest (Lin 1994).

In Central China, unusually high density of WBPH was first found in a hybrid rice Shanyou 6 in Zhejiang Province in 1979. Observations at farmer's fields for 3 years from 1980 to 1982 showed that the population density of WBPH was 8–38 times higher than that in inbred rice (Ruan 1983). After that, it was demonstrated that rate of WBPH reproduction in Shanyou 6 was 2.6–3.9 times higher as compared with that in three inbred rice varieties (Huang et al. 1985). Higher fecundity of WBPH on hybrid rice such as Shanyou 6, Shanyou 63, and Weiyou 35 was also recorded (Zhu et al. 1990; Yu et al. 1991; Shi and Lei 1992; Cooperative Research Group on the Population Dynamics and Ecology of White-backed Planthopper 1992; Huang et al. 1994). These field evidence and observations showed that WBPH is much more reproductive in Chinese hybrid rice than in inbred rice.

High susceptibility to WBPH in a Chinese hybrid rice Shunyou 63 is primarily inherited from the WA-CMS (wild abortive cytoplasmic male sterile) line, which is extremely vulnerable to the WBPH infestation (Sogawa et al. 2003b). Field experiments revealed that population density of WBPH in the CMS lines “Zhenshan 97A” and “Xieqingzao A” was much higher than that in the susceptible TN1 (Liu et al. 2003). In addition, greater tolerance to WBPH infestations in Shanyou 6 due to heterotic vigorous growth is further attributed to the unusual upsurge of WBPH populations on it (Sogawa et al. 2003b).

WBPH has been only a minor insect pest of monsoon rice in the Red River Delta (RRD) in Vietnam. WBPH caused, however, a historical outbreak in about 153,000 ha of the winter–spring rice planted with Chinese hybrid rice in the RRD in 2000 (Dinh et al. 2001, 2002). Since then, WBPH is steadily increasing as a new important economic insect pest of rice in the rice granary of Vietnam. Chinese hybrid rice was first introduced to Vietnam in early 1990s and quickly extended over 70–80 % of rice areas in the RRD. Subsequent intensive applications of insecticides are spoiling the previous great efforts for the implementation of IPM and causing the paddy ecosystem crisis. In the northern Laos, possible influx of insecticide-resistant WBPH from adjacent to the northern Vietnam and China was pointed out (Komine et al. 2008).

Prevalence of WBPH in Chinese hybrid rice caused significant increase of overseas migrations of this insect from China to Japan. Immigration density of WBPH started to increase from the mid-1970s, which coincides introduction of hybrid rice in China (Naba 1991; Watanabe et al. 1994). Massive immigration surges reached not only to the southwestern Japan facing directly to China, but also to the distant northern Japan, where WBPH caused unusual economic damages to rice in the 1980s (Takano et al. 1984; Murai et al. 1986; Araya et al. 1989).

In addition, the prevalence of WBPH, a new virus disease, southern rice black-streaked dwarf virus, which is transmitted persistently by WBPH, became epidemic in the hybrid rice areas in China and Vietnam since 2008 (Zhang et al. 2008). Prevalence of WBPH and new virus disease are attributed to the nationwide extension of WBPH-susceptible hybrid rice with heavy inputs of insecticides and nitrogenous fertilizers in the WBPH-dominated insect migration areas.

5. Ovicidal resistance in *japonica* rice

It has been well known the WBPH immigrants produce conspicuous necrotic symptoms to the leaf sheaths of newly transplanted rice seedlings by intensive oviposition. *Indica* rice oviposited by WBPH does not exhibit such symptoms. The necrosis is one of the damages to deter the initial plant growth, but at the same time, it is a sign of unique self-defense mechanism against the rice planthoppers in *japonica* rice. The WBPH eggs deposited in the rice plants suffer high mortality by an ovicidal substance, benzyl benzoate, which is induced in situ in the plants laid eggs within 1–2 days after oviposition (Suzuki et al. 1996; Seino et al. 1996). Egg mortality due to the ovicidal response increases as host plants grow during the tillering stage, but decreases after the heading stage and declined to negligible levels in the ripening stage (Suzuki et al. 1993; Kiyonaga and Suzuki 1998).

Because *japonica* rice in Japan commonly has the ovicidal trait, it has been remained unaware until recently. Also, it has long been ignored because in the routine breeding process, it is an invisible and neutral trait. The ovicidal trait was discovered as an “hyper-susceptibility” to WBPH in the *japonica/indica* hybridized lines that lost the ovicidal trait intrinsic in the *japonica* parent due to a cryptic erosion during the breeding process (Sogawa 1991). *Japonica* varieties “Musashikogane” and “Asahinoyume” lost the ovicidal trait insidiously during the breeding process to incorporate rice stripe virus (RSV) resistance gene from a Pakistani *indica* rice “Modan” to *japonica* rice. As the result, “Musashikogane” and “Asahinoyume” became highly susceptible to WBPH, though it was highly

resistant to RSV (Hara and Saito 1984; Murakami and Kanda 1984; Nakamura et al. 2009). Likewise, WBPH populations increase easily on some forage rice varieties, which lost the ovicidal resistance during the process of *japonica/indica* hybridization breeding (Sogawa 1991; Matsumura 2006).

The ovicidal resistance to WBPH was found restrictedly in the *japonica* rice germplasm. Almost recent Japanese *japonica* paddy rices have distinct ovicidal resistance (Suzuku 1996), but some upland rice varieties lack the ovicidal resistance (Sogawa 2007). About 24 % of *japonica* rice improved in China also shows the ovicidal response to the WBPH eggs. Similar ovicidal response was found in the landraces of native *japonica* in Zhejaing Province, East China (Sogawa et al. 2003c). Those landraces show continuous variations in the level of ovicidal activities. For example, “Sanqianhuang” and “Changhongdao” show strong ovicidal response, while “Laohudao” and “Jijiaohuang” entirely lack it. Furthermore, the ovicidal response is induced in a strain of perennial wild rice, *O. rufipogon*, when oviposited by WBPH (Sogawa 2007). On the other hand, the ovicidal resistance to WBPH does not distributed among the *indica* and tropical *japonica* (*javanica*) varieties (Sogawa et al. 2003c). A strain of annual wild rice, *Oryza nivara*, has no ovicidal function (Sogawa 2007). A single dominant gene *Ovc* on chromosome 6 mainly governs the ovicidal trait in *japonica* rice (Yamasaki et al. 1999a, b; Sogawa et al. 2003a, d).

The ovicidal response is an important component of field resistance or self-defense mechanism to protect *japonica* rice from sudden massive overseas immigrations of rice planthoppers in the temperate Asia, where the paddy ecosystems exist only in the summer season and natural enemies are not enough to cope with the massive immigrant planthoppers in the newly prepared paddy fields. The ovicidal response explains why WBPH is not so destructive to the rice plants as is BPH in Japan, in spite of its 100 or higher immigration density than that of BPH and high intrinsic fecundity as a typical *r*-strategist. The ovicidal resistance has no other antibiosis to the planthopper nymphs and adults. Therefore, the *japonica* rice plants allow WBPH to establish a low density of populations from the eggs that escaped from the ovicidal reaction, but vegetative growth of host plants usually compensates such limited infestations with WBPH. The ovicidal response is also found to be effective against the BPH eggs to some extent, which may contribute to suppress the population buildup of BPH on *japonica* rice plants during the vegetative growth stage (Kiyonaga et al. 1997; Yamasaki et al. 2000).

If *japonica* rice had not ovicidal resistance, WBPH could be a much greater threat to traditional rice farming in Japan. This is a typical example of field resistance to WBPH in *japonica* rice, which cannot be evaluated by the SSST.

2.6 Rice Planthoppers: A Health Barometer of Paddy Ecosystem

High reproductive potential of rice monophagous and *r*-strategic BPH and WBPH evolved in order to balance with defensive traits of rice plants and intensive biotic pressure by natural enemies. Thus, field resistance in rice plants and natural

enemies are essential ecological and genetic components to keep balance of tri-trophic interactions among the rice plants, planthoppers, and natural enemies in the paddy ecosystems (Verkerk et al. 1998).

Depending on the paddy ecosystem conditions and crop management practices, the planthoppers perform two distinct population trends, namely the endemic and epidemic patterns. IPM is an ecological approach to keep the population density of planthoppers to the endemic level, where natural enemies and indigenous field resistance in rice plants play key roles. Mismanagement of paddy ecosystem by prophylactic sprays of insecticides induces resurgence of the planthoppers. We have to recall to our mind why the BPH outbreak prevailed over the tropical rice areas during the process of “green revolution,” which was embarked with easy adoption of insecticides as an essential high-yielding input.

At the same time, the *r*-strategic planthoppers have a potential to reproduce beyond endemic level escaping biological control by natural enemies on the highly susceptible HYVs, which lost field resistance traits due to genetic erosions during breeding process. Field resistance in rice plants is an intrinsic self-defense mechanism to suppress the planthopper populations to the levels that natural enemies are controllable and host plants enable to compensate. Therefore, field resistance in rice plants and natural enemies are the basic components to ensure the sustainable management of *r*-strategic rice planthoppers. A concept of the preventive breeding has been proposed so as to prevent the epidemic boom of indigenous endemic pests and pathogens already present in the crop ecosystem in the tropics (Buddenhagen and Ponti 1983). In the preventive breeding for the endemic pests, the significance of durable field resistance was anticipated to be the basic foundation of sustainable crop and pest managements. The use of temporary (transient) vertical resistance conferred by the monogenic factors isolated by the SSST should be tried to avoid against highly mobile *r*-strategic insect pests such as BPH and WBPH in the tropical rice areas, which only encouraged the biotype shifts of the planthoppers. In this connection, the SSST-based resistance breeding should be redressed, because the SSST cannot evaluate field resistance mediated in the various phases of post-feeding interactions between the host plants and planthoppers, which commits a great risk of insidious erosion of useful field resistance traits from breeding materials.

Both the rice monophagous BPH and WBPH are a sensitive barometer to alert paddy ecosystem crisis. Recent revival of BPH outbreaks and unusual population upsurges of WBPH are warning the crisis of paddy ecosystems due to misuse of insecticides, misdeployment of host plant resistance, and mismanagement of farm environment.

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